MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

On the applicability of SDMs fit at large extents to projections onto small study areas

verfasst von / submitted by

Moritz Fallgatter BSc

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2024 / Vienna, 2024

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	UA 066 833
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Ecology and Ecosystems
Betreut von / Supervisor:	Univ.-Prof. Mag. Dr. Stefan Dullinger

Acknowledgements

I would like to thank Stefan Dullinger, Karl Hülber and Johannes Wessely for their excellent supervision during numerous meetings. In particular, I would like to thank Johannes Wessely for his great guidance throughout the process. I would also like to thank the entire working group for creating a pleasant working atmosphere and supporting me with their knowledge. Finally, I would like to thank my family and friends for their great support.

Abstract

Facing the global biodiversity crisis, species distribution models (hereafter SDMs) have the potential to be a powerful tool in nature conservation by identifying suitable conservation areas. However, the applicability of SDMs fit at large extents to projections onto small study areas, such as conversation areas, remains uncertain. In this study, I calibrated SDMs for 16 alpine plant species relating their observations across the Alps to six topo-climatic predictors at a spatial resolution of 100 x 100 meters using two pseudo-absence selection approaches. Subsequently, I predicted the species distributions across the Alps and evaluated the model's accuracy according to TSS, AUC and Boyce index at the extent of the Alps, as well as at three individual mountains, keeping the resolution of model projections constant. The results show that the accuracy of the model predictions can vary considerably between the extent of the Alps and the individual mountains. Further, model accuracy depends on the pseudo-absence selection approach and the evaluation metric used. However, the difference in accuracy between the extent of the Alps and the individual mountains is not linear and seems to depend on the specific environmental conditions of the individual mountains. In general, the difference apparently increases with the marginality of conditions on a mountain as compared to the average conditions across the Alps. When designing nature conservation areas, I emphasize that the evaluation of model predictions over a large spatial extent should be treated with caution as it does not necessarily reflect the accuracy at smaller extents.

Abstrakt (deutsch)

In Anbetracht der weltweiten Biodiversitätskrise können Verbreitungsmodelle ein wirksames Instrument für den Naturschutz darstellen, indem sie zur Ausweisung von geeigneten Naturschutzgebieten beitragen. Die Anwendbarkeit von Verbreitungsmodellen, die auf großen Gebieten kalibriert wurden, auf kleinere Untersuchungsgebiete wie Naturschutzgebiete, ist jedoch ungewiss. In dieser Studie habe ich Verbreitungsmodelle für 16 alpine Pflanzenarten erstellt, indem ich ihre Beobachtungen in den Alpen mit sechs topo-klimatischen Prädiktoren bei einer räumlichen Auflösung von 100 x 100 Metern in Beziehung gesetzt habe. Dabei habe ich zwei verschiedene Ansätze der Pseudo-Absenz Auswahl verwendet. Anschließend wurde die Verbreitung der Arten in den Alpen vorhergesagt und die Genauigkeit des Modells anhand von TSS, AUC und Boyce Index für die gesamten Alpen, sowie für drei einzelne Berge ermittlet, wobei die Auflösung der Modellprojektionen konstant gehalten wurde. Die Ergebnisse zeigen, dass die Genauigkeit der Modellvorhersagen zwischen den Alpen und den einzelnen Bergen stark variieren kann und zudem vom Ansatz der Pseudo-Absenzauswahl und der verwendeten Bewertungsmetrik abhängt. Der Unterschied in der Modellgenauigkeit zwischen den Alpen und den einzelnen Bergen ist jedoch nicht linear und scheint mit den spezifischen Umweltbedingungen auf den einzelnen Bergen zusammenzuhängen. Generell scheint der Unterschied in der Modellgenauigkeit mit der Marginalität der Bedingungen auf einem Berg im Vergleich zu den durchschnittlichen Bedingungen in den Alpen zuzunehmen. Bei der Ausweisung von Naturschutzgebieten möchte ich hervorheben, dass eine Bewertung der Modellvorhersagen über eine große räumliche Ausdehnung mit Vorsicht zu behandeln ist, da sie nicht unbedingt die Genauigkeit auf kleineren räumlichen Ausdehnungen widerspiegelt.

Keywords: model evaluation, habitat suitability, fine-scale distribution, environmental predictors, pseudo-absence selection approach, presence-only data.

