Master Thesis

Modelling the Habitat Suitability of the Hazel Grouse (*Tetrastes bonasia*) in Salzburg, using Maxent

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Affidavit

I hereby declare that I have authored this master thesis independently, and that I have not used any assistance other than that which is permitted. The work contained herein is my own except where explicitly stated otherwise. All ideas taken in wording or in basic content from unpublished sources or from published literature, as well as those which were generated using artificial intelligence tools, are duly identified and cited, and the precise references included.

I further declare that this master thesis has not been submitted, in whole or in part, in the same or a similar form, to any other educational institution as part of the requirements for an academic degree.

I hereby confirm that I am familiar with the standards of Scientific Integrity and with the guidelines of Good Scientific Practice, and that this work fully complies with these standards and guidelines.

Vienna, 24. September 2025 Gabriel STAUBMANN *(manu propria)*

Preface

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Abstract

In this master's thesis, a Maxent based species distribution model was created to identify suitable habitats of the hazel grouse (*Tetrastes bonasia*) and to evaluate habitat suitability across Salzburg using presence records of the Naturpark-Weißbach and the Bavarian Saalforsten. The hazel grouse is a small and elusive grouse species inhabiting mountainous forests of central Europe, with the alps representing a major stronghold for European populations. Increased pressures from intensive forestry and other human land uses, fragment, degrade and isolate near-natural, structurally diverse forests, required by this bird. Understanding and spatially depicting these habitat requirements is essential for effective conservation management. The Maxent model was built using 34 presence records together with environmental predictors selected for ecological relevance to the hazel grouse. The final model indicated that habitat suitability was most strongly influenced by the aspect of slopes, as well as by the increasing distance to forest roads and the presence of mixed coniferous stands. Unexpectedly, increased vertical heterogeneity of forest structure, measured as the Gini-coefficient of tree heights, was associated with reduced habitat suitability. Approximately 25 % (= 665 km^2) of Salzburg's forested area was identified as suitable habitat for the hazel grouse, with larger continuous patches occurring primarily in the inner mountain valleys and more fragmented suitable areas found in the north of Salzburg. Suitable habitats were characterised by a higher proportion of mixed coniferous forest stands and reduced proportions of single-species deciduous forest stands, greater distance to forest roads, closer proximity to lotic waterbodies and a notable predominance of northern facing slopes. The results of this master's thesis are intended to serve as a foundation for decision making regarding the conservation of hazel grouse populations and habitats in Salzburg.

Kurzfassung

In dieser Masterarbeit wurde ein auf Maxent basiertes räumliches Lebensraummodell erstellt, um geeignete Lebensräume des Haselhuhns (*Tetrastes bonasia*) zu identifizieren und das Lebensraumpotenzial für das gesamte Bundesland Salzburg darzustellen. Das Haselhuhn ist eine kleine und seltene Raufußhuhnart, die in Gebirgswäldern Mitteleuropas, darunter im Alpenraum und Salzburg, heimisch ist. Aufgrund zunehmender Landnutzung in Form von intensiver Waldbewirtschaftung und anderen Formen anthropogener Landnutzung werden unabdingbare naturnahe Waldhabitate für Haselhühner immer weniger, fragmentierter und isolierter. Ein besseres Verständnis dieser Habitatansprüche sowie deren räumliche Verbreitung ist ein wesentlicher Aspekt für wirksame Artenschutz- und Managementkonzepte. Das Modell wurde auf Basis von 34 Vorkommensnachweisen aus dem Naturpark-Weißbach und den bayerischen Saalforsten sowie ökologisch relevanten Umweltvariablen erstellt. Die Ergebnisse zeigen, dass das Lebensraumpotenzial insbesondere durch die Hangexposition, die Distanz zu Forststraßen sowie das Vorhandensein gemischter Koniferenbestände beeinflusst wird. Unerwartet zeigte sich, dass eine erhöhte vertikale Bestandsheterogenität, gemessen über den Gini-Koeffizienten der Baumhöhen, mit geringerem Lebensraumpotenzial einherging. Rund 25 % (= 665 km^2) der Salzburger Waldfläche wurde als geeignet eingestuft, wobei größere, zusammenhängender Flächen vor allem in inneralpinen Tälern im Süden Salzburgs liegen, während im Norden vermehrt fragmentierte Habitate vorhanden sind. Geeignete Lebensräume waren gekennzeichnet durch einen höheren Anteil gemischter Nadelwälder, geringere Anteile reiner Laubwälder, größere Distanzen zu Forststraßen, die Nähe zu Fließgewässern sowie ein überwiegen nördlich exponierter Hänge. Die Ergebnisse dieser Arbeit dienen als Grundlage für zukünftige Schutz- und Managementmaßnahmen von Haselhühnern und deren Habitaten in Salzburg.

1. Introduction

European forests experienced a severe decline in extent and conditions throughout the 19th century and beyond, as expanding agricultural areas, demand for fuel and industrial purposes reduced continuous woodlands to highly fragmented forests stands (Pommerening et al. 2025). Beginning in the mid 20th century, forest ecosystems started to recover, largely driven by socioeconomic changes such as agricultural intensification, change of silvicultural practices and migration of people from rural areas into cities (Gingrich et al. 2022). This resulted in an increase of 25 % forest cover over the last 70 years and improved ecological quality throughout Europe (Fuchs et al. 2012). The Alpine region exemplifies this recovery trend. Over the past century, the abandonment of small-scale agricultural plots has allowed forests to recolonise former farmland at an average rate of approximately 0.64 % per year (Anselmetto et al. 2024). Despite these positive developments, increasing human land use pressures continue to fragment and degrade alpine forest ecosystems. Intensive silvicultural practices that include mandatory clearcutting and monoculture plantation simplify stand structure and diversity of forests, while the expansion of human infrastructure isolate habitat patches and influence disturbances. Landscape alterations such as these affect the ecological functions of forest ecosystems as well as overall biodiversity (Zimmermann et al. 2010; Pardini et al. 2017; Diaz et al. 2019).

Among wildlife taxa in central Europe, the predominantly forest dwelling grouse-species of the tribe Tetraonini illustrate the responses to these dynamics: the Western capercaillie (*Tetrao urogallus*), the black grouse (*Tetrao tetrix*) and the hazel grouse (*Tetrastes bonasia)* and notably the rock ptarmigan (*Lagopus muta*) which is occurring above the treeline. All these grouse species are native to Austria and of conservation and management concern and particularly susceptible to habitat alterations (Ram et al. 2017). Mountainous regions of Europe such as the Pyrenees and the Alps represent the westernmost distribution of this group of forest birds, whose limited dispersal abilities, specific habitat requirements and life-histories presents them particularly vulnerable to habitat changes. Human land use in the form of intensive forest practices appears to be the strongest physical factor affecting habitats (Elvesveen et al. 2023), while disturbances through mountain tourism as well as anthropogenic infrastructures such as ski-lifts or wind power plants, have been shown to alter and often degrade the quality of grouse habitats (Hovick et al. 2014; Coppes et al. 2019; Jäger et al. 2020). Within the European Union, hazel grouse, black grouse and capercaillie are categorised as “Vulnerable” by the ICUN Red List and the capercaillie as “Least concerned”, yet all species exhibit declining population trends (BirdLife-International 2021).

Given the vulnerabilities and conservational importance of these forest grouse species, spatially explicit information on the potential distribution and habitat suitability is needed to guide monitoring efforts, aid in conservation- planning and to assess potential impacts of human land use, such as silvicultural practices and infrastructural planning. While there have been previous studies investigating the habitat use of capercaillie and black grouse in Austria (Zohmann et al. 2014; Sachser et al. 2017), almost no publicly accessible information on Austrian Hazel Grouse populations, conditions and distribution is available from within Austria, which is largely due to the birds elusive lifestyle and increasing rarity. However, large scale spatial information on the potential distribution of hazel grouse has been provided by Kunz et al. (2021) for the state of Styria, yet information on its potential distribution and habitats remain absent for most of Austria, including the state of Salzburg.

1.1. Hazel Grouse – Species Profile and Habitat Requirements

The Hazel Grouse (*Tetrastes bonasia*) is the smallest member of the grouse species in Europe, native to the Palaearctic region. Its distribution is wide but patchy, spanning from central Europe eastwards across Eurasia up to northern Japan. In Europe, hazel grouse occupy montane coniferous-deciduous mixed forests, with large populations in Fennoscandia and mountainous regions of central Europe such as the Dinaric Mountains, Carpathians and the Alps (Rózsa et al. 2016). Austria, especially its alpine regions are considered important for hazel grouse in Central Europe. Data on population sizes and trends were originally published in 2018, estimating a national population size between 5000 to 10000 breeding pairs. However, these figures may be imprecise and current number are probably lower due to the lack of systematic and comprehensive data not only in Austria, but for most of Europe (BirdLife-International 2024).

The hazel grouse is protected under the EU Birds Directive (2009/147/EC), listed in both Annex I, requiring special habitat conservation measures, and Annex II, which allows for regulated hunting on a national level. In Austria hunting legislature and regulations are subject to federal-state level that implement species specific regulations, aligning with national and international conservation and species-protection laws. Currently, hazel grouse hunting is permitted in six of Austrias nine provinces. However, the province of Burgenland recorded the last official harvest in 1968, while the provinces of Vienna, Vorarlberg and Salzburg, have incrementally suspended hunting completely, with Salzburg being the last state to do so in 1995, implementing a year-round protection status. Provinces where hunting remains permitted are experiencing a reduction of annual harvest from 800 individuals to 100 individuals per year from 1948 to 2022 (Reimoser 2024). According to the International Union for Conservation of Nature (IUCN), the hazel grouse is classified as “Least Concerned” in Europe, largely due to the inclusion of estimations from territories of the Russian Federation, which account for approximately 66 % of Europe’s total hazel grouse populations (BirdLife-International 2021). However, within the European Union, this forest-bird is classified as “Vulnerable” and exhibiting population decline or unknown trends across almost all its member-states.

Habitat Requirements and Vulnerabilities

A habitat, as defined by Hall et al. (1997), are “*the resources and conditions present in an area that produce occupancy, including survival and reproduction, by a given organism*” and the hazel grouses requirements to its habitat are largely determined by its ground-dwelling and cryptic lifestyle. The availability of perennial food sources in addition to vegetation structures providing shelter, nesting sites and protective cover from predators are essential requirements on its habitat throughout the seasons. Previous studies have addressed the importance of structurally heterogeneous and complex forest stands, characterised by mixed-species composition and multi-layered vertical structures and variability in canopy-closure as aspects of high quality habitats (Åberg et al. 2003; Sitzia et al. 2014; Braunisch et al. 2019).

While this species predominantly occupies conifer-dominated stands comprising of spruce (*Picea abies*) and often silver fir (*Abies alba*), a substantial dependency on deciduous tree species as food sources and shelter throughout the seasons has been documented (Mathys et al. 2006; Müller et al. 2012). Deciduous species like poplar (*Populus spp.),* rowans (*Sorbus spp.),* and birch (*Betula spp.),* together with shrubs such as hazel (*Coryllus avellana*), willow (*Salix spp*.), and bilberry (*Vaccinum spp*.) provide essential food sources and breeding habitats during spring (Matysek et al. 2017). In the post-breeding period of autumn and in winter, the amount of deciduous tree species in habitats is reduced in favour of forest stands consisting of dense understories of young spruce together with shrubs providing cover(Sachot et al. 2003; Schäublin and Bollmann 2011; Ludwig and Klaus 2016). Forest stands undergoing early natural succession after experiencing disturbances such as bark-beetle infestations, provide high-quality habitats for the hazel grouse (Kortmann et al. 2018). These areas are often colonised by pioneer-species such as elder and hazel provide both dense ground layer cover and food sources. In winter, early succession stages of coniferous stands become particularly important for cover (Scridel et al. 2022). Additionally, the hazel grouse shows a preference for linear forest structures such as edges, forest aisles and riparian zones, as these structures enhance structural diversity in canopy-closure by supporting species like alnus, birch and alder among others (Müller et al. 2012; Matysek et al. 2019). Conversely, hazel grouse avoid open landscapes such as clear-cut areas, agricultural fields and transitional zones between forests and open-lands due to increased predation risk (Huhta et al. 2017). Human land use, particularly intensive silvicultural practices and touristic activity influence hazel grouse habitat selection as these birds have been shown to spatially avoid these areas (Matysek et al. 2020). A long term study focusing on a population in the bohemian forest report negative impact of intensive logging, clear-cutting and removal of pioneer-species, causing habitat loss, increasing fragmentation and resulting in a population decline of approximately -3.8 % per year from 2006-2019 (Klaus and Ludwig 2021). The hazel grouse's limited dispersal abilities enhance their vulnerability to habitat degradation and fragmentation (Sahlsten et al. 2010). Consequently, they require relatively large, continuous forest patches rather than small isolated high-quality habitats (Sahlsten et al. 2010; Åberg et al. 2011; Kajtoch et al. 2012). Such fragmentation and isolation dynamics have previously led to a decreased genetic diversity in a Carpathian hazel grouse population (Rutkowski et al. 2016), with similar findings affecting other European grouse species (Jimenez et al. 2022; Kunz et al. 2022). In order to assess and mitigate the impact of potential threats on hazel grouse habitats, large scale spatial analyses provide the foundation for applied conservation efforts by assessing the distribution and quality of potential habitats.

1.2. Species Distribution Modelling and Maxent

Species Distribution Models (SDMs) are statistical tools to predict the distribution of a species across a landscape in relation to environmental conditions often derived from satellite remote sensing data (Guisan and Zimmermann 2000; He et al. 2015). While there are several different families from which SDM's can originate, the general approach of correlative models involves georeferenced spatial information in the form of presence-records of a species, often accompanied by corresponding absence-data, linked to topographic, climatic and other ecological habitat conditions of a species to model its distribution (Elith and Leathwick 2009). The outputs of SDM contribute to ecological insight about the spatial distribution of the target species and the quality of its habitats. Thereby, SDM's allow for the identification of suitable areas for conservation measures, support spatial conservation planning by guiding monitoring, restoration and protection efforts and assist in decision-making by assessing the impact of management actions (Lawler et al. 2011; Guisan et al. 2013) including potential risk assessment regarding invasive species (Srivastava et al. 2019).

Traditionally, SDM's have relied on regression based approaches like generalised linear models or generalised additive models to predict a species probability of distribution by using the maximum likelihood method which often relies on absence data of the species to contrast against occurrences to create predictions (Norberg et al. 2019). However, obtaining robust absence-records can be problematic since differentiating between true-absences and non-detections can be methodologically difficult (Gu and Swihart 2004) and often resource intensive, particularly in wildlife sciences (MacKenzie 2005). However, in recent decades, due to theoretical and computational advancements, machine learning models such as random forests, artificial neural networks and maximum entropy (Maxent) (Phillips et al. 2006; Phillips and Dudík 2008) have become increasingly popular for managing large, complex datasets, such as remote sensing satellite data, to model species-environment relationships by using presence-only data (Zhang and Li 2017).