Table of Contents

Rahmenschrift

In Hinblick auf den Klimawandel und dem damit verbundenen Rückgang der globalen Biodiversität (Ceballos et al. 2015) ist es notwendig, zukünftige Risiken frühzeitig abzuwägen, um entsprechende Gegenmaßnahmen einleiten zu können. Das Forschungsfeld von Verbreitungsmodellen hat in den letzten Jahrzehnten zunehmend an Bedeutung gewonnen (Lobo et al. 2010, Guisan et al. 2013) und bietet die Möglichkeit, die potentielle Verbreitung von Arten unter vergangenen, gegenwärtigen und zukünftigen Umweltbedingungen vorherzusagen (Elith and Leathwick 2009, Guisan et al. 2017). Dabei besteht das zugrundeliegende Prinzip von Verbreitungsmodellen darin, die geeigneten Umweltbedingungen unter welchen eine Art vorkommt zu quantifizieren (Guisan and Zimmermann 2000). Auf dieselbe Weise lassen sich auch Verbreitungen von Genen, Populationen, Gesellschaften oder Habitaten untersuchen (Guisan et al. 2017). In den frühen 1970er Jahren wurden die ersten computerbasierten Modelle zur Untersuchung der Beziehung zwischen einer Art und ihrer Umwelt erstellt (Austin and Noy-Meir 1971). Seitdem wurde die Methodik von Verbreitungsmodellen deutlich verbessert und mit ökologischen Theorien verknüpft (Guisan and Thuiller 2005). Kontextabhängig werden im Englischen verschiedene Bezeichnungen für Verbreitungsmodelle benutzt. Unter den am häufigsten verwendeten Begriffen sind neben habitat suitability models, species distribution models, habitat distribution models, ecological niche models und climate-envelope models viele weitere zu finden (Elith and Leathwick 2009, Guisan et al. 2017). Ungeachtet der Namensgebung bleibt jedoch die Ermittlung von geeigneten Umweltbedingungen das grundlegende Prinzip von Verbreitungsmodellen (Guisan and Zimmermann 2000).

Um die Verbreitung einer Art zu modellieren, ist es notwendig die Ökologie einer Art, also die Wechselbeziehungen einer Art mit ihrer Umwelt, zu verstehen (Elith et al. 2006). In der Biogeographie wird untersucht, welche Faktoren die geographische Verbreitung einer Art bestimmen (Brown and Lomolino 1998). Dabei stellt sich die Frage, weshalb eine Art an einem bestimmten Ort vorkommt und an einem anderen nicht. Während die globale Verbreitung einer Art meist durch klimatische Bedingungen bestimmt wird, prägen weitere Faktoren wie Topographie und Geologie die Verbreitung auf kleineren räumlichen Ebenen (Elith and Leathwick 2009). Neben den abiotischen Umweltbedingungen hängt die Verbreitung einer Art jedoch auch von biotischen Interaktionen ab (Araújo and Luoto 2007). Während Mutualismus dazu führen kann, dass eine Art unter abiotisch eher ungeeigneten Umweltbedingugnen vorkommt (Afkhami et al. 2014), kann interspezifische Konkurrenz eine Art aus einem Gebiet mit eigentlich geeigneten Umweltbedingungen ausschließen (Goldberg and Barton 1992, Leathwick and Austin 2001). Ob eine Art an einem bestimmten Ort vorkommt, hängt also davon ab, ob die Kombination von lokalen abiotischen und biotischen Umweltbedingungen für diese Art geeignet ist (Guisan and Thuiller 2005, Soberon and Peterson 2005). Zudem ist für das Vorkommen einer Art entscheidend, ob die Ausbreitungsfähigkeit der Art ein Besiedeln der Fläche ermöglicht

(Guisan and Thuiller 2005, Soberon and Peterson 2005). So wurde beispielsweise gezeigt, dass die heutige Verbreitung von europäischen Buchenwaldarten stark mit den Rückzugsgebieten während des letzten glacialen Maximums und folglich mit einer begrenzten Ausbreitungsfähigkeit zusammenhängt (Willner et al. 2009). Zudem ist zu beachten, dass die Verbreitung einer Art durch verschiedene Faktoren auf unterschiedlichen räumlichen und zeitlichen Ebenen beeinflusst wird (Wiens 1989, Levin 1992, Mackey and Lindenmayer 2001). Eine Art ist dabei die grundlegende Einheit der Evolution (Mayr 1996) und hat sich infolge dieser an gewisse Umweltbedingungen angepasst (Schluter 2001). Diese physiologischen Anpassungen sorgen dafür, dass eine Art unter bestimmten Umweltbedingungen eine höhere Fitness als unter anderen Umweltbedingungen besitzt (Kearney and Porter 2009, Hector et al. 2012). Durch die Spezialisierungen entlang von mehreren Umweltgradienten ergibt sich eine artspezifische Nische, auf welcher Verbreitungsmodelle aufbauen (Guisan and Zimmermann 2000). In verschiedenen Theorien wird die Nische einer Art als die Gesamtheit der Umweltbedingungen, unter welchen eine Art überlebensfähige Populationen erhalten kann oder hinsichtlich des Einflusses, welchen eine Art auf ihre Umwelt hat, beschrieben (Chase and Leibold 2009). Verbreitungsmodelle folgen dabei der Nischen Theorie von Hutchinson (Guisan and Thuiller 2005), welcher die Nische einer Art als ein n-dimensionales Hypervolumen an Umweltbedingungen beschreibt (Hutchinson 1957, Guisan et al. 2017). Dabei kann jeder Umweltgradient als eine eigene Dimension in Hutchinsons n-dimensionalem Hypervolumen angesehen werden (Miller 2010). Die Gesamtheit der abiotischen Umweltbedingungen, unter denen eine Art lebensfähige Populationen aufrechterhalten kann, wird als fundamentale Nische bezeichnet (Soberon and Peterson 2005). Die Gesamtheit der abiotischen Umweltbedingungen, unter denen eine Art in Interaktion mit anderen Arten lebensfähige Populationen aufrechterhalten kann, wird als realisierte Nische bezeichnet (Soberon and Peterson 2005). Während die realisierte Nische aus der realen Verbreitung einer Art ermittelt werden kann, lässt sich die fundamentale Nische einer Art nur durch aufwändige Experimente erforschen (Guisan et al. 2017). Da Verbreitungsmodelle mit realen Vorkommen, also Vorkommen mit biotischer Interaktion erstellt werden, quantifizieren sie die realisierte Nische einer Art (Austin 2002, Pearman et al. 2008, Guisan et al. 2017).

Als Voraussetzung von Verbreitungsmodellen muss zudem angenommen werden, dass sich die Beziehung einer Art zu ihrer Umwelt im Gleichgewicht befindet und sich im Laufe der Zeit nicht, oder nur extrem langsam, verändert (Austin 2002, Elith and Leathwick 2009). Grundlegende Schritte von Verbreitungsmodellen beinhalten Konzeptualisierung, Vorbereitung der Daten, Kalibrierung, Evaluierung und Prädiktion (Guisan and Thuiller 2005). Dabei ist es wichtig, dass die Modelle auf soliden methodischen und theoretischen Grundlagen beruhen (Guisan et al. 2017). Zum Erstellen von Verbreitungsmodellen werden geographische Vorkommensinformationen einer Art mit den vorherrschenden Umweltbedingugen in Verbindung gesetzt (Guisan et al. 2017). Verbreitungsmodelle werden dabei mit einer bestimmten Auflösung und innerhalb eines definierten geographischen Raumes

erstellt (Barve et al. 2011, Guisan et al. 2017). Um die gesamte Nische eine Art abzubilden, sollte der geographische Raum, in dem Verbreitungsmodelle erstellt werden, entweder die gesamte geographische Verbreitung einer Art umfassen, oder zumindest so groß sein, dass alle Umweltbedingungen unter welchen eine Art vorkommt, abgebildet werden (Guisan et al. 2017). Die räumliche Auflösung eines Modells bezieht sich auf die minimale räumliche Distanz zwischen Punkten mit unterschiedlichen Umweltbedingungen. Diese Umweltbedingungen werden in Verbreitungsmodellen üblicher Weise als geographische Raster dargestellt, die Auflösung entspricht daher der Größe der einzelnen Rasterzelle. . Ein Modell mit hoher räumlicher Auflösung verwendet dabei eine geringe Zellgröße. Des weiteren ist es wichtig, dass die Auflösung der Prädiktoren mit der räumlichen Genauigkeit der Vorkommensinformationen übereinstimmt (Guisan et al. 2017).

Da die Auswahl der Prädiktoren maßgeblich über die Modellvorhersagen entscheidet, sollten diese aufgrund fundierter ökologischer Kentnisse ausgewählt werden (Araújo and Guisan 2006). Häufig verwendete Prädiktoren für das Vorkommen von Arten sind abiotische Umweltbedingungen wie Klima, Geograhie und Topographie (Guisan et al. 2017). Des weiteren können aber auch beispielsweise das Vorkommen einer dominanten Art (Pellissier et al. 2010) oder die Ausbreitungsfähigkeit einer Art als Prädiktoren verwendet werden (D'Amen et al. 2018). Als Vorkommensinformationen einer Art können Präsenzen, Absenzen oder Abundanzen verwendet werden (Guisan et al. 2017). Während Präsenzen Informationen über geeignete Umweltbedingungen liefern und Abundanzen diese Informationen gewichten, sollen Absenzen Informationen über ungeeignete Umweltbedingungen liefern (Lobo et al. 2010). Jedoch können Präsenzen irreführende Informationen beinhalten, wenn eine Art unter ungeeigneten Umweltbedingungen vorkommt. Dies ist beispielsweise der Fall, wenn eine Population nur aufgrund einer kontinuierlich Zuwanderung von Individuen aus anderen Populationen bestehen bleibt (Pulliam 2000). Andersherum können Absenzen irreführende Informationen beinhalten, wenn eine Art unter geeigneten Umweltbedingungen als absent beobachtet wird (Elith et al. 2006). Dabei können biotische Interaktionen oder eine beschränkte Ausbreitungsfähigkeit zur Absenz einer Art führen (Lobo et al. 2010). Während mittlerweile eine enorme Anzahl an Präsenzendaten in diversen Datenbanken verfügbar ist, sind Informationen über Absenzen aufgrund des hohen Auswands während der Probenahme rar (Guisan et al. 2017). Aufgrund des Mangels an Absenzen werden deshalb oft so genannte Pseudo-Absenzen zum Erstellen von Verbreitungsmodellen verwendet (Elith and Leathwick 2009), welche die Umweltbedingungen im Untersuchungsgebiet widerspiegeln sollen (Barbet-Massin et al. 2012). Trotz diverser Probleme konnte gezeigt werden, dass auf diese Weise qualitativ hochwertige Vorhersagen getroffen werden können (Elith et al. 2006).