Maxent

The species distribution modelling software Maxent, developed by Phillips et al. (2006) has established itself as one of the most widely used and well-performing presence-only modelling approaches, particularly in situations of rare and cryptic species with limited presence records (Fois et al. 2018; Radomski et al. 2022). Since its establishment, this software has been widely used and experienced a number of adaptations by the creators over the years, ultimately resulting in this software becoming open source, which led to numerous implementations in statistical software such as R (Phillips et al. 2017).

Maxent employs the Maximum-Entropy-Method to estimate model parameters and to create predictions. In information theory, entropy quantifies the average uncertainty predicting an outcome of random variables, where the lowest entropy indicates perfect certainty and the highest entropy represents perfect uncertainty (Shannon 1948). In the context of species distribution modelling using Maxent, the maximum-entropy-method assumes a uniform prior distribution of uncertainty across the study areas, representing an equal a-priori uncertainty regarding the species occurrence. The model only deviates from this prior assumption by including empirical evidence of environmental conditions at known presence sites, estimating the corresponding habitat suitability values (Elith et al. 2010). An advantage of Maxent is its ability to produce predictions using presence-only data, contrasted against background points which are randomly sampled non-occurrence locations representing environmental conditions of potentially available habitats to the species. Additionally, the internal model tuning and regularisation parameters of Maxent penalise complexity, thereby preventing overfitting and overly complex models with regards to varying sample sizes. Additional features implemented into Maxent are the abilities to project or transfer a model fitted to specific environmental conditions onto different geographic areas (Phillips and Dudík 2008) as well as defining suitability-thresholds to binarize a continuous map to distinguish between "suitable/unsuitable" habitats or "presence/absence", particularly for practical purposes (Phillips et al. 2006). These feature have been applied in previous studies to assess the invasion risk of non-native species (Fernández and Hamilton 2015) and predicting climate change impacts on species distribution by transferring models trained on native or known ranges to novel areas or future scenarios (Karuppaiah et al. 2023; Kang et al. 2025) and to define and compare specific suitability thresholds (Liu et al. 2016; Shabani et al. 2018).

However, while many studies report the ease of applicability, overall robustness and high predictive performance of Maxent compared to other presence-only approaches (Ray et al. 2017; Elith et al. 2020; Valavi et al. 2021; Ahmadi et al. 2023), there are several aspects that need carful consideration throughout the modelling process. Addressing potential sampling-bias due to uneven sampling effort, background sampling, multicollinearity among predictor variables and appropriate model tuning have been reported to be crucial aspects to consider when modelling (Merow et al. 2013; Lissovsky and Dudov 2021), as well as the choice and quality of predictor variables (Bradie and Leung 2016).

The resulting output of a Maxent analysis includes a spatial map depicting the potential distribution of a species and quantifying the corresponding habitat suitability through a continuous gradient from 0 to 1, with 0 indicating least suitable habitats and areas closest to 1 the most suitable. Additionally, Maxent generates graphical representations depicting individual environmental variables responses regarding species occurrence and quantifies the relative contribution of each predictor variable to model performance and explanatory power. When adequately implemented and interpreted, Maxent modelling can provide valuable ecological insights into a species-environment relationship and practical utility for wildlife management and conservation planning.

1.3. Research Goal and Hypotheses

The main objective of this master's thesis is to develop a Maxent based species distribution model to predict and describe suitable habitats for the Hazel Grouse (*Tetrastes bonasia*) across the Austrian province of Salzburg, using signs of occurrence obtained from the Naturpark-Weißbach and the Bavarian Saalforsten.

Hypotheses

H1) Vertical Heterogeneity

Since Hazel Grouse require a multi-layered forest stands of mixed age classes, I hypothesised that habitat suitability increases with increasing vertical heterogeneity. In this work, heterogeneity is represented as the Gini coefficient of tree-height distributions, calculated in a 150 m moving window.

H2) Edge Proximity

Hazel Grouse have been reported to show preference towards edge structures within forests such as forest aisles, waterbodies and others as these structures increase structural heterogeneity of habitats and provide additional food sources of corresponding edge vegetation. I hypothesised that habitat suitability increases with increasing proximity to a) forest roads, b) lotic-waterbodies and c) forest edges, measured as the Euclidean distance to the nearest edge-structures.

H3) Transferability – Training extent

Since Hazel Grouse occurrences were obtained exclusively from parts of the Saalachtal region which covers about 4.2 % of Salzburg's total area, two modelling strategies have been compared:

1. "Saalachtal-extent" Model: training the model on the area where data has been collected followed by projecting the fitted model onto all of Salzburg.
2. "Full-extent" Model: training the model directly on the total area of Salzburg.

I hypothesised that the local extent and projection approach will outperform the full-extent model when evaluated by model selection criteria as the projection feature allows for the model to be trained within the actual sampled area, thereby avoiding the influence of unsampled areas.

2. Methodology

2.1. Study Areas – Salzburg and the Saalachtal

Full Extent – Salzburg

The province of Salzburg covers an area of 7154 km^2 in west-central Austria, bordering Bavaria in the north and west, and the provinces of Upper Austria, Styria, Carinthia and Tyrol to the northeast, east, south and southwest, respectively. Geographically, approximately 90 % of Salzburg state territory lies within the Alps, extending both into the Central Eastern Alps, primarily the Hohe Tauern range in the south, and the Northern Limestone Alps in the north central region. These alpine areas are separated by the Salzach and Enns river valley, which present corridors of lower elevations and smoother relief, allowing for agricultural land use and the development of urban areas. Salzburg is traditionally partitioned into five distinct regions: Flachgau, Tennengau, Pongau, Pinzgau and Lungau. The Flachgau and Tennengau, encompass the northernmost extent of Salzburg, surrounding the city of Salzburg and the city of Hallein. The regions of Pinzgau, Pongau and Lungau, collectively known as the "Innergebirg-Regions", are located in the west, south and east respectively, containing the highest elevations within Salzburg, particularly within the Hohe Tauern mountain ranges.

Forests constitute the largest land cover type of Salzburg, comprising approximately 52 % of the total area, equating to 3750 km^2. Of these, 67 % are coniferous forests, dominated by Spruce, European beech, Larch and others. More than half of these forests are considered "Schutzwald", essential for mitigating natural hazards such as avalanches, mudslides and erosion of terrain. The distribution of forested areas varies across the region with the "Innergebirgs" -regions Pinzgau (110,909 ha), Pongau (96,157 ha) and Lungau (50,438 ha) making up the majority of forested areas over Flachgau (38,443 ha) and Tennengau (38,443 ha) (Lackner 2023). Agricultural land occupies around 14 % (1000 km^2) of Salzburg's area and is largely concentrated within the valley floors of lower elevation in the northern regions. Traditional land use in the form of alpine pasture farming is occurring only in higher elevation regions. Urban Development is consisting around 4 % of the land area and is mostly concentrated around larger urban areas such as Zell am See, St. Johann and Hallein, in addition to large suburban areas around the capital city of Salzburg.

Small Extent – Saalachtal

The study area where hazel grouse presence has been recorded, lies within sections of the Salzburger Saalachtal valley, located in the Pinzgau region of Salzburg. The Saalachtal valley is characterised by a mosaic of landscapes ranging from valley floors at approximately 600 m a.s.l to high peaks exceeding 2500 m a.s.l. It encompasses several municipalities, comprising of Lofer, St. Martin bei Lofer, Unken and Weißbach bei Lofer, collectively encompassing 297 km^2, of which 193 km^2 are forested and considered to be available habitat to the hazel grouse. The valley is flanked by pronounced mountain groups such as the Reiter Alpe in the north, the Loferer massifs to the west, and the Steinernes Meer plateau to the east, creating a diverse topographic alpine relief.

Within the Saalachtal valley lies the Naturpark Weißbach, established in 2007 and covering about 27.8 km^2 of which, 21 km^2 are forested. The nature park is located between the Loferer, Leoganger and Reiter Steinberge limestone massifs, adjacent to the Bavarian border and bordered on its Austrian side by the Northern Kalkhochalpen protected area and on the Bavarian side by the Berchtesgaden National Park and Biosphere Reserve. The majority of non-urban or agricultural areas within the Saalachtal, including most forested areas within the Naturpark Weißbach are owned and managed by the Bavarian State Forests Administration of Germany, comprising a total area of 185 km^2, of which 60 % (approximately 112 km^2) are forested areas. The forests within the Saalachtal valley at lower and middle elevations are predominantly mixed deciduous-coniferous stands consisting of Norway spruce (*Picea abies*), European beech (*Fagus sylvatica*), Silver fir (*Abies alba*) and various shrubs species like hazel (*Corylus avellana*) and alder (*Sambucus sp.*). Higher elevations transition into subalpine coniferous forests characterised by European larch, Spruce and large areas of dwarf pine (*Pinus mugo*) near the timberline. The Saalforsten span from approximately 540 m a.s.l in the valley, up to 2643 m a.s.l at the Birkhorn peak and are characterised by steep slopes, rugged cliffs and variable altitudinal gradients.

2.2. Presence Records and Bias File

Occurrences of the hazel grouse (*Figure 1*) have been obtained from forest district managers of the Bavarian Saalforsten, who have been recording presence evidence of the grouse within their respective forest districts. These records were not collected through a systematic survey but rather originate from opportunistic form of evidence, which were georeferenced and archived with potential future habitat analyses, such as this study, in mind. The questionnaire was distributed in March of 2023 to the forest district managers of the Saalforsten and peers managing the Bavarian Saalforsten, which was completed by April 2023.

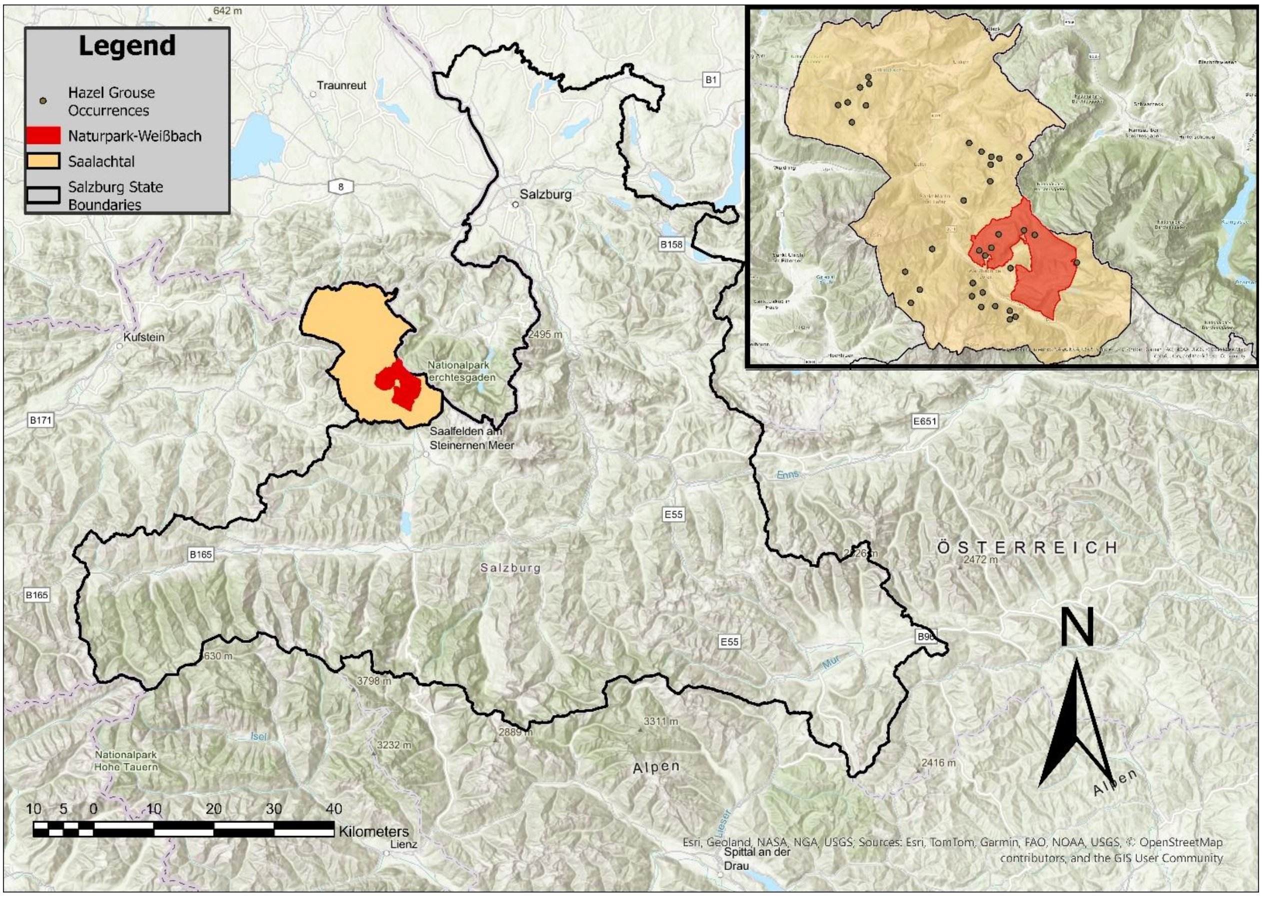

Figure 1: Map depicting the administrative boundaries of Salzburg, parts of the Saalachtal and the Naturpark Weißbach as well as occurrence records of the hazel grouse. Basemap sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors and the GIS User Community.

In this questionnaire the date, longitudinal and latitudinal coordinates, the number and sex of individuals was asked (male, female, unknown), the type of evidence of presence (direct observation, acoustic-identification, photo/video, carcasses, faeces, feathers, tracks, nests, or "other"), as well as some information on the participants professional background (forestry, hunters, local expert, governmental or scientific personnel), with the option to leave additional comments or habitat descriptions relevant to the observation. In addition, the perceived georeferenced accuracy was asked (low, medium, high). The survey resulted in 44 unique responses of evidence of presence overall, including one entry noted as an error by a participant. Of the remaining 43 responses, 7 were located within the boundaries of the Naturpark-Weißbach and the others within a 17 km radius to the west and south of the park all lying within the Saalachtal. 14 observations were dated and obtained between October 2020 and October 2022, whereas 21 were undated, 8 have been classified "historic" referring to observations made 10 to 30 years ago. Excluding historic records, the overall presence records are 35 comprising 21 unsexed individuals, 8 males, 6 females, of which 4 were carrying 4-6 chick (totalling 19 chicks). Thirteen observations originated from direct sightings, 1 found-dead individual documented on a camera trap and 21 from unclassified evidence-types. Self reported accuracy of the participants was high in 5 cases, moderate in 22 and low in 8 cases.

Sampling bias was addressed through a spatial thinning procedure using the 'spThin'-package (Aiello-Lammens et al. 2015), by applying a minimum distance of 500 meters between observations, thereby reducing spatial clustering and overrepresentation of frequently detected locations. The threshold was chosen, based on the hazel grouses observed mean daily migration distance, reducing the number of available presence records for modelling to n=34.

Subsequently, a bias file was generated, following the recommendations of (Inman et al. 2021), by calculating a gaussian kernel density estimation with a bandwidth of 300m. The kernel density estimation way calculated on the thinned presence records with the "density()" function using the 'terra' package (Hijmans et al. 2022), producing a continuous sampling density surface. This raster was then normalised to a range of 0-1 using "calc()"-function of the 'raster'-package and masked to forested areas using the "terra::mask()" function, following the background-point selection approach described in chapter 2.4.

2.3. Data Collection and Software

The remote-sensing datasets obtained to create variables representing the habitat requirements of the hazel grouse are listed in (*Table 1*). The monthly mean precipitation and temperature data for the months of April, May, and June were obtained from GeoSphere Austria Bundesanstalt für Geologie, Geophysik, Klimatologie und Meteorologie (Hiebl and Frei 2016). Topographic datasets consisted of elevation, slope, and aspect, derived from the 5 m ALS-DGM, were provided by the Land Salzburg (data.salzburg.gv.at) in ESRI ASCII Grid format. Ecological datasets included a tree species map (Baumartenkarte) with 26 classes, provided in GeoTIFF format at 10 m resolution by the Bundesforschungszentrum für Wald (Schadauer et al. 2024), based on Sentinel-2 data alongside a canopy-closure layer, a normalized digital surface model (nDSM), and a binary forest mask, all in 1 m resolution GeoTIFF format. Vector data representing forest roads and lotic waterbodies and municipal boundaries of Salzburg, were obtained from Land Salzburg (data.salzburg.gv.at). The anonymised survey of hazel grouse occurrences in hunting territories of Austria was provided by the director of the hunting association of Salzburg, to be used for validating the results of habitat suitability mapping.

Table 1: Topographic, ecologic and climatic datasets used in this study, including resolution, unit, format and sources.

Data-Type	**Data-set**	**Period/Temporal Extent**	**Spatial Extent**	**Resolution**	**Data Unit**	**Format**	**Source**
Topographic	Digital Terrain Model	May, 2024	Salzburg	5 m	Meters a.s.l.	GeoTIFF	Land Salzburg – data.salzburg.gv.at
Topographic	Slope			5 m	Percent (0-90)	GeoTIFF	Land Salzburg – data.salzburg.gv.at
Topographic	Aspect			5 m	Degree (0-365)	GeoTIFF	Land Salzburg – data.salzburg.gv.at
Ecological	Tree-Species-Map	November, 2024	Austria	10 m	Classes	GeoTIFF	Bundesforschungszentrum für Wald
Ecological	Normalised Digital Surface Model (nDSM)	August, 2024	Salzburg	1x1 m	Meters a.s.l.	GeoTIFF	Bundesforschungszentrum für Wald
Ecological	Canopy-Closure			1x1 m	Percentage (0-100)	GeoTIFF	Bundesforschungszentrum für Wald
	Forest-Roads	NA		NA	Line	Vector	Land Salzburg – data.salzburg.gv.at
Ecological	Lotic Waterbodies			NA			
Climatic	Mean Temperature	April-June 2024		1000 x 1000 m	C°/day	GeoJSON	GeoSphere Austria – Bundesanstalt für Geologie, Geophysik, Klimatologie und Meteorologie
Climatic	Mean Precipitation			1000 x 1000 m	mm/day		GeoSphere Austria – Bundesanstalt für Geologie, Geophysik, Klimatologie und Meteorologie
Processing	Forest-Mask	June 2024		10 x 10 m	Binary	GeoTIFF	Bundesforschungszentrum für Wald
Processing	Salzburg Municipal Boundaries	NA		NA	Polygon	Vector	Land Salzburg – data.salzburg.gv.at

All aspects regarding data-preparation and variable calculations and descriptive analyses have been performed using R Statistical Software v.4.4.1 (R_Core_Team 2024). All visual inspection during the data-preparation, variable-calculation and modelling process of R and Maxent output, as well as visual depictions including the creation of maps was conducted in ArcGIS Pro version 3.5.

2.4. Data Pre-Processing and Background Selection

Data Pre-Processing

For environmental layers to be compatible with Maxent, they must share the same spatial extent, spatial resolution and coordinate reference system. Due to most of the original datasets having been provided in high-resolution, a resolution of 10x10m has been decided for analyses, allowing for fine-grain analyses of potential hazel grouse habitats. The coordinate reference system chosen for this study was ETRS89/Austria Lambert (EPSG:3416), as it employs a Lambert Conformal Conic projection, specifically designed for Austria, reducing spatial distortion and ensuring high positional accuracy suitable for small scale geospatial analyses (Ihde et al. 2000). Additionally, most Austrian remote sensing data are provided in ETRS89 based projections, facilitating model integration and minimising potential transformation errors.

Spatial alignment was performed using the "Municipal_Boundaries"-shapefile as a reference mask, ensuring consistency across spatial extent and verifying alignment in with functions provided by the R package 'terra', specifically the "project()", "resample()", "crop()" and "mask()" functions. This first spatial mask standardised all layers to the ETRS89/Austria Lambert CRS at the resolution of 10x10-meter, restricting data processing to the state areas of Salzburg. In order to create the spatial mask for the smaller Saalachtal valley modelling extent, municipalities containing occurrence records were manually selected from the same "Salzburg_Municipal_Boundaries"-shapefile in ArcGIS and exported as binary raster mask.

Background Point Selection

Previous studies noted the importance of appropriately defining the spatial extent of available habitats to the target species, which is represented as the "background" in species distribution models (Acevedo et al. 2012; Northrup et al. 2021) to avoid over estimating the potential distribution when fitting a model. With regards to Maxent, (Merow et al. 2013) emphasised that the background selection fundamentally influences Maxent inferential abilities and must be conducted with the species ecology in mind. It has been recommended by (Phillips 2008; Vanderwal et al. 2009; Castillo and Higa 2025), that restricting background-point-selection to areas in area which the target species can potentially occur and exclude non-habitats in order to avoid losing detailed habitat boundaries, an approach demonstrated to improve model accuracy and overall performance in a comparative study (Castillo and Higa 2025). The background-point selection strategy for modelling in this study involved restricting all calculations of model variables and the modelling process to forested areas only, as the hazel grouse does not realistically occupy landcover types such as agricultural areas, urban areas or large scale open lands. To do this, the forest-cover map, was used as a spatial mask using the "terra::mask()" function, constraining all valid cells within each dataset exclusively to forested areas of Salzburg. To create the spatial mask for the smaller modelling extent, the same process of restricting valid cells to forested areas was applied to the smaller Saalachtal extent. However, the actual restriction of environmental predictor layers to forested areas, is applied after variable calculation in the following chapter, ensuring that calculations were performed exclusively on valid cells and avoiding interpolation due to the inclusion of missing or invalid data after masking, especially during moving-window calculations.

2.5. Variable Calculation

Topographic variables: The data set of the "Aspect" predictor variable, originally provided in degrees from 0-360° representing the compass direction of slope orientation, was classified into eight categorical directional classes to simplify interpretation and facilitate practical interpretability. The reclassification was based standard directional groupings: North: 0-22.5°, Northeast: 22.5-67.5°, East: 67.5-112.5°, Southeast: 112.5-157.5°, South: 157.5°-202.5°, Southwest: 202.5-247.5°, West: 247.5-337.5°, Northwest: 292.5-337.5°, North: 337-360°. This has been done using the "classify()"-function from the "terra"-package", resulting in classification of values representing cardinal directions from 1-8 as a categorical variable of "Aspect". For the variables "Elevation" and "Slope", no additional calculations were necessary.

Climatic variables: To represent climatic conditions during the core breeding period of the hazel grouse, monthly climate data for precipitation and temperature were merged for the months of April, May and June respectively. The averaging of the three months was performed using the "app()" function from the terra package, calculating the mean value across April, May, June aka. the spring period, from the "terra"-package. The resulting variables were a single raster layer for temperature in C° and for precipitation in mm. Both layers were subsequently renamed "Seasonal_Temperature" and "Seasonal_Precipitation" as model variables.

Ecological variables: To quantify vertical forest heterogeneity of tree heights, the Gini coefficient was calculated based on nDSM raster layer, using a moving window approach. The Gini coefficient is a statistical measure, originally intended to assess income inequality (Catalano et al. 2009), that is expressed on a normalised scale from 0 representing perfect equality to 1 maximum inequality. In previous studies the Gini-coefficient has been calculated from forest related data such as diameter of breast height or tree-height, derived by LIDAR data, to measure structural heterogeneity (Kukunda et al. 2019; Paluch 2021; Valbuena et al. 2021). Particularly the Gini-coefficient of tree heights has been shown to be an effective parametrisation measuring forest heterogeneity (Reich et al. 2022). The Gini-coefficient has been derived from the dataset using the moving window approach with a spatial diameter of 300m, representing the average daily movement of hazel grouse. The Gini coefficient was calculated using the "Gini()"-function from the "ineq" package (Zeileis et al. 2009). The moving window calculations were applied to each cell using a 150 meter focal window (15x15 cells at 10 m resolution) using the "focal()" function from the "terra"-package. The resulting predictor variable was names "Gini-tree-height". In order to create the predictor variable "Standard-deviation-canopy-closure" representing the variability in forest canopy structure, the standard deviation of canopy closure was calculated, using the same moving window approach. The input raster represented canopy closure as continuous percentage values, from which the standard deviation in a moving window was calculated following the same approach and parameters as performed in the Gini-coefficient calculations.

The original tree-species-dataset representing tree-species composition, has been provided as a categorical raster layer with 26 distinct tree species and tree species assemblages, which was reclassified into five ecologically meaningful forest type categories to improve interpretability and to reduce model complexity. The five resulting categories were: 1) Single-Species Conifers, 2) Mixed-Species Conifers, 3) Coniferous-Deciduous mixed, 4) Single-Species-Deciduous and 5) Undergrowth. The reclassification was performed using the "classify()" function from the "terra"-package and resulted in the variable "Tree-species-composition".

To quantify the spatial proximity of edge structures relevant to hazel grouse habitat use, three distance based raster layers were calculated representing the Euclidean distance to forest-edges, lotic-waterbodies and forest-roads, respectively. All calculations were performed in R using the 'terra' and 'sf' package (Pebesma 2018). Vector layers representing the before mentioned habitat-features were rasterised onto a reference grid encompassing the same dimensions as the other raster layer, assigning values to cells intersecting the cell-grid. By applying the "distance"-function from the terra package, the Euclidean distance was calculated for each cell. This resulted in three distance raster layers, “Distance_forest-edge”, “Distance_lotic-waterbodies” and “Distance_forest-roads”.

2.6. Multicollinearity Diagnostics and Description of Environmental Predictors

To assess multicollinearity among candidate environmental predictors used for modelling, a Pearsons product-moment correlation was conducted to identify pairwise correlation between numeric and ordinal variables, and the Variance Inflation Factors (VIF), were calculated to identify higher order collinearity. The correlation analysis was performed by calculating a heterogeneous correlations matrix using the “hetcor()” function from the R package ‘polycor’, with a threshold of r ≥ 0.7 to identify correlation among predictors (Fox and Fox 2022). The correlation analysis (*Appendix A 1*) revealed a high negative correlation (r = -0.85) between “Seasonal_Temperature” and “Elevation”, leading to the exclusion of “Seasonal_Temperature” due to redundancy and data quality concerns of the climate data, while “Elevation” was retained as a candidate predictor variable. Additionally, despite the variable “Seasonal_Precipitation”, showing no statistically significant correlations with other predictors, it was excluded from further analysis due to data quality concerns and to reduce model complexity by limiting the number of potential predictors. To further investigate potential higher order collinearity issues, the VIF scores for all the variables were calculated using the “vifstep()” function from the ‘usdm’ R package developed by (Naimi and Naimi 2017), applying a threshold of 5, with variables showing VIF values ≥3 intended for iterative removal. During the VIF assessment, no further variables were excluded from the set of candidate predictors, thereby only retaining uncorrelated candidate predictor variables. In addition to collinearity diagnostics, descriptive statistics were calculated to provide an overview of the predictor variables prior to modelling. This was carried out for the full modelling extent as well as the small modelling extent to document potential differences in predictor characteristics between spatial extents. For continuous predictors (*Table 2*), the mean, standard deviation (SD) and interquartile range (IQR) were calculated and for categorical predictors (*Table 3*), the proportional representation (%) of each class.

Table 2: Descriptive statistics (mean, standard deviation and interquartile range) of continuous environmental predictors for both study extents (small extent – Saalachtal, full extent – Salzburg IQR describes the range between the 25th and 75th percentile, capturing the central spread of the data.

Variable (Small Extent)	**Unit**	**Mean ± SD**	**IQR**
Distance_lotic_waterbodies	meter	578.33 ± 447	580.853
Distance_forest_roads	meter	1913.535 ± 1343	2010.51
Distance_forest_edge	meter	81.668 ± 104.386	115.55
Elevation	meter a.s.l.	1147.461 ± 293.697	437.068
Standard-deviation-canopy-closure	Index (0-1)	0.155 ± 0.075	0.102
Gini-tree-height	Index (0-1)	0.252 ± 0.099	0.138
Variable (Full Extent)	**Unit**	**Mean ± SD**	**IQR**
Distance_lotic_waterbodies	meter	381.755 ± 369.054	391.438
Distance_forest_roads	meter	998.807 ± 1150.370	1115.198
Distance_forest_edge	meter	111.762 ± 154.824	155.451
Elevation	meter a.s.l.	1269.092 ± 368.648	539.319
Standard-deviation-canopy-closure	Index (0-1)	0.177 ± 0.094	0.138
Gini-tree-height	Index (0-1)	0.266 ± 0.115	0.159

Table 3: Descriptive statistics (class-proportions) of categorical predictors for both study extents.