Dabei liegt die Nützlichkeit von Verbreitungsmodellen darin, die ökologische Beziehung einer Art zu ihrer Umwelt zu ermitteln und in den geographischen Raum zu projezieren (Miller 2010). Mithilfe von Techniken wie beispielsweise Regressionsanalysen oder Methoden aus dem Bereich des maschinellen Lernens wird die Verbreitung einer Art entlang von Umweltgradienten erfasst und als kontinuierliche

Vorkommenswahrscheinlichkeit in den geographischen Raum prädiziert (Guisan and Thuiller 2005). Mithilfe eines Grenzwertes werden die kontinuierlichen Vorkommenswahrscheinlichkeiten dann meist in binäre Prädiktionen von Präsenzen und Absenzen oder, genauer, von geeigneten und ungeeigneten Standorten umgewandelt (Liu et al. 2013). Ziel der Prädiktion kann es sein, unbekannte Vorkommen innerhalb des Untersuchungsgebiets oder neuen Gebieten zu erfassen, oder die Verbreitung einer Art unter zukünftigen, gegenwärtigen oder vergangenen Umweltbedingungen zu untersuchen (Elith and Leathwick 2009, Miller 2010). Infolgedessen können Verbreitungsmodelle dazu genutzt werden, ökologische Theorien zu untersuchen (Austin 2002) oder im Naturschutz Anwendung zu finden (Guisan et al. 2013). In der Vergangenheit wurden Verbreitungsmodelle beispielsweise dazu genutzt um biotische Interaktionen zu erforschen (Anderson et al. 2002, Pellissier et al. 2010) oder die Folgen des Klimawandels vorherzusagen (Wessely et al. 2022). Im angewandten Naturschutz können Verbreitungsmodelle zur Risikobewertung biologischer Invasionen (Pyšek et al. 2020), zur Identifizierung kritischer Lebensräume (Lyet et al. 2013, Charbonnel et al. 2023), zur regionalen Naturschutzplanung (Esselman and Allan 2011) oder zur Umsiedlung gefährdeter Arten eingesetzt werden (Engler et al. 2004).

Im Rahmen einer Verbreitungsmodellierung ist es essentiell, die Genauigkeit und Verlässlichkeit eines Modells einschätzen zu können. Ein zentraler Schritt ist daher die Evaluierung der Modellprädiktionen (Barry and Elith 2006). Um die Genauigkeit eines Models zu erfassen wird überprüft, ob die Vorhersagen eines Modells mit realen Vorkommensinformationen übereinstimmen. Dabei werden meist unabhängige Vorkommensinformationen herangezogen, oder im Fall der Nutzung statistischer Methoden wie bootstrapping oder crossvalidation ausgewählte Vorkommensinformationen wiederholt verwendet (Guisan and Thuiller 2005). Zusammenfassend gibt es in einem Verbreitungsmodell mit Präsenzen und Absenzen zwei Arten von möglichen Fehlern (Fielding and Bell 1997). So kann eine Art an einem Ort vorhergesagt werden, wo sie nicht vorkommt oder eine Art an einem Ort nicht vorhergesagt werden, wo sie vorkommt (Fielding and Bell 1997, Guisan and Thuiller 2005).