Aspect (cardinal directions)	Proportion (%) - Small	Proportion (%) - Full
1 - North	1.49	2.89
2 - Northeast	11.95	12.66
3 - East	15	14.56
4 - Southeast	15.45	13.33
5 - South	15.34	13.32
6 - Southwest	14.76	13.54
7 - West	13.74	15.76
8 - Northwest	12.25	13.92
Tree-species-composition		
1 - Single-Species-Coniferous	41.18	38.89
2 - Mixed-Species-Coniferous	16.21	21.89
3 - Coniferous-Deciduous mixed	26.54	17.07
4 - Single-Species-Deciduous	11.58	13.83
5 - Undergrowth	4.49	8.31

2.7. Model Predictor Sets

For modelling, nine different candidate predictor sets comprising varying amounts of the eight derived environmental predictors were constructed (*Table 4*), based on ecological knowledge of the target species and in alignment with best practices in species distribution modelling using Maxent. This approach aimed at balancing ecological relevance, interpretability and methodological robustness in order to minimise risks associated with model overfitting. The methodological approach aligns with principles outlines in the work of (Leitão and Santos 2019) who emphasized iteratively assessing the importance of predictor variable selection to ensure accurate predictions while allowing for practical ecological interpretation of model results and (Warren et al. 2014), suggesting that fewer predictors tend to produce more robust models while avoiding overfitting.

Table 4: Candidate predictor sets, including core predictor variables and respective predictor combinations used for modelling.

Candidate Set				**Topographic Variable**	**Vertical heterogeneity**	**Distance-Variables**		
Set-1	Aspect	Tree-species-composition	Gini-tree-height	Elevation			Distance_forest_road	Distance_lotic_waterbodies
Set-2	Aspect	Tree-species-composition	Gini-tree-height	Elevation				
Set-3	Aspect	Tree-species-composition	Gini-tree-height		Standard-deviation-canopy-closure		Distance_forest_road	Distance_lotic_waterbodies
Set-4	Aspect	Tree-species-composition	Gini-tree-height		Standard-deviation-canopy-closure			
Set-5	Aspect	Tree-species-composition	Gini-tree-height			Distance_forest_edge		
Set-6	Aspect	Tree-species-composition	Gini-tree-height	Elevation		Distance_forest_edge		
Set-7	Aspect	Tree-species-composition	Gini-tree-height		Standard-deviation-canopy-closure		Distance_forest_road	
Set-8	Aspect	Tree-species-composition	Gini-tree-height		Standard-deviation-canopy-closure	Distance_forest_edge		
Set-9	Aspect	Tree-species-composition	Gini-tree-height	Elevation	Standard-deviation-canopy-closure	Distance_forest_edge		

In this work, a set of core variables across all candidate sets were selected based on ecological knowledge of habitat-feature importance and on initial model testing. The topographic predictor "Aspect", consistently showing high predictive performance and explanatory contribution to model performance in preliminary test runs, was included due its potential ecological influence on microclimate and vegetation. The ecological variable "Tree-species-composition" was also included as a core predictor as it represents key habitat components such as food-sources and shelter reflected by fundamental tree species or tree species composition, thereby influencing habitat selection of the hazel grouse. In addition, the variable "Gini-tree-height", representing vertical structural heterogeneity, was implemented as a core predictor due to its superior predictive performance over "Standard-deviation-canopy-closure" in preliminary testing and due to its ecological importance for hazel grouse habitats.

In order to evaluate the contribution of additional predictor variables, the remaining ecological and topographic variables, as well as distance-related variables, were implemented incrementally across all candidate sets, to asses individual contributions to model performance and ecological and practical interpretability. Variables such as "Elevation" and "Standard-deviation-canopy-closure" were selectively incorporated to assess their ecological relevance and contribution to model performance. Additionally, the integration of distance-based predictors "Distance_forest_edge", "Distance_forest_roads" and "Distance_lotic_waterbodies" was constrained to either one or two layers per set to prevent redundancy and avoid inflating model complexity. The selection and systematic rotation of the predictor variables across all candidate sets is intended to assess the predictive importances and their combined or individual roles in influencing the predictive power of the model.

2.8. Model Fitting and Selection

Model fitting was conducted using the Maxent Java Software and model calibration was conducted in R. To assess the effect of spatial scale and evaluate robustness across varying spatial extents, the entire modelling and model selection procedure was independently conducted at two spatial scales, yet with identical model settings and predictor sets. In the first "traditional" approach, a model is directly trained on the full extent of Salzburg without projection and with the inclusion of the created bias file. In the second modelling approach, outlined by (Phillips 2008), a model is trained on the environmental predictor set of the smaller "Saalachtal" extent and subsequently projected onto the environmental predictor set covering the full study area (Salzburg).

All model runs employed a fixed combinations of three feature types: linear, quadratic and hinge which were chosen, based on the recommendations provided by (Merow et al. 2014) advocating for fewer and simpler feature types, given the amount of presence-records used in this work (n=34). More complex feature-types such as the product- and threshold-feature should be avoided from using below a sample size of n=80, and were not used in this work (Elith et al. 2010). In order to balance model complexity and predictive generalisation, three different regularisation multipliers (RM's) were used: 0.5, 1 and 2. The choice of regularisation multipliers are based on recommendations provided by (Ahmadi et al. 2023), suggesting that regularisation multiplier values are adequate for the given sample size (n=34) and supported by findings from (Morales et al. 2017) indicating that lower regularisation parameters tend to produce more robust models with fewer sample sizes. Each model was run using 80 % of the occurrence records for training and 20 % for testing, with model robustness assessed via 20 bootstrap replicates and jackknife-test to assess variable-importance on model performance. This ensures that each model replication samples different subsets of the data, therefore accounting for potential variability in model performance due to the effect of randomly sampling training- and test-data. All model outputs are set to be generated using the recommended cloglog transformation. The model fitting process resulted in 27 candidate models for each modelling extent, totalling in 54 unique models overall.

Model Selection

After model fitting, model selection was performed separately for each modelling extent using a systematic sequential approach following the "ORTEST" framework described by (Dorji et al. 2020). For each extent, the 27 candidate models were first evaluated using 10th percentile training presence omission rate as the primary criterion. This threshold was chosen because it balances sensitivity to presence records with predictive generalisability and is particularly suitable for small sample sizes. In the first step, the models with the lowest omission rates were retained. If multiple models shared the lowest omission rates, the AUC for test data (AUC_test) was used as a secondary criterion, with higher values indicating better discriminatory ability. As an additional indicator of overfitting, the difference between training and test AUC (AUC_Diff) was examined, with smaller values indicating greater generalisability. Based on this ranking, the two best performing models of each spatial extent were selected, resulting in a total of four candidate models for further consideration.

The final model was chosen in two rounds. In the first round, four candidate models were evaluated and compared based on model performance metrics, predictor set and environmental predictor response curves, as well as ecological plausibility through visual inspection in ArcGIS and in consultation with my supervisors. After this evaluation, the four candidate models were reduced to two, from which one was selected as the preliminary final model. In the second round, both remaining candidate models were presented to the director and head-forester to discuss and interpret the models' output with regards to ecological realism and habitat prediction of the model, particularly focusing on the areas of the Naturpark-Weißbach and the surrounding Saalforsten.

2.9. Post-Modelling Processing and Validation of Suitability Map

Post-Processing

The final continuous cloglog raster layer from Maxent was converted into a binary map of "suitable" and "unsuitable" habitats, using the "10th-percentile training presence threshold (10PT). This threshold defines the suitability-cutoff under which 10 % of training occurrences fall, thereby only including the 90 % of presence records with a suitability score above the lowest 10 %. Among the multiple potential thresholds available to binarize a continuous Maxent output, the 10PT is one of the most widely used thresholds (Rhoden et al. ; Liu et al. 2016; Shabani et al. 2018) in Maxent modelling. Additionally, findings from (Radosavljevic and Anderson 2013) suggest that, among other candidate thresholds, the 10PT is less sensitive to extreme low suitability scores and more conservative compared to other threshold options.

To describe the environmental differences between areas classified as "suitable" and "unsuitable", descriptive statistics were calculated for all model predictors. For continuous predictors the mean, standard deviation and interquartile range were calculated. For categorical predictors the proportional representation (%) of each class as well as Joint Count Statistics (JCS) were calculated, to quantify the clustering of identical categorical values "like-values" and different categorical values "unlike-values" among neighbouring cells. This allows for the calculation of "like-ratios" which provide a measure of spatial clustering of categorical classes with like-ratios close to 1 indicating clustering of the same class and like-ratios close to 0 more spatially dispersed classes. Additionally, the difference in like-ratios between suitable and unsuitable areas (like-ratio difference) was calculated to better describe differences in the degree of spatial clustering of individual classes between "suitable" and "unsuitable" areas, with positive values indicating stronger clustering in "suitable" and negative in "unsuitable areas".

Validation

To validate the resulting binary threshold, Maxent's built in post-hoc binomial-test was used to assess whether the number of independent test records falling into "suitable" areas are statistically significantly higher than random chance, in contrast to the proportion of the landscape defined as “suitable”. A significant p-value < 0.05 indicates that the model predicts test localities in suitable areas better than random chance. Both the continuous and binary suitability maps were qualitatively evaluated, together with the director of the hunting association of Salzburg, by comparing its predictions against a survey conducted in 2023 by the Salzburger hunting association (*Figure 2*), assessing presence of hazel grouse in hunting territories . In this evaluation process, five large, continuous, high-suitability areas, one from each of the five regions of Salzburg were identified, which were present in both the continuous and binary map, to be selected for external validation. In this external validation approach, the respective hunting- or forest-district managers of these areas were directly contacted, assessing/confirming the presence and perceived habitat suitability for the hazel grouse in that forest territory.

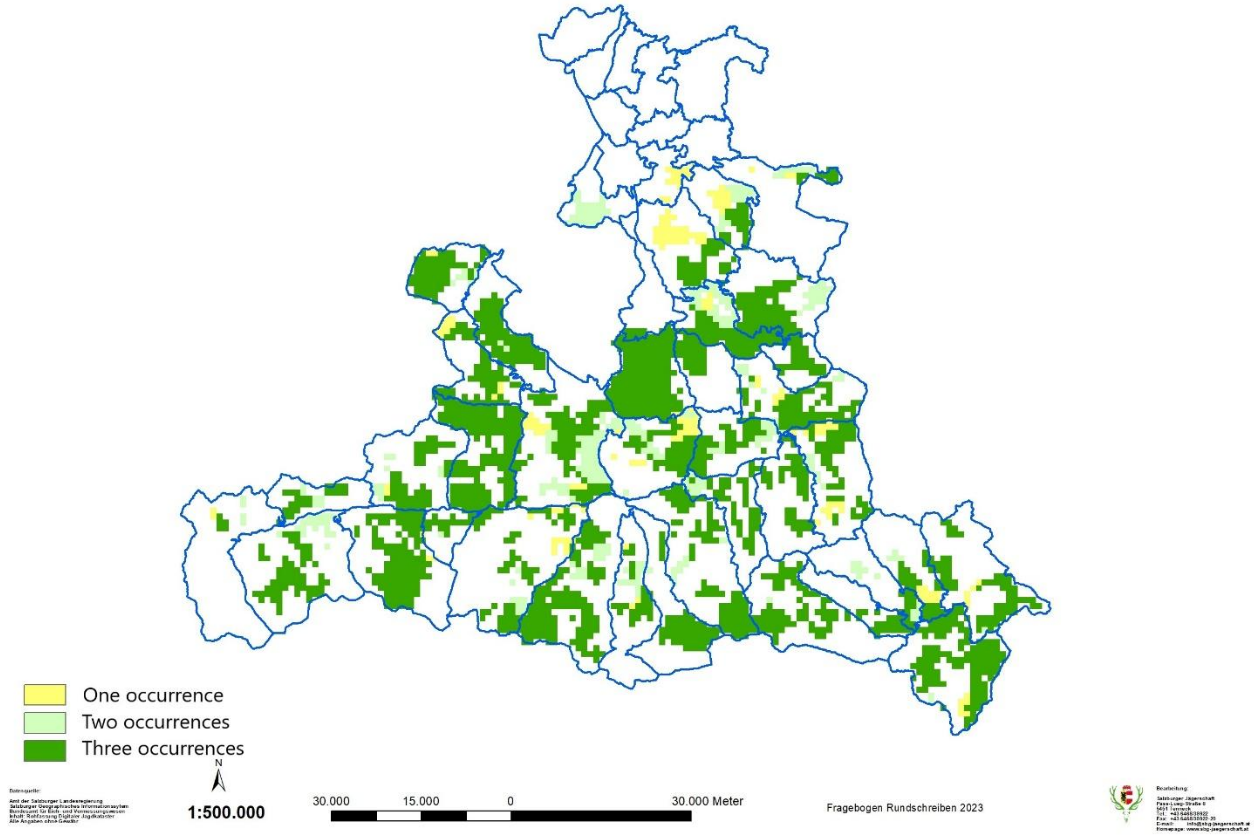

Figure 2: Anonymised map of the 2023 survey of the Salzburger hunting association assessing hazel grouse occurrences across Salzburg with yellow areas experiencing one occurrence, light-green two occurrences and dark-green three occurrences.

3. Results

3.1. Model Selection

Model selection was carried out by the ORTEST approach to balance performance against model complexity across different predictor sets and regularisation multipliers, for both spatial modelling extents (*Table 5*). For the Saalachtal extent the top ranked model (ID_Model_1) resulted in a training AUC of 0.8345, a test AUC of 0.7831, a 10 % omission rate of 0.0714 and an AUC difference of 0.0514. It was closely followed by Model 10 and Model 19. Model 2 showed the highest test discrimination (test AUC = 0.0.8636) and lowest AUC_difference (0.051) but at as higher omission rate of 6.9 %, while Model 2 (Set-2, RM = 2) ranked fifth with comparable metrics. In contrast, for the full-extent of Salzburg, Model 10 (Predictor Set 1; RM = 1), scored the highest rank within its spatial extent and overall across all models with best discriminatory ability (AUC_train = 0.9081, AUC_test = 0.8297), low overfitting (AUC_Diff = 0.0784) and a low omission rate (6 %), outperforming all other models across both spatial extents. On the basis of this trade-off between predictive accuracy and model balance, Model 10 of the full-extent was selected as the final model for habitat suitability mapping.

Table 5: Top 5 ranked Maxent models for both study extents (small extent – Saalachtal, full extent – Salzburg) under the ORTEST selection framework. Models were ranked by the 10th percentile training presence threshold, ties were broken by AUC_test and the AUC_diff and subsequently compared for both study extents.

Extent	Model-ID	Rank_ORTEST	ß-Multiplier	Predictor-Set	AUC_ train	AUC. test	Omission-rate (10%)	AUCdiff
Salzburg (full)	10	1	1	Set-1	0.9081	0.8297	0.0643	0.0784
Salzburg (full)	12	2	1	Set-3	0.8915	0.826	0.0678	0.0655
Salzburg (full)	6	3	0.5	Set-6	0.8872	0.8202	0.0678	0.067
Salzburg (full)	22	4	2	Set-4	0.8663	0.8103	0.0607	0.056
Salzburg (full)	14	5	1	Set-5	0.8952	0.8047	0.0714	0.0905
Saalachtal (small)	1	1	1	Set-1	0.8345	0.7831	0.0714	0.0514
Saalachtal (small)	10	2	0.5	Set-9	0.8579	0.7764	0.0643	0.815
Saalachtal (small)	19	3	2	Set-7	0.8436	0.659	0.0678	0.1209
Saalachtal (small)	11	4	2	Set-2	0.8417	0.7727	0.0714	0.0514
Saalachtal (small)	2	5	0.5	Set-7	0.8636	0.7534	0.0678	0.069

3.2. Final Maxent Model

The final Maxent model was built on 34 presence records and 10028 background points, converging after a mean of 391 iterations. The model shows strong discriminatory power with a regularised training gain of 0.556, a mean test gain of 0.746, and a mean training AUC of 0.908 and a mean test AUC of 0.830 ± 0.072. Variable contribution (*Table 6*) showed the variables "Aspect" to be the largest contributor (29.61 %), followed by "Distance_forest_roads" (18.72 %),"tree-species category" (16.11 %), "Gini-tree-height" (14.67 %), "Elevation" (9.96 %) and "Distance_lotic_waterbodies" (10.92 %). Additionally, permutation importance highlighted "Distance_forest_roads" (38.83 %) and "Elevation" (22.24 %) as the most influential environmental predictors.

Table 6: Model predictor variables and respective variable contribution (%) and permutation importance (%).

Variable	**Model Contribution (%)**	**Permutation Importance (%)**
Aspect	29.6	9.7
Distance_forest_roads	18.7	38.7
Tree-Species	16.1	7.3
Gini-tree-height	14.7	15.8
Distance_lotic_waterbodies	10.9	6.1
Elevation	10	22.2

The Jackknife tests of the regularised training gain from the model (*Figure 3*) resulted in an overall model gain of 0.5565 including all variables. The variable "Aspect" alone resulted in the highest explanatory power when used in isolation, whereas the variable "Distance_lotic_waterbodies" contributed the least. In contrast, the omission of "Aspect" from the full-extent model caused the largest drop in training gain, while removing "Elevation" produced the smallest decrease. The remaining predictors "Tree-species-composition", "Distance_forest_roads" and "Gini-tree-height" each experienced intermediate solo gains and omission effects.

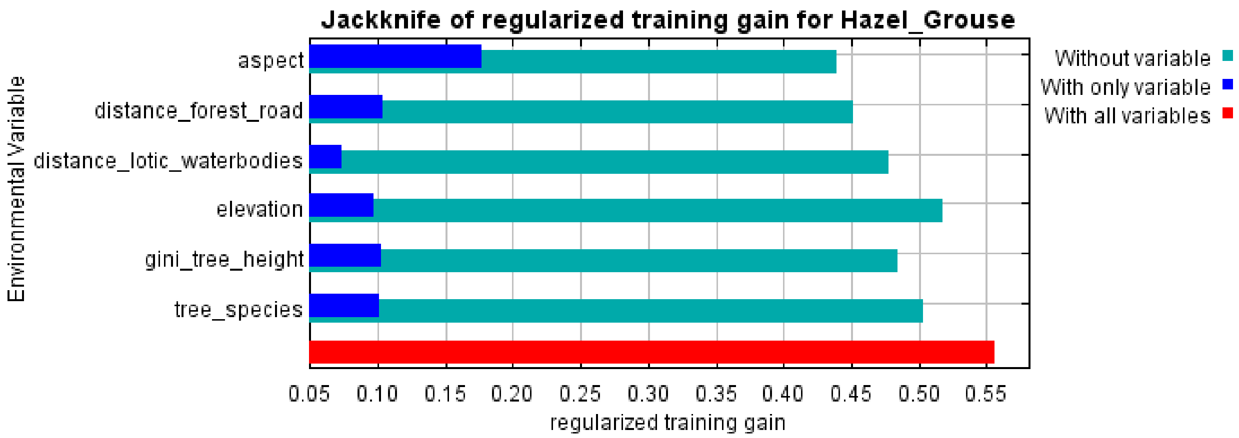

Figure 3: Bar chart of the jackknife analysis for each model predictor depicting the relative influence on model performance with- and without omission – blue bars depict the single standalone contribution to the model, the turquoise bars represent model contribution with omission of the respective variable and the red bar depicts overall model performance including all variables.

Analysis of the model response-curves revealed the influence of each predictor on habitat suitability. "Distance_lotic_waterbodies" (*Figure 4*) showed that suitability is relatively high with close proximity peaking at approximately 100m, then declining steadily, falling below ≈ 0,5 beyond 1900m. "Elevation" (*Appendix B 1*) showed a unimodal response, with suitability increasing from peaking between 1100-1400, before declining with increasing altitude. "Gini-tree-height" (*Figure 5*) showed highest suitability at low vertical heterogeneity, followed by a steady decline with increasing vertical heterogeneity. The response-curve of "Distance_forest_roads" (*Figure 6*) showed that suitability is lowest in close proximity to forest roads which sharply rises with increasing distance before plateauing around a maximum suitability. "Tree-species composition" (*Appendix B 2*) showed that category 5 "undergrowth" results in the highest mean suitability, followed by category 2 "Mixed-Species-Conifers", category 3 "Coniferous-Deciduous-Mixed", category 1 "Single-Species-Conifers" and lowest mean suitability in category 4 "Single-Species-Deciduous". The response of the variable "Aspect" (*Appendix B 3*) revealed that north-eastern slopes (category 2) are most suitable, with north (category 1) and northwest (category 8) being also favoured, while east (category 3) and west facing slopes (category 7) experience intermediate suitability and south-eastern (category 4) and southern aspects (category 5) showed lowest suitability.

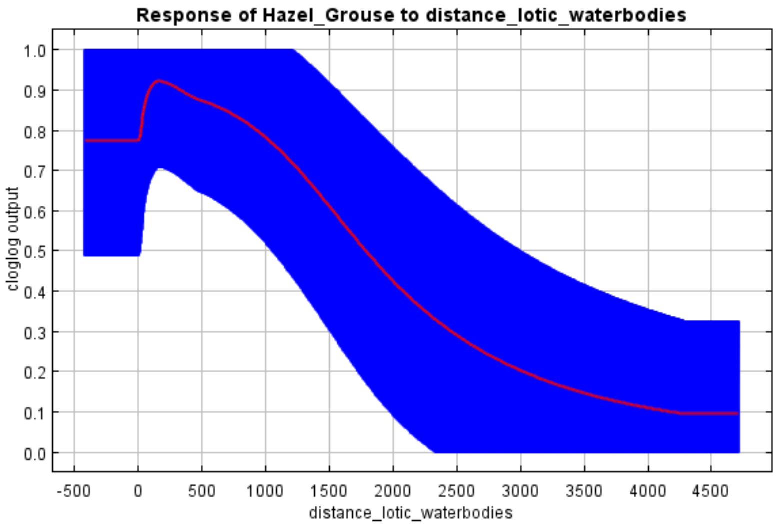

Figure 4: Maxent response curve of "Distance_lotic_waterbodies" in isolated runs. On the x-axis, the value of the predictor (m) is depicted and on the y-axis the habitat suitability on a cloglog scale (0 to 1) is depicted. The red curve depicts the average suitability value and the blue areas indicate 1 standard deviation from the mean.

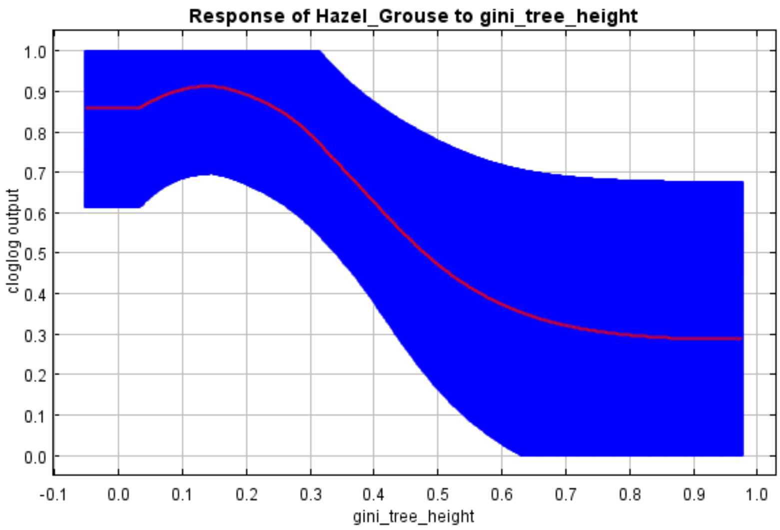

Figure 5: Maxent response curve of "Gini-tree-height" in isolated runs. On the x-axis, the value of the predictor (Index = 0 to 1) is depicted and on the y-axis the habitat suitability on a cloglog scale (0 to 1) is depicted. The red curve depicts the average suitability value and the blue areas indicate 1 standard deviation from the mean.

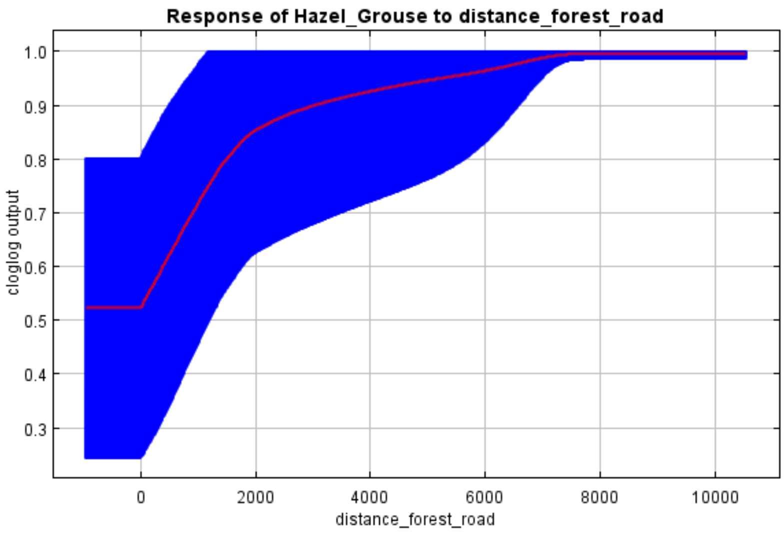

Figure 6: Maxent response curve of "Distance_forest_road" in isolated runs. On the x-axis, the value of the predictor (m) is depicted and on the y-axis the habitat suitability on a cloglog scale (0 to 1) is depicted. The red curve depicts the average suitability value and the blue areas indicate 1 standard deviation from the mean.

3.3. Habitat Suitability Mapping

The continuous Maxent cloglog habitat suitability map (*Figure 7*), confined to forest landcover, encompasses approximately 3750 km^2 of Salzburg. The predicted suitability values range from 0.002 to 0.997 and are depicted in a continuous colour spectrum with blue-shades indicating very low suitability and red coloured areas very high suitability. Spatially, the highest suitability zones concentrate in the densely forested southern districts of Pinzgau, Pongau and Lungau. By contrast, the northern region of Flachgau, including the surroundings of the capital city of Salzburg show very few forested areas which comprise of low suitability apart from forests in the very south of the region. The Tennengau region exhibits moderate to high suitability, primarily along its eastern border to Upper Austria.

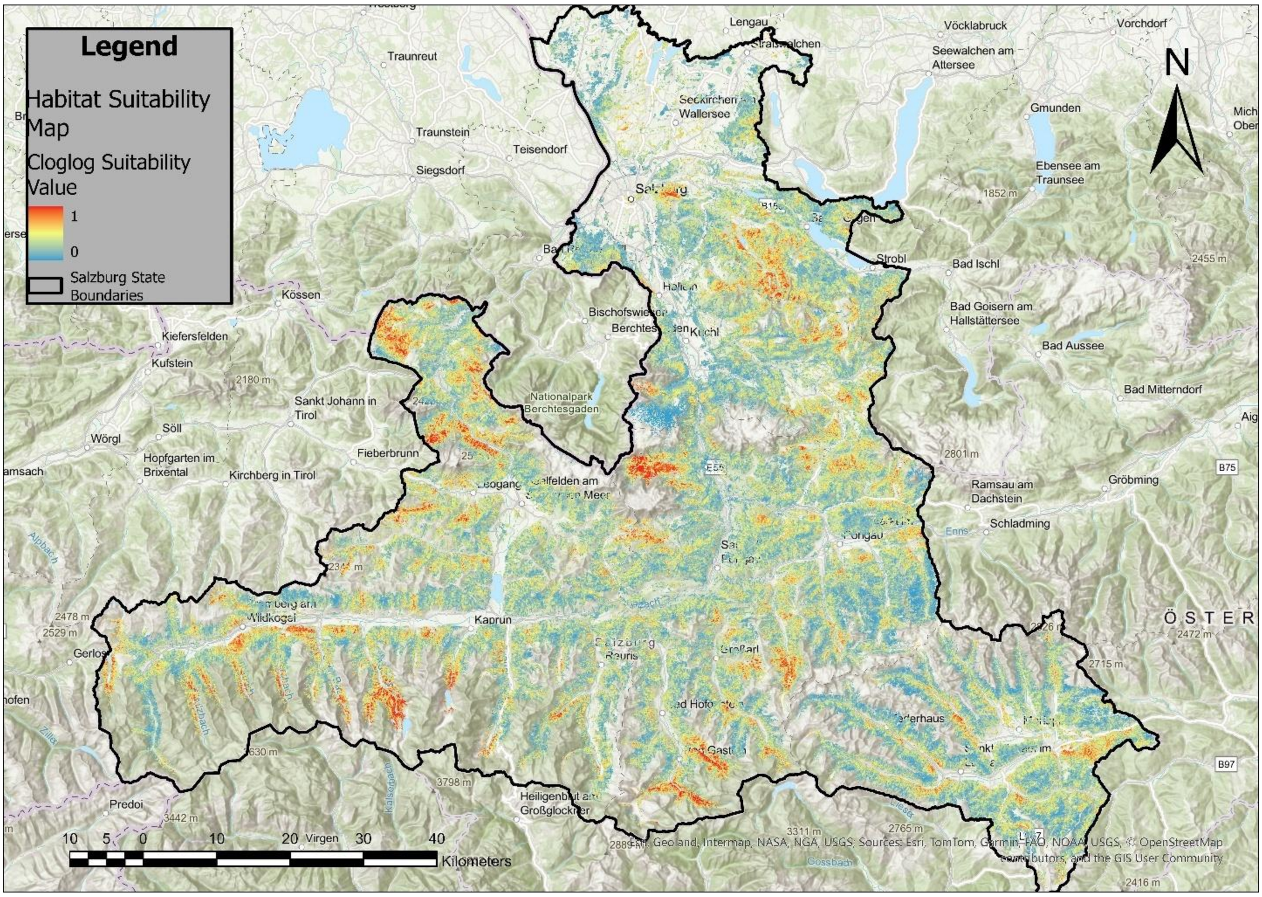

Figure 7: Habitat suitability map depicting continuous cloglog suitability-scores in a colour gradient. Red shades represent high suitability values, yellow intermediate and blue shades low habitat suitability scores. Basemap sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors and the GIS User Community.