Introduction

The relationship between species and their environment is a fundamental aspect of vegetation research. Species occurrence can provide information about the environmental conditions of a specific site, while environmental conditions can indicate the presence or absence of species (Ellenberg 1974, Landolt et al. 2010). Linking species observations with environmental predictors enables ecological modellers to predict the distribution, or at least the potential distribution of species under past, present and future environmental conditions (Elith and Leathwick 2009, Guisan et al. 2017). By identifying the suitable habitat of a species (Guisan and Zimmermann 2000), SDMs can be a powerful tool in nature conservation (Guisan et al. 2013). To address the global biodiversity crisis (Pereira et al. 2010) SDMs can be used to designate protected areas, for example (Tulloch et al. 2016). However, the practical application of SDMs in nature conservation remains sparse (Guisan et al. 2013). For applicability in nature conservation, SDMs should be able to distinguish between suitable and unsuitable habitats at fine spatial scales (Oliveira et al. 2021), with the meaning of 'fine' depending on the context, e.g. the size and mobility of species or the usual patch size of their habitats . In SDMs, the term scale refers to the parameters of spatial resolution, often referred to as grain size, i.e. the size of the individual spatial subunit, e.g. the raster cell, and spatial extent, which corresponds to the size of the study area (Guisan et al. 2017). As the distribution of species depends on various factors acting at different spatial scales, observing ecological patterns is associated with both the resolution and extent of an investigation (Wiens 1989). To investigate the distribution of species in the context of nature conservation, it is recommended to apply SDMs at small spatial extents with high spatial resolution (Oliveira et al. 2021). However, to avoid model misspecification, the extent of the study area used for model calibration should cover the entire range of a species or an area large enough to represent all environmental conditions occupied by a species (Guisan et al. 2017). Therefore, areas considered in nature conservation planning are often much smaller than the area considered in SDMs, leading to a mismatch between the spatial extent of model parameterization and application. Furthermore, SDMs are usually projected and evaluated within the area, in which they were calibrated (Randin et al. 2006). Calibrating and evaluating SDMs over a large spatial extent could therefore lead to a strong overconfidence in the model's accuracy at smaller spatial extents, such as nature conservation areas. This is especially likely when the fine-scale distribution of a species is influenced by additional environmental gradients that are not accounted for by models calibrated at large spatial extents (Mackey and Lindenmayer 2001). In such cases, SDMs calibrated at a large extent may accurately capture the general distribution pattern, but may lose discriminative ability at smaller extents, even if they are calibrated with high spatial resolution. This might be a serious issue when establishing nature conservation areas or studying the fine-scale distribution of a species.

In this study I investigated whether SDMs calibrated over a large spatial extent can make reasonable predictions at smaller spatial extents. Therefore, I generated SDMs for 16 alpine plant species by relating their observations in the European Alps to six topo-climatic predictors at a spatial resolution of 100 x 100 meters using artificial neural networks, generalized boosted models, and random forest as modeling techniques. Since reliable absences are often lacking due to a high sampling effort, so-called pseudo-absences are increasingly used, which are supposed to represent the environmental conditions within the study area (Barbet-Massin et al. 2012). However, it has been shown that the approach of pseudo-absence selection can influence the predictive outcome of SDMs (Chefaoui and Lobo 2008, VanDerWal et al. 2009, Wisz and Guisan 2009, Lobo et al. 2010, Barbet-Massin et al. 2012, Hanberry et al. 2012). Depending on whether the pseudo-absences are selected in areas with more similar or dissimilar environmental conditions to those of the species presence observations, it can result in overprediction or underprediction, respectively (Chefaoui and Lobo 2008, VanDerWal et al. 2009, Lobo et al. 2010, Barbet-Massin et al. 2012, Hanberry et al. 2012). Consequently, I independently calibrated SDMs with two different approaches of pseudo-absence selection. Firstly, I selected pseudo-absences randomly over the whole study area represented by the Alps including a 20-kilometer buffer. Secondly, I sampled pseudo-absences within a 20-kilometer, disk shaped buffer around the species observations. Another important issue in SDMs is the assessment of the model´s predictive accuracy (Guisan and Thuiller 2005, Elith et al. 2006). Since different evaluation metrics provide varying information about the accuracy of the model predictions (Hernandez et al. 2006, Elith 2009), I evaluated the model predictions by applying three different evaluation metrics: the true skill statistic (hereafter TSS) (Allouche et al. 2006), the area under the curve (hereafter AUC) (Fielding and Bell 1997) and the Boyce index (Boyce et al. 2002). The most commonly used evaluation metrics are the TSS (Allouche et al. 2006) and the AUC (Fielding and Bell 1997). However, these metrics have been widely criticized (Lobo et al. 2008, Leroy et al. 2018). One reason for this is that TSS and AUC necessarily require presence-absence observations but are often calculated using pseudo-absences instead of true absences (Jiménez-Valverde 2012, Leroy et al. 2018). To avoid an evaluation based on pseudo-absences, I included the Boyce index, which is calculated on the continuous probabilities of presence observations (Boyce et al. 2002) and is considered to be an appropriate metric for presence-only data (Leroy et al. 2018).