The procedure of binarizing the continuous cloglog output at the 10 % training-presence threshold (cloglog = 0,428), resulted in 25.5 % (≈ 665 km^2) of the study area after exclusion of non-forested areas being classified as "suitable" for the hazel grouse. Below this cutoff, the model shows a training omission rate of 7 % and a test omission rate of 21.7 %, and a post-hoc binomial test showed that the model predicts true presences in areas defined as "suitable" above the before mentioned threshold, statistically significantly more often than random chance (p = 0.045).

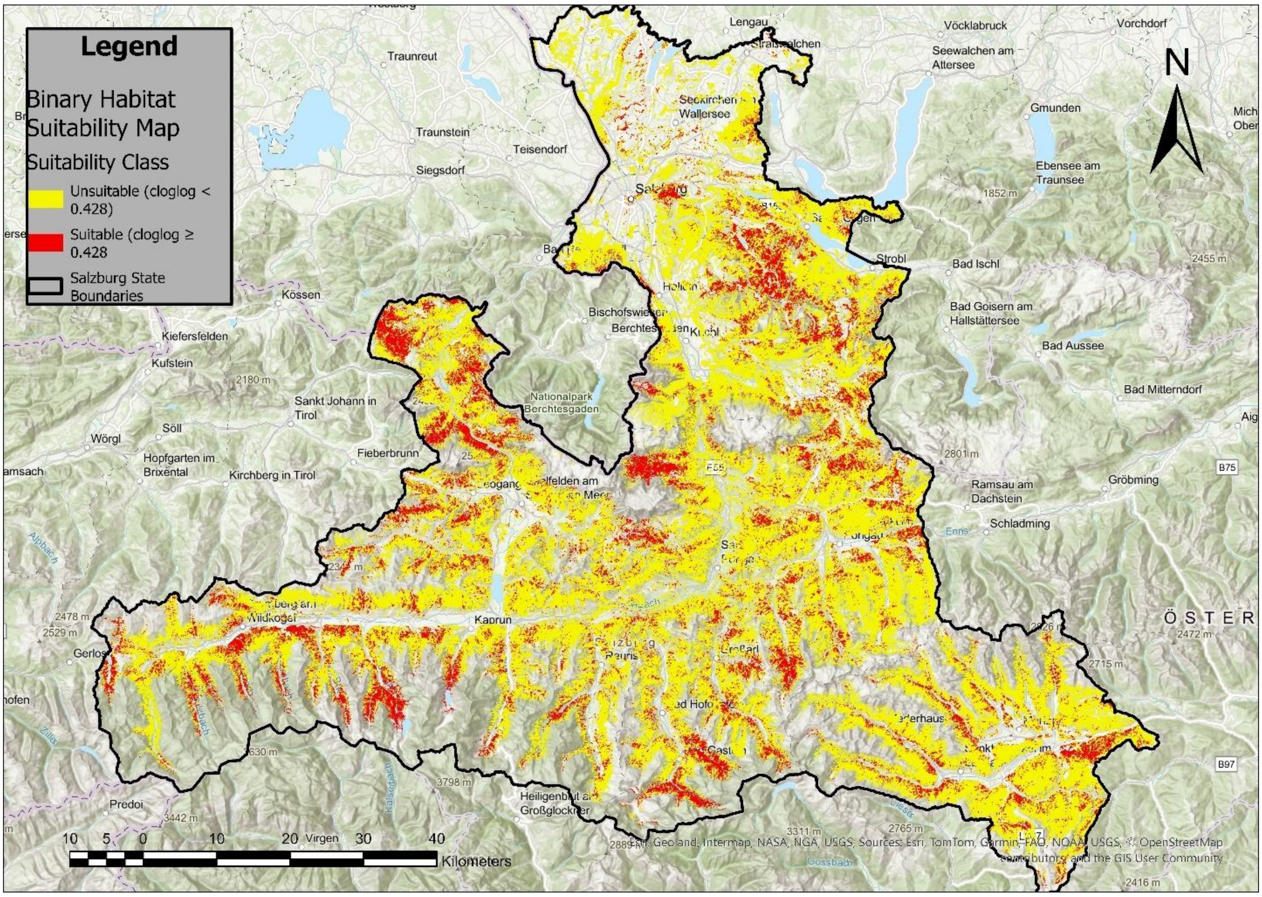

Figure 8: Binarized habitat suitability map depicting predicted "suitable" and "unsuitable" habitats across Salzburg based on the 10th-percentile training presence threshold (cloglog = 0,428). Basemap sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors and the GIS User Community.

The difference in environmental predictor expressions is compared for areas predicted as "suitable" and "unsuitable" for the hazel grouse. For continuous predictors (*Table 7*), suitable areas were characterised by a mean distance to lotic waterbodies of 316.6 m ± 285.9 m, which is on average 83.7 m closer than in unsuitable areas (400.3 m ± 386.2 m). The mean distance to forest roads in suitable areas was 1769.9 m ± 1538,3 m, more than twice the average distance observed in unsuitable areas (808.9 m ± 946.6 m). Elevation showed almost identical averages between suitable and unsuitable areas of ≈ 1200 m. Tree height heterogeneity, expressed as the Gini-coefficient, was lower in suitable areas (0.21 ± 0.089) than in unsuitable areas (0.28 ± 0.12), indicating less vertical heterogeneity in suitable areas.

Table 7: Descriptive statistics (mean, standard deviation and interquartile range) for continuous predictors of predicted "suitable" and "unsuitable" areas. IQR describes the range between the 25th and 75th percentile, capturing the central spread of the data.

Variables (Suitable Areas)	**Unit**	**Mean ± SD**	**IQR**
Distance_lotic_waterbodies	meter	316.637 ± 285.868	290.352
Distance_forest_roads	meter	1769.877 ± 1538.274	1721.947
Elevation	meter a.s.l.	1271.904 ± 312.950	406.017
Gini-tree-height	Index 0-1	0.21 ± 0.089	0.114
Variables (Unsuitable Areas)			
Distance_lotic_waterbodies	meter	400.335 ± 391.900	420.424
Distance_forest_roads	meter	808.94 ± 946.628	902.044
Elevation	meter a.s.l.	1270.087 ± 386.174	590.325
Gini-tree-heights	Index 0-1	0.281 ± 0.117	0.16

For categorical predictors (*Table 8*), "Aspect" and "Tree-species-composition" distribution differed between suitability classes, with the like ratio difference (LRD) indicating the degree and direction of relative spatial clustering across the two suitability classes. For "Aspect", the highest positive LRD and thereby indicating ting spatial clustering in suitable areas, was found for northeast facing slopes (LRD = 0.117; 26,5 % in suitable and 9 % in unsuitable), followed by southwest (0.027; 18 % vs. 12 %) northwest (0.027; 20.9 % vs. 12 %) and north (0.026; 4.6 % vs. 2.4 %). Smaller positive values were found in for west (0,019; 9% vs. 17,5 %), south (0.016; 4,5 % vs 15.8 %) and east (0.011; 7 % vs. 16.7 %). The only negative LRD was for southeast facing slopes (-0.260; 9.5 % vs. 14.5 %). For "Tree-species-composition" the strongest positive LRD occurred for coniferous-deciduous mixed stands (0.294; 16.5 % in suitable vs. 17.2 % in unsuitable), followed by single species deciduous stands (0.139; 6.2 % vs. 15.7 %), undergrowth (0.088; 7 % vs. 8.7 %) and mixed species coniferous stands (0.148; 33.9 % vs. 19 %). Single species conifers had the only negative LRD (-0.161; 36.4 % vs. 39.5 %).

Table 8: Descriptive statistics - proportions (%) and Joint Count Statistics (JCS) like-ratio's for categorical variables of predicted "suitable" and "unsuitable" areas. Like ratios quantify the clustering of identical neighbouring classes (1 = strong clustering; 0 = dispersed). The like ratio difference (LRD) is the like-ratio in suitable minus unsuitable areas, indicating where clustering is stronger.

Aspect (cardinal directions)	**Proportion (%) - Suitable**	**Like ratio - Suitable**	**Proportion (%) - Unsuitable**	**Like ratio - Unsuitable**	**Like Ratio Difference**
1 - North	4.6	0.339	2.4	0.313	0.026
2 - Northeast	26.5	0.213	9	0.096	0.117
3 - East	7	0.359	16.7	0.348	0.011
4 - Southeast	9.5	0.393	14.5	0.653	-0.26
5 - South	4.5	0.338	15.8	0.322	0.016
6 - Southwest	18	0.306	12	0.279	0.027
7 - West	9	0.299	17.5	0.28	0.019
8 - Northwest	20.9	0.357	12	0.33	0.027
Tree-species-composition					
1 - Single-Species-Coniferous	36.4	0.451	39.5	0.612	-0.161
2 - Mixed-Species-Coniferous	33.9	0.582	19	0.434	0.148
3 - Coniferous-Deciduous mixed	16.5	0.732	17.2	0.438	0.294
4 - Single-Species-Deciduous	6.2	0.516	15.7	0.377	0.139
5 - Undergrowth	7	0.281	8.7	0.193	0.088

3.4. Model Validation

Both continuous cloglog habitat suitability map as well as the binary suitability map were first evaluated by qualitatively comparing it to the anonymised survey-map provided by experts of the Salzburger hunting association. Despite the intentional distortion of hunting-territory boundaries, by visual inspection, regions of high predicted suitability largely corresponded with the survey results.

Five core areas were selected, one in each of the five regions of Salzburg. These areas were “Gaisberg” in Flachgau, “Blühnbachtal” in Tennengau, “Stubach” in Pinzgau, “Kleinarl” in Pongau and “Tamsweg” in the Lungau region. Each area was remotely validated for hazel grouse presence and for perceived habitat suitability (*Figure 9*).

The hunting district managers of Blühnbachtal, Stubach, Kleinarl and the forest district manager of Tamsweg confirmed continuous hazel grouse occurrences and reported high perceived habitat suitability within their territories. The validation of the Gaisberg location failed, with the forest district manager reporting no current hazel grouse occurrences. However, it has been reported, that the available habitats appear to be suitable for the hazel grouse.

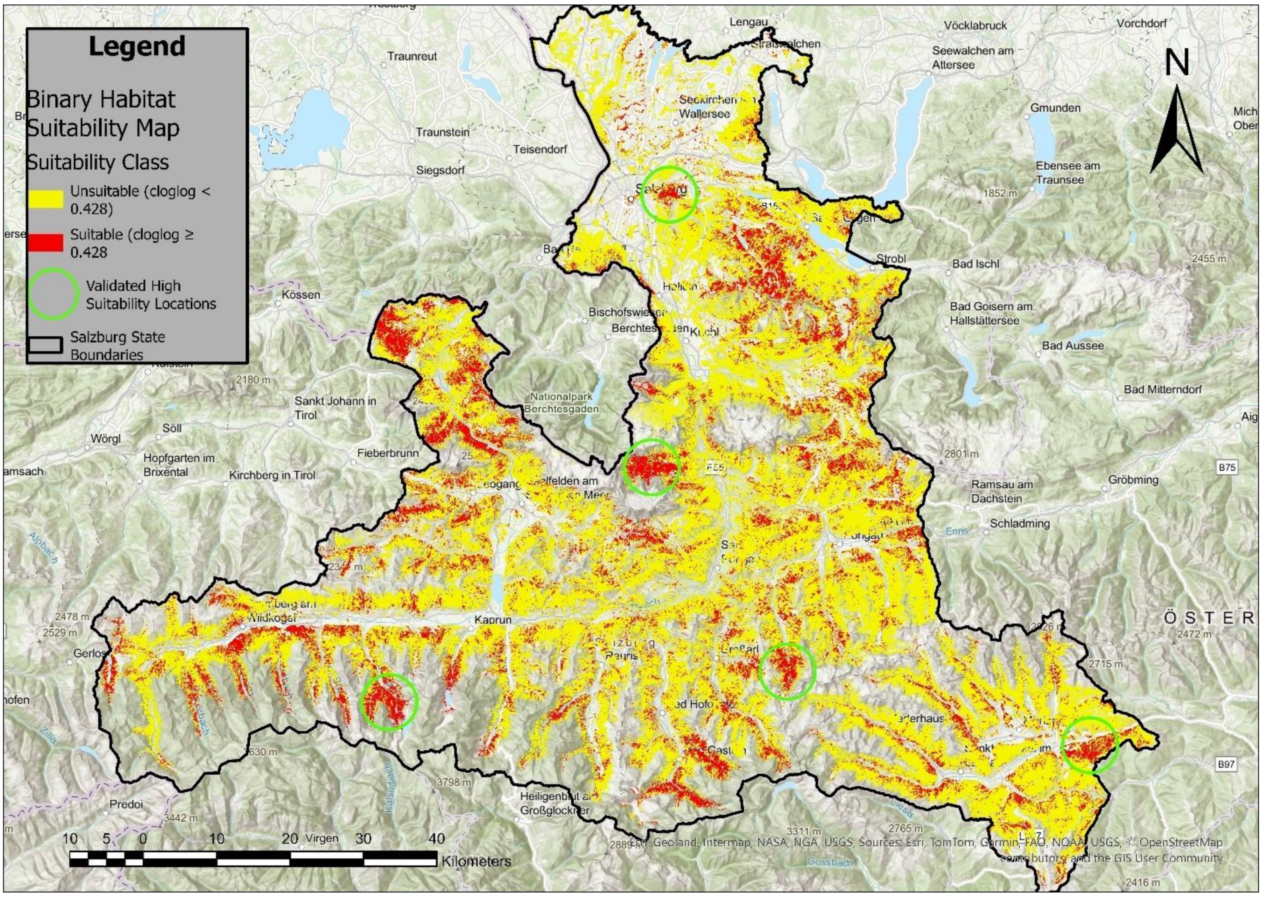

Figure 9: Binarized suitability map depicting suitable and unsuitable habitats in Salzburg with validated locations marked in green circles. Basemap sources: Esri, TomTom, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors and the GIS User Community.

4. Discussion

4.1. Summary of Key Findings

In this study, a Maxent based species distribution model was created to identify suitable habitats for the hazel grouse and evaluate habitat suitability across the province of Salzburg. The final, full-extent model demonstrated strong predictive performance (mean training AUC = 0.908; test AUC = 0,830; omission rate = 7 %), outperforming all alternative candidate models for both spatial extents. Suitability of habitats was most strongly influenced by the slope aspect, was well as by the increasing distance to forest roads and the presence of mixed coniferous stands. Unexpectedly, increased vertical heterogeneity of forest structure, measured as the Gini-coefficient of tree heights, was associated with reduced habitat suitability. Approximately 25 % (= 665 km^2) of Salzburg's forested area was identified as suitable habitat for the hazel grouse, with larger continuous patches occurring primarily in the inner mountain valleys and more fragmented suitable areas found in the north of Salzburg. Suitable habitats were characterised by a higher proportion of mixed coniferous forest stands and reduced proportions of single-species deciduous forest stands, greater distance to forest roads, closer proximity to lotic waterbodies and a notable predominance of northern facing slopes. In addition, suitable habitats are characterised by more spatially self associated or "continuous" forest stand types and slope aspect/orientation as described by the joint count statistics. Unexpectedly, and contrary to hypothesis 3, the full extent model outperformed the small extent projection model. These findings of this study partially support the initial hypothesis regarding the influence of edge-related variables but contradicted expectations regarding the influence of structural heterogeneity.

4.2. Model Performance and Relationship between Environmental Predictors on Habitat Suitability

The final model was built on the full-extent, outperforming all other candidate models from both sets of the small extent and the full-extent. The chosen model scores the highest mean traing AUC (0.908) and test AUC (0.830 ± 0.072), indicating strong discriminatory abilities. The model showed modest overfitting (AUC_diff = 0.078) and a low 10 percent omission rate (6 %), outperforming the best small extent model. In addition to evaluating model performance diagnostics, a qualitative visual comparison of the best small extent projection model with my supervisors and associates of the Naturpark Weißbach respectively suggested the full-extent model to be the better fitting. This led to the rejection of the third hypothesis of spatial transferability, namely that the small extent model following a projection outperforms the full-extent model based on the used model selection approach. While there is currently no review study comparing Maxent projection model performance, findings from Sutton and Martin (2022) comparing projected vs. non-projected models suggest that non-projected models perform better under certain conditions. In addition, Merow et al. (2014) suggested that creating a robust and valid projection model requires specific model tuning which was not the case in this study, as the projection feature was mainly used for comparative model selection.

In the following section, the environmental predictors are discussed, based on the results of the jackknife-test as well as response-curves depicting the relationship between a variable and its influence on habitat suitability.

Topographic Variables

The jackknife analysis revealed the importance of slope orientation, with the variable "Aspect" alone yielded the highest gain when used in isolation and its omission caused the greatest drop in overall model performance. The responses of "Aspect" revealed a clear north/south gradient. According to model results, northern slopes are most suitable while western aspects are providing intermediate suitability and southern slopes area least suitable. This suggest that hazel grouse may prefer cooler and more moist northern facing slopes in Salzburg. It has been reported in a quantitative synthesis by Bradie and Leung (2016) who analysed multiple variables used in Maxent models, that high-quality datasets, such as digital terrain models derived by remote sensing data, contribute most to model performance. Apart from ecological effects, this can explain the strong observed influence of the variable "Aspect" in this model. However, the jackknife test showed that the variable "Elevation" which is based on a dataset of equal quality and origin, contributed second to last to overall model performance which is in contrast to these findings. However, it has been reported by Smith and Santos (2020) that Maxent is able to correctly discriminate between true and false influences of environmental predictor, particularly when data quality and the resolution of environmental layers is high, and assigning correct variable importance. This suggests that the strong influence of "Aspect" in this study, may reflect actual ecological factors, rather than modelling artifacts.

Additionally, while the variable "Elevation" contributed the least to overall model performance, in preliminary testing and comparisons of candidate predictor sets, elevation appeared to have a subjectively important perceived effect of influencing the model prediction of forest-composition in high altitude areas. For example, visual inspections of models with and without revealed that incorporating "elevation" into the model allows for correctly identifying high-altitude forests i.e "Krummholzzone" as unsuitable habitats for the hazel grouse. However, since not all permutations of potential predictors sets were tested, it is not possible to confidently attribute the proposed discrimination ability by incorporating "Elevation" into the model.

Structural Variables

Results of the Maxent analysis and visual inspection of the response-curves suggest that suitability of Hazel Grouse habitats declines with increasing vertical heterogeneity (=Gini Coefficient) with the highest predicted suitability being expressed in low Gini indices (0,1 – 0,2) and dropping off as structural complexity increased. This relationship directly contradicts the first hypotheses, which proposes that greater vertical heterogeneity would increase habitat suitability and is therefore rejected. However, while this led to rejecting the first hypothesis (H1), this is in accordance with findings from Sitzia et al. (2014) who analysed stand structure and composition in 30x30m cells derived from a field survey, suggesting that hazel grouse prefer more homogeneous stands with no more than one layer, but with a rich and diverse understory. While the regular Gini-coefficient is to be interpreted where 0 represent perfect homogeneity and 1 represent perfect heterogeneity, research from Valbuena et al. (2021) suggest that Gini-coefficients calculated for one-dimensional forest variables such as "tree-heights", as in this study, maximum realistic vertical heterogeneity is expressed at a Gini-coefficent of 0.33. As the results of the Maxent response curve of "Gini-tree-heights" (*Figure 5*) suggest that hazel grouse prefer lower vertical heterogeneity further qualitative analysis is needed to directly link a Gini-coefficient to vertical heterogeneity in Austrian forests. Additionally, the moving window size (150 m), which was originally chosen based on the mean daily movement range of hazel grouse, may be too large to capture fine scale variation in forest-structure due to the increased smoothing effect of the moving window calculation. It has been suggested by Paluch (2021) that appropriate moving window sizes are around 15 m for capturing variation in forest structure. In the light of this, the numerical results regarding the Gini-coefficient of tree heights reported in this study must be interpreted with caution as they may be not meaningful due to the misconstruction of the moving window.

The variable "Tree-species-composition" emerged as a predictor of medium importance on overall model performance. The classes within show similarly strong influence on habitat suitability with the category "Undergrowth" emerging as the class depicting the highest mean suitability with "single-species deciduous" experiencing the least. While the difference is only marginal across classes, "undergrowth" emerging as the most suitable class is supported by findings of Sitzia et al. (2014) who found that ground layer composition to be one of the most important habitat factors positively influencing suitability. Conversely, “single-species deciduous” emerging as the least suitable class is reasonable, as montane forests containing large proportions of coniferous tree species are the primary forest habitats in Europe. It must be noted that the authors of the original dataset Schadauer et al. (2024) report a potential underrepresentation of mixed tree-species classes in the dataset, as two tree-species contribute to a single cell of the original size of 10x10 m, thereby posing difficulties to the classification algorithm. This was not addressed in the modelling process of this study, which may result in overrepresentation of single-species classes and underrepresentation of mixed-species classes.

Edge-Distance-Based Variables

The second hypothesis proposed that habitat suitability increases with proximity to egde structures such as waterbodies and forest roads. The results of this study led to accepting the hypothesis regarding “Distance_lotic_waterbodies” but rejecting it for “Distance_forest_roads”. The response curves (*Figure 6*) depicting “Distance_lotic_waterbodies” (H2a) experience the expected effect where suitability is peaking) at around 100-500 m from streams, which remain relatively high up to 1000 meters and then declining with increasing distance. However, while the relationship appears relative clear in the response of habitat suitability values, the jackknife-test revealed that the variable “Distance_lotic_waterbodies” contributes the least to overall model performance. In contrast, the response curves for “Distance_forest_roads” (*Figure 6*) is inverted, depicting lowest suitability within 500m of forest roads and only rising from a distance of 2000m upwards, led to rejecting the second hypotheses (H2b). The jackknife test revealed that the variable “Distance_forest_roads” contributed modestly to model performance, similar to “Gini-tree-heights” and “Tree-species-composition”.

The effect and influence of forest roads and other linear structure such as hiking trails on hazel grouse appears to be highly variable and often revealing contradicting impact depending on the context of the study. Several studies (Müller et al. 2012; Matysek et al. 2019; Scridel et al. 2022) attribute presence or close proximity of edge structures like forest roads a positive effect on habitat quality by increasing diversification of vegetation assemblages and variability in canopy-closures regimes. Additionally, findings from Matysek et al. (2022) suggest that hazel grouse brood and chick survival is increased within a 100m radius of forest roads. However, the same or similar structures as forest roads, such as hiking trails are not only a potential source of disturbance but can also increase predation risk for ground-dwelling birds by facilitating access for predators such as foxes, martens and corvids(Kämmerle and Storch 2019; Matysek et al. 2020; Klaus and Ludwig 2021). Notably, findings from Sachot et al. (2003) did not find any statistically significant influence of forest roads presence within a 1 km^2 radius on hazel grouse occurrence, attributing it to the cryptic avoidance behaviour of the hazel grouse. This suggests, that the effect and impact of structures such as forest roads and hiking trails may be highly variable, depending on locality and context. Based on this, the effect captured by implementing the variable “Distance_forest_roads” in this study appears to have identified forest roads as a source of disturbance rather than a feature of structural enrichment in hazel grouse habitats.

4.3. Characteristics and Spatial Patterns of Suitable Habitats across Salzburg

The binary classification of the Maxent cloglog output at the 10th-percentile training presence threshold, representing the threshold under which the lowest 10 % of suitability scores of presence records, reveals spatial distinction between "suitable" and "unsuitable" habitats for the hazel grouse across Salzburg. The post-hoc binomial test (p = 0.045) confirmed that hazel grouse presences occur statistically significantly more often in areas defined as "suitable" by the aforementioned threshold than expected by random chance. Suitable areas comprise approximately 25.5 % (=665 km^2), of the overall potential habitat of the hazel grouse across Salzburg. Similar estimations on the amount of suitable habitats are reported in a long term study from a finish island (Saari et al. 1998), investigating the habitat selection of the hazel grouse based on quantitative and qualitative patch metrics, who estimated the amount of suitable habitat to be 32 % across all landcover types.

Based on visual inspection, a large amount of non-continuous forest patches as well as isolated pixels of high-suitability cells is present across Salzburg, particularly in the northern region. However, large and continuous forest patches predicted as potentially suitable for the hazel grouse were present, particularly in secluded valleys of the regions of Pinzgau, Pongau and Lungau. These predictions are largely in accordance with the survey of the hunting association of Salzburg (*Figure 2*). In the south-west Pinzgau region of Salzburg, areas predicted as "suitable" occur to a large degree in the valleys south of the Salzach river, particularly in the secluded lower valleys of the Hohe Tauern mountain range. Among the subgroups of the Hohe Tauern range, suitable habitats are predicted to occur in the east and west valleys of the "Granatspitzgruppe" and "Venedigergruppe" with the valleys of the adjacent "Glocknergruppe" providing fewer suitable areas. In the central-south Pongau region large continuous areas of predicted suitability were identified around the "Radstädter Tauern" near the city of Sankt Johann and the "Ankogelgruppe" to the east of the city of Bad Gastein, as well as in the very southern valleys of the "Goldberggruppe". The easternmost Lungau regions is orographically separated by the Niedere Tauern from the rest of Salzburg. Predicted suitable areas are largely occring in the east of the region bordering Styria. In particular south of the city of Tamsweg, within the "Schladminger Tauern" and the northern extensions of the Hafnergruppe in the south bordering the state of Carinthia provide suitable habitats for the hazel grouse. In the north-central Flachgau region of Salzburg, large areas of predicted suitability were identified in the Osterhorngruppe and parts of the Salzkammergut. In the central Region of Salzburg, large continuous areas of high predicted suitability are located in the Blühnbachtal valley which is flanked by the Hochkönigstock mountain range in the south and the Hagengebirge of the Berchtesgadener Apen to the north, in addition to being separated in the east by the Salzach river.

Characteristics of Suitable Habitats

Tree-species-composition (*Table 8*) in predicted "suitable" areas are dominated by mixed-species coniferous stands compared to unsuitable areas, with similarly high proportions of single species coniferous stands of in suitable and unsuitable areas. The proportion of single species deciduous stands are reduced in "unsuitable" compared to "suitable" areas with similar proportions of undergrowth for both suitability classes. The proportions of coniferous and deciduous mixed stands is similar in for both suitable and unsuitable areas. The like ratio difference (LRD) derived from the Joint Count Statistics indicates how strongly and in which suitability class, the respective classes of categorical variables tend to be more spatially aggregated or clustered. For "Tree-species-composition", the largest positive LRD values was observed for coniferous-deciduous mixed species suggesting that these stands tend to occur in more spatially continuous amounts compared to unsuitable patches. Mixed species coniferous stands also showed a positive LRD similar to single-species deciduous. In contrast, the largest negative LRD values is exhibited for single-species coniferous stands indicating a greater clustering in unsuitable areas. Undergrowth showed a smaller positive LRD. These proportion patterns are largely consistent with previous findings from Klaus and Ludwig (2021) in the bohemian forests reporting that habitat suitability increases from 10 %

deciduous tree species proportion with an optimum between 30 to 40 % and a maximum of 85 % coniferous amount and Mathys et al. (2006) who found that an amount of 35 % deciduous species together with 45 % coniferous species and shrubs comprise suitable hazel grouse habitats and Åberg et al. (2003) who reported similar proportions of deciduous species between 5-40 %.

The variable "Aspect" (*Table 8*) is prominently different in suitable and unsuitable areas. Proportionally, north eastern and north-western aspects were more common in suitable areas, while east, south, and west were less common. LRD's indicate stronger spatial clustering in suitable areas for northeast , southwest and north , while west , south and east showed smaller positive LRD values. The only negative LRD occurred for southeast, indicating greater clustering in unsuitable areas. While there is no clear preference reported of hazel grouse towards aspect direction, some studies report tendencies towards southern exposures (Steiner 2007; Matysek et al. 2019). The clear prominence and clustering of northern aspects in suitable areas may reflect cooler and shaded areas, allowing for the establishment of a dense understory and larger amounts of mixed forests, which are favoured by the hazel grouse (Kortmann 2022).