Applying the aforementioned methods, I predicted the distribution of 16 alpine plant species throughout the Alps, including three individual mountains with a particularly high number of species observations. Subsequently, I evaluated the accuracy of the model predictions at the extent of the Alps as well as at each of the individual mountains. By comparing the accuracy between the extent of the Alps and the individual mountains, I investigated whether SDMs calibrated at a large spatial extent perform equally well at large and small extents. As SDMs calibrated over a large extent are likely to identify mainly the gradients determining the species distributions at a broad scale, while additional factors may come into play at smaller extents, I hypothesized that the accuracy of the model predictions decreases from the

large (i.e., the Alps) to the small extent (i.e., the individual mountains). In addition, I explored what causes such a difference in model accuracy between large and small extents. Since the model predictions ultimately rely on which environmental conditions are included into the calibration of the SDMs through species observations, the model accuracy at smaller extents might depend on the similarity between the environmental conditions at large (i.e., the Alps) and at small extents (i.e., the individual mountains). Consequently, I assessed the dissimilarity between the environmental predictors of the species presences across the Alps and the individual mountains and investigated whether the difference in model accuracy between the spatial extent of the Alps and the individual mountains can be explained by the dissimilarity of environmental conditions experienced at the extent of the Alps and the individual mountains. Here, I hypothesized that the difference in model accuracy between the large (i.e., the Alps) and small spatial extent (i.e., the individual mountains) increases with increasing dissimilarity.

Material and Methods

Study area and study organisms

As a study area, I chose the mountain range of the European Alps, as well as three individual mountains, namely Hochschwab (2277 m a.s.l., 47°37'05.5"N 15°08'35.5"E), Racherin (3092 m a.s.l., 47°04'50.9"N 12°47'39.5"E) and Schrankogel (3497 m a.s.l., 47°02'38.1"N 11°05'56.5"E). These mountains were selected because they offer particularly high observation density of 16 shared alpine plant species in the data sources used in this study. As study organisms, I included all plant species with at least 20 observations on each of the three individual mountains. Due to the geographical distance and geological differences of the individual mountains, the following geologically indifferent species with an alpine-wide distribution were selected: *Agrostis alpina, Anthoxanthum alpinum, Bartsia alpina, Campanula scheuchzeri, Carex sempervirens, Geum montanum, Homogyne alpina, Leontodon hispidus, Mutellina adonidifolia, Myosotis alpestris, Persicaria vivipara, Poa alpina, Potentilla aurea, Selaginella selaginoides, Thymus praecox subsp. polytrichus, Vaccinium vitis-idaea*. Species presence observations were extracted from the Global Diversity Information Facility (hereafter GBIF) (GBIF.org 2024) using the R rgibf package (Chamberlain et al. 2017) and the Austrian Vegetation Database (Willner et al. 2012). Additional species presence observations at Mount Schrankogel were contributed by the Microclim project (MICROCLIM (mountainresearch.at)). For the calibration of the SDMs, I limited the species data to observations collected within the European Alps, including a 20-kilometer buffer. Additionally, I only used observations with a minimum spatial accuracy of 100 meters that were collected between 1980 and 2022. Duplicate observations for one and the same grid cell were merged. Further, I ensured that the data did not contain erroneous locations such as capitals, countries, equal latitudes and longitudes, GBIF headquarters, biodiversity institutions and missing coordinates by using the CoordinateCleaner package (Zizka et al. 2019). An overview of the species observations at the extent of the Alps and the individual mountains is given in Table 2 in the appendix.

Predictor variables

The climatic predictors used in this study include temperature seasonality, temperature and precipitation of the warmest quarter, as well as precipitation of the coldest quarter. All climatic predictors were retrieved from the CHELSA Climate database (Karger et al. 2017) available at http://chelsa-climate.org/. The data was further downscaled to a 100 x 100 meter resolution (original resolution of 30 arcsec) using the Delta method as in (Dullinger et al. 2012). The temperature seasonality was calculated using the standard deviation of the monthly mean temperature and is thus a measure for the temperature fluctuations in a year. The temperature and the precipitation of the warmest quarter reflect the climatic conditions during the growing season, while the precipitation of the coldest quarter can be seen as indicator of insulation against the cold by snow cover. Additionally, I included the heat load index and the topographical wetness index as topo-climatic predictors. The heat load index provides

information on cooling effects and heat accumulation, while the topographical wetness index reflects topographically controlled water availability. The heat load index and the topographical wetness index were calculated at a resolution of 100 x 100 meters, using the spatialEco package (Evans and Ram 2015) and the software SAGA GIS (Conrad et al. 2015), respectively. With this set of predictors, I aimed to capture the major environmental gradients that drive the species distribution at both large and small spatial scales, apart from soil attributes. The correlation between predictors was tested for all species and both approaches of pseudo-absence selection at the spatial extent of the Alps. All predictors were intercorrelated with less than r = 0.85 (see Table 3 in the appendix).