For continuous environmental variables (*Table 7*), the distances to lotic waterbodies were on average closer and with fewer variations in distances, in suitable areas than in unsuitable areas. These results are in accordance with previous findings from (Matysek et al. 2019) who found that occupied sites hat a statistically higher occurrence of streams available within a 300m radius than non-occurrence sites. The average distance to forest roads was much greater in suitable areas than in unsuitable areas. This indicates, as mentioned in the previous chapter, that suitable habitats tend to be more remote and potentially less affected by anthropogenic disturbances and silvicultural practices. Tree height heterogeneity, expressed as the Gini-coefficient of tree heights, was lower in suitable areas than in unsuitable areas indicating a more even vertical forest structure in suitable habitats, whereas unsuitable habitats tend to exhibit greater vertical heterogeneity. However, as mentioned in the previous chapter, the interpretation of the Gini-cofficient has presented itself as a challenge to be interpreted, due to the moving window size calculations. The average altitude of both suitable and unsuitable habitats in the model is largely the same around 1270 m a.s.l., with similar variation across suitability classes. This pattern reflects the broad ecological plasticity of the hazel grouse, which is known to occur across a wide altitudinal gradient from lower mixed forests, up to avalanche paths near the treeline(Kunz et al. 2021). However, despite this flexibility with regard to elevation, the hazel grouse consistently depends on small scale habitat structures such as forest edges as well as certain tree species, which may occur only locally or temporarily.

4.4. Limitations and Improvements

In this study, limitations must be considered when interpreting the outcomes. The number of occurrence records of the hazel grouse in this study, while sufficient enough for robust modelling, were largely clustered within a discrete region of Salzburg. Although, best-practice efforts were made to address uneven sampling effort by mitigating spatial sampling bias, incorporating additional occurrence records will most likely result in a more robust and precise model. Furthermore, the computational resources imposed constraints, especially regarding the intensive memory and processing requirements associated with handling large geospatial datasets, particularly with a given cell size of 10m. These limitations restricted certain analyses such as calculating density-based metrics instead to Euclidean distance metrics. Another aspect that needs to be addressed is the exclusion of climatic and seasonal habitat use from modelling. Although climatic variables were selected as candidate models and are recognised as important predictors in a Maxent analyses (Bradie and Leung 2016), these predictors were excluded due to multicollinearity issues and stark differences in spatial resolution of the datasets and due to data quality concerns. The climate data were available in 1000x1000 m resolution, and the subsequent resampling to the target resolution of 10x10 m would lead to a generating smoothed values through interpolation across the study extent. Not only is using this climate dataset in this analysis problematic regarding the modelling process, but according to the authors, climate predictions tend to be particularly prone to inaccuracies, in mountainous regions such as is the case in this study (Hiebl and Frei 2016). Nonetheless, previous research comparing seasonal habitat selection patterns of the hazel grouse indicated minor differences in variation of habitat use, notably a higher reliance on coniferous tree species during winter, as elaborated in chapter 1.2. Factors such as predation and human disturbance were not explicitly accounted for in this study. Efforts were made to incorporate human disturbance into the study design by implementing data reflecting recreational land-use (Strava), yet these data were unobtainable for this study. The most recent review study on the impact of predation on grouse species found a negative impact of predator abundance on chick and nest survival (Kämmerle and Storch 2019), particularly affecting hazel grouse in fragmented habitat patches, and patches in close proximity to agricultural areas (Saniga 2002; Huhta et al. 2017).

Certain methodological refinements could further enhance the robustness and ecological validity of this research. Implementing quantitative model selection and -tuning approaches such as the R packages KUENM or ENMeval could improve the optimisation of predictor combinations as well as model parameters. These methods utilise derivatives of the Akaike Information Criterion (AIC), assessing model performance, which were not applied in the current study. The present study followed a semi-qualitative and quantitative approach, based on the recommendations by (Dorji et al. 2020), prioritising ecological relevance and expert evaluation. Integrating the aforementioned mathematically driven model-tuning methods may offer more precise parameter estimates and an overall more robust modelling approach. However, this was not possible in this study, due to computational limitations. While the background point selection performed in this study appears to have contributed to overall accuracy of model predictions, further improvements may be achieved by not only spatially restricting the background of the model, but adapt the number of background points in relation to the size of the study area (Rausell-Moreno et al. 2025). Regarding model variables, calculating distance based metrics for frequent or large-scale landscape structures such as wind power plants or ski-lifts and implementing these aspect as potential sources of disturbance in the model (Coppes et al. 2019). Further refinement could be achieved by reassessing the application of the Gini-coefficient of tree heights and comparing it to other continuous and non-discrete alternatives, capable of capturing fine-scale variation in vegetation structure, while offering a more interpretable and practically applicable parametrisation. Lastly, since studies report variable effect of linear forest structures such as forest roads and hiking trails on habitat suitability, it is essential to address that these habitat features can either act as a source of disturbance or as elements of structural enrichment, thereby positively or negatively affecting hazel grouse habitats. Therefore, I recommend that future habitat modelling should pre-assess any potential effects of linear forest structure both qualitatively and quantitatively before modelling.

4.5. Future Research and Management Implications

Future Research

Validation remains an important aspect for evaluating and confirming model predictions. While remote validation of larger, high-suitability patches in cooperation with the director of the Salzburger hunting association and district forest managers has contributed to initial validation, systematic field validation is necessary to further attribute validity to the model. Conducting systematic surveys across both areas predicted as “suitable” and “unsuitable” would enhance understanding of the model accuracy and contributing habitat features, thereby providing more reliable information for conservation decisions.

Future research could further refine the present habitat suitability maps by excluding small individual high-suitability cells, and assessing a minimum continuous patch size necessary for harbouring continuous hazel grouse populations and comparing it to the findings of (Sahlsten et al. 2010; Kajtoch et al. 2012). Subsequently, the degree of fragmentation across these defined patches can be assessed based on an approach proposed by (Rivas et al. 2022). Additionally, integrating connectivity metrics may offer insights in the dispersal potential of the hazel grouse, resulting in a more coherent and comprehensive understanding of the conditions and distribution of hazel grouse habitats throughout Salzburg.

Moreover, future research and conservation efforts must extend beyond local or regional scales. Management and conservation efforts with the goal of sustaining viable wildlife populations, such as the hazel grouse, cannot be restricted to small scale local or regional units. Assessing habitat connectivity and suitability across administrative and national boundaries is a necessary aspect in order to sustain a viable and long-term hazel grouse populations within Austria and throughout the alpine region. These large-scale approaches can allow for the identification of potential corridors for the target species that support migrations processes, genetic exchange and population resilience.

Management Implications and Recommendations

From an applied management perspective, several implications arise from this study. For wildlife management, the habitat suitability map can guide targeted monitoring efforts, allowing for the efficient allocation of resources. Conservation and maintenance of identified high-suitability habitats with confirmed continuous occurrences should be prioritised to sustain existing hazel grouse populations. Additionally, the identification of suitable yet unoccupied habitats can inform efforts aimed at habitat conservation and restoration for potential colonisation of the hazel grouse. In order to keep the habitat model and the habitat suitability map relevant for conservation and management purposes over time, the model framework used in this study can be repeated at regular intervals. Using the same set of environmental predictors, while incorporating additional presence records and updated environmental data allows for the re-evaluation of habitat suitability across Salzburg and the detection of shifts in model outputs, driven by environmental changes or sampling effort. Future presence data should be collected systematically, including in currently unsampled but potentially suitable areas, using targeted point-checks in predicted habitats without prior evidence of occurrence using acoustic monitoring devices such as AudioMoth.

Forest management strategies should emphasize the establishment and maintenance of multi-species mixed forests, characterized by diverse stand structures and a proportion of deciduous tree species and shrubs between 10-15 %. Specifically, forest management should actively promote species beneficial to the hazel grouse such as poplar, alder, willow, birch and shrubs, particularly bilberry. Intensive silvicultural practices, including ground-clearing and clearcutting should be avoided, with selective logging practices being preferred to sustain habitat integrity. It is recommended to reduce forest road usage during sensitive periods, notably the breeding and chick rearing period from April to June. Additionally, allowing for natural succession, particularly in coniferous stands offer essential winter shelter and mixed stands for vital summer brooding can provide essential elements of high suitable habitats. In the context of tourism and landscape planning, directing human recreational activities away from secluded, high-suitability areas is recommended, particularly during critical episodes from April to June. The created habitat suitability maps can be integrated into ecological landscape planning, by providing a basis for assessing and mitigating the potential impacts of infrastructure development and increased human presence on hazel grouse populations.

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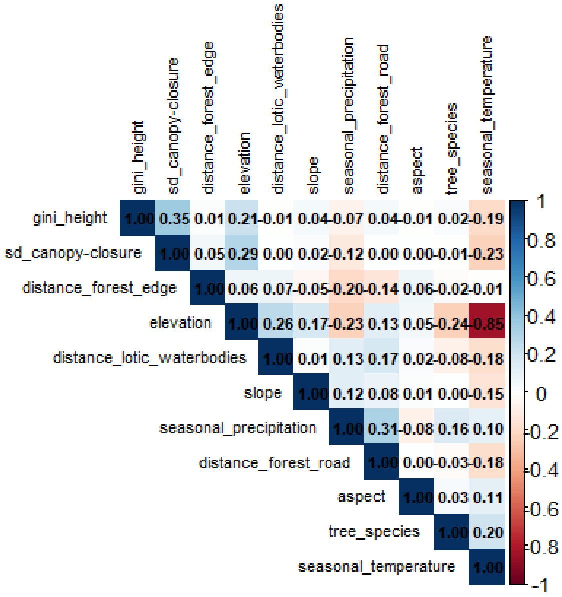
Declaration of the use of generative AI tools

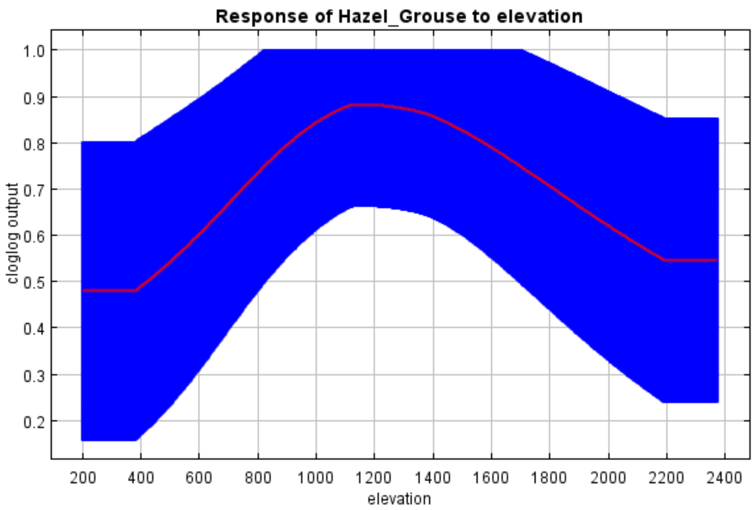
I used ChatPDF to manage a library of publications and summaries for literature screening. I used ChatGPT to check grammar, improve phrasing and to aid in the data preparation process, in particular with regards to avoiding and identifying potential mistakes during the coding in RStudio. Apart from these uses, no generative AI systems were employed for creating this thesis.

Appendix A: Correlation Matrix

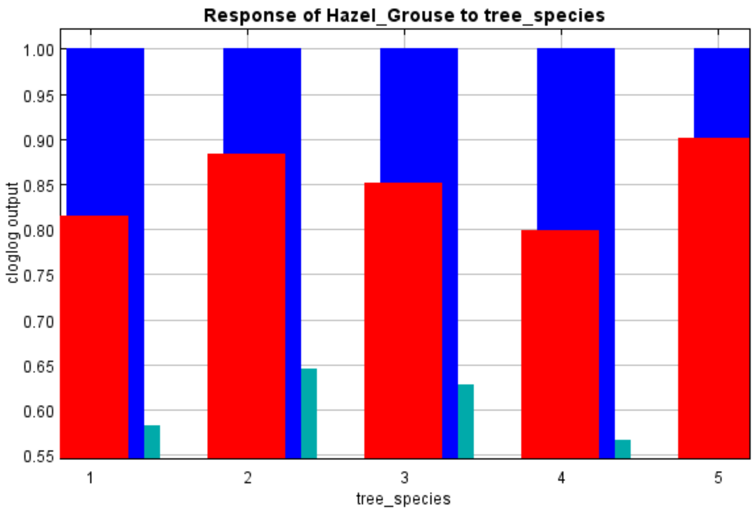


Appendix A 1: Correlation matrix of the pearson product moment correlation.

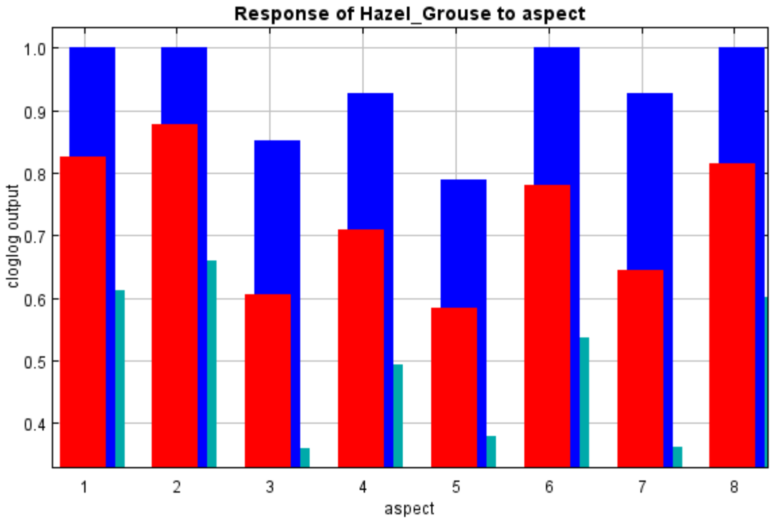
Appendix B: Response Curves



Appendix B 1: Maxent response curve of "Elevation" in isolated runs. On the x-axis, the value of the predictor (m) is depicted and on the y-axis the habitat suitability on a cloglog scale (0 to 1) is depicted. The red curve depicts the average suitability value and the blue areas indicate 1 standard deviation from the mean.



Appendix B 2: Maxent response bar chart of "Tree-species-composition" in isolated runs. On the x-axis, the categories of the predictor (tree-species-classes) is depicted and on the y-axis the mean habitat suitability on a cloglog scale (0 to 1) is depicted. The red bars depict the average suitability value and the blue bars indicate 1 standard deviation from the mean.



Appendix B 3: Maxent response bar chart of "Aspect" in isolated runs. On the x-axis, the categories of the predictor (tree-species-classes) is depicted and on the y-axis the mean habitat suitability on a cloglog scale (0 to 1) is depicted. The red bars depict the average suitability value and the blue bars indicate 1 standard deviation from the mean.