Model calibration

The SDMs were calibrated using the biomod2 package, allowing for ensemble model forecasting (Thuiller et al. 2016). For model calibration I used the species observations of the Alps but excluded the species observations of the three individual mountains. Calibrating the SDMs, I choose two approaches of pseudo-absence selection. On one hand, I selected the pseudo-absences randomly over the whole study area represented by the Alps including a 20-kilometer buffer. On the other hand, I selected pseudo-absences within a 20-kilometer disk-shaped buffer around the species observations. The pseudo-absences were selected five times for each approach of pseudo-absence selection. To achieve a well-balanced prevalence, I selected as many pseudo-absences for each species as presence observations available at the spatial extent of the Alps. As modelling techniques, I used artificial neuronal networks, generalized boosted models and random forest. Each modeling technique was used three times with each of the five sets of pseudo-absences resulting in 15 single models per modeling technique. As I used three different modeling techniques, I generated 45 single models per species for each pseudo-absence selection approach. During each single model run, the input data was split into 80 percent for model calibration and 20 percent for model evaluation. Thereby, the model accuracy of each single model was assessed regarding the TSS, and the variable importance of each predictor variable was calculated. For each species, the 45 single models were then weighted by their TSS value and combined into an ensemble model. Only single models with a TSS evaluation higher than 0.7 were included in the ensemble model. Single models with lower TSS evaluations were dropped. The species distribution was then predicted as a continuous probability of occurrence throughout the Alps. To convert the continuous predictions into binary predictions, the threshold was chosen to maximize the TSS value (Liu et al. 2013). Model calibration and prediction were conducted separately for both approaches of pseudo-absence selection.

Model evaluation

The accuracy of the model predictions was evaluated at the extent of the Alps and at each individual mountain separately. On the extent of the Alps, I reevaluated how well the SDMs fitted the species observations used for model calibration. Further, I evaluated how well the SDMs fitted independent observations on the three individual mountains located in the eastern Alps. The accuracy of the SDMs

was assessed using the TSS (Allouche et al. 2006), the AUC (Fielding and Bell 1997) and the Boyce index (Boyce et al. 2002). The TSS is calculated as the sum of sensitivity and specificity minus 1 (Allouche et al. 2006). Sensitivity and specificity represent the proportion of correctly predicted presences and absences, respectively (Allouche et al. 2006). The AUC refers to the area under the curve obtained when all true-positive values on the y-axis are plotted against the corresponding false-positive values on the x-axis (Fielding and Bell 1997). Therefore, TSS and AUC indicate the ability of the model's binary predictions to correctly predict presences and absences, in this case presences and pseudo-absences. Unlike TSS and AUC, the Boyce index assesses model accuracy solely based on the comparison of continuous predictions and presence observations. The Boyce index divides the continuous suitability predictions into an arbitrary number of intervals, so called windows (Hirzel et al. 2006), and calculates the ratio between the frequency of predicted and expected observation points for each window (Hirzel et al. 2006). The number of expected observation points in a window is the number of observations under the assumption of the random distribution, i.e. the percentage of all observations equal to the percentage of all cells in the respective window. The minimum requirement for a model to be useful is that windows with low suitability should contain fewer predicted observations, while windows with high suitability should contain more predicted observations than expected by chance. Thus, the ratio between the frequency of predicted to expected observation points should increase with increasing habitat suitability. The Boyce index measures this increase calculating the Spearman rank correlation coefficient between the ratio of predicted and expected observation points of each window and the corresponding rank of habitat suitability. Therefore, the Boyce index indicates whether the predicted habitat suitability aligns with the distribution of presence observations in the evaluation dataset. To reduce its sensitivity to the number of windows, the Boyce index was calculated using a moving window (Hirzel et al. 2006). While the TSS was calculated using the formula described above, the AUC and Boyce index were calculated using the Metrics (Hamner et al. 2018) and ecospat (Di Cola et al. 2017) packages, respectively. The TSS and Boyce index range from -1 to 1, with 0 indicating a model with random predictions. The AUC ranges from 0 to 1, with 0.5 indicating a model with random predictions. To ensure a fair comparison between the extent of the Alps and the individual mountains, I calculated the Boyce index using the continuous predictions of presence observations at the respective extent and the continuous predictions of the Alps. For the same reason, I calculated the TSS and AUC using the presence observations of the respective extent and pseudo-absences of the Alps. Due to the lack of true species absences, I selected pseudo-absences for the model evaluation with TSS and AUC in the same way as they were selected for model calibration. In order to evaluate SDMs with random pseudo-absence selection across the Alps for model calibration, I selected pseudo-absences for model evaluation randomly across the Alps. To evaluate SDMs with a pseudo-absence selection within a 20-kilometer disk around the species observations for model calibration, I sampled pseudo-absences for model evaluation within a 20-kilometer disk around the species observations. For model evaluation, I selected the same number of pseudo-absences as presence observations of each species available at the

respective extent. The predictions of the two approaches of pseudo-absence selection were evaluated separately.

Data analysis

To test whether there is a difference in model accuracy between the extent of the Alps and the individual mountains, I conducted an ANOVA as well as post hoc TukeyHSD tests, comparing the model accuracy at the spatial extent of the Alps to the model accuracy at each of the individual mountains for both approaches of pseudo-absence selection and each evaluation metric separately. Further I investigated whether the difference in model accuracy between the Alps and the individual mountains is dependent on whether the species occupies similar intervals of the environmental predictors used in model fitting at the extent of the Alps and each individual mountain. For each combination of species and predictor, I therefore calculated the Kolmogorov-Smirnov-statistic *D*, by using the stats package (R Core Team 2023). *D* measures the difference between two empirical distributions as the maximal distance of their cumulative distribution functions. The distributions to be compared were those of the predictor values of the species presence observations across the Alps and on the focal mountain, respectively. Since *D* is a distance, it is a measure of dissimilarity. The smaller *D* is, the more similar the distribution of species along the gradient on a mountain is to the one across the Alps. Finally, I fitted linear models relating the difference in model accuracy to *D* by using the lm function from the stats package (R Core Team 2023) for both approaches of pseudo-absence selection, each evaluation metric and each predictor separately. I corrected for multiple testing by adjusting the p-values with the p.adjust function from the stats package using the Bonferroni method (R Core Team 2023). All statistical analyses were conducted using the software R (R Core Team 2023).

Results

Regardless of the approach of pseudo-absence selection, the SDMs were mainly influenced by the mean temperature of the warmest quarter, followed by the precipitation of the warmest quarter (Figure 1). For SDMs with random pseudo-absence selection, model accuracy was high at the extent of the Alps (mean TSS = 0.81, AUC = 0.9, Boyce index = 0.95), Hochschwab (mean TSS = 0.88, AUC = 0.94, Boyce index = 0.72) and Racherin (mean TSS = 0.83, AUC = 0.91, Boyce index = 0.81), but low at Schrankogel (mean TSS = 0.3, AUC = 0.65, Boyce index = 0.39). Furthermore, the accuracy of the model predictions significantly decreased from the extent of the Alps to Schrankogel for all evaluation metrics. For SDMs with a pseudo-absence selection within a 20-kilometer disk around the species observations I observed an intermediate accuracy at the spatial extent of the Alps according to TSS and AUC (mean TSS = 0.57, AUC = 0.78), whereas the accuracy was high regarding the Boyce index (mean Boyce index = 0.99). At the individual mountains, the accuracy of the model predictions was highest at Hochschwab (mean TSS = 0.79, AUC = 0.9, Boyce index = 0.71), intermediate at Racherin (mean TSS = 0.31, AUC = 0.66, Boyce index = 0.54) and lowest at Schrankogel (mean TSS = 0.12, AUC = 0.56, Boyce index = 0.15). Additionally, there were significant differences in model accuracy between the Alps and Hochschwab, Racherin, and Schrankogel for model evaluation with TSS and AUC. The model accuracy significantly decreased from the Alps to Hochschwab and Schrankogel, according to the Boyce index. More detailed results of the TukeyHSD test are displayed in Table 1 in the Appendix. For SDMs with random pseudo-absence selection, I found that *D* of the temperature seasonality was most strongly correlated with the difference in model accuracy between models fitted at the extent of the Alps and at each mountain, followed by *D* of the temperature of the warmest quarter for all evaluation metrics. Furthermore, the difference in model accuracy between the Alps and each mountain when measured as TSS and AUC was partly explained by the precipitation of the coldest quarter. For SDMs with pseudo-absence selection within a 20-kilometer disk around the species observations, I found that *D* of the heat load index was correlated most closely with to the difference in model accuracy, followed by *D* of the temperature seasonality and temperature of the warmest quarter when accuracy was measured by TSS and AUC. For the Boyce index *D* of the temperature seasonality was most closely correlated with the deviance in model accuracy of the model predictions, followed by *D* of the temperature of the warmest quarter. Table 1 displays more detailed results of the linear regression models. As an example, the binary model predictions of *Geum montanum* at the extent of the Alps and the individual mountains are displayed in Figure 5 for both approaches of pseudo-absence selection separately.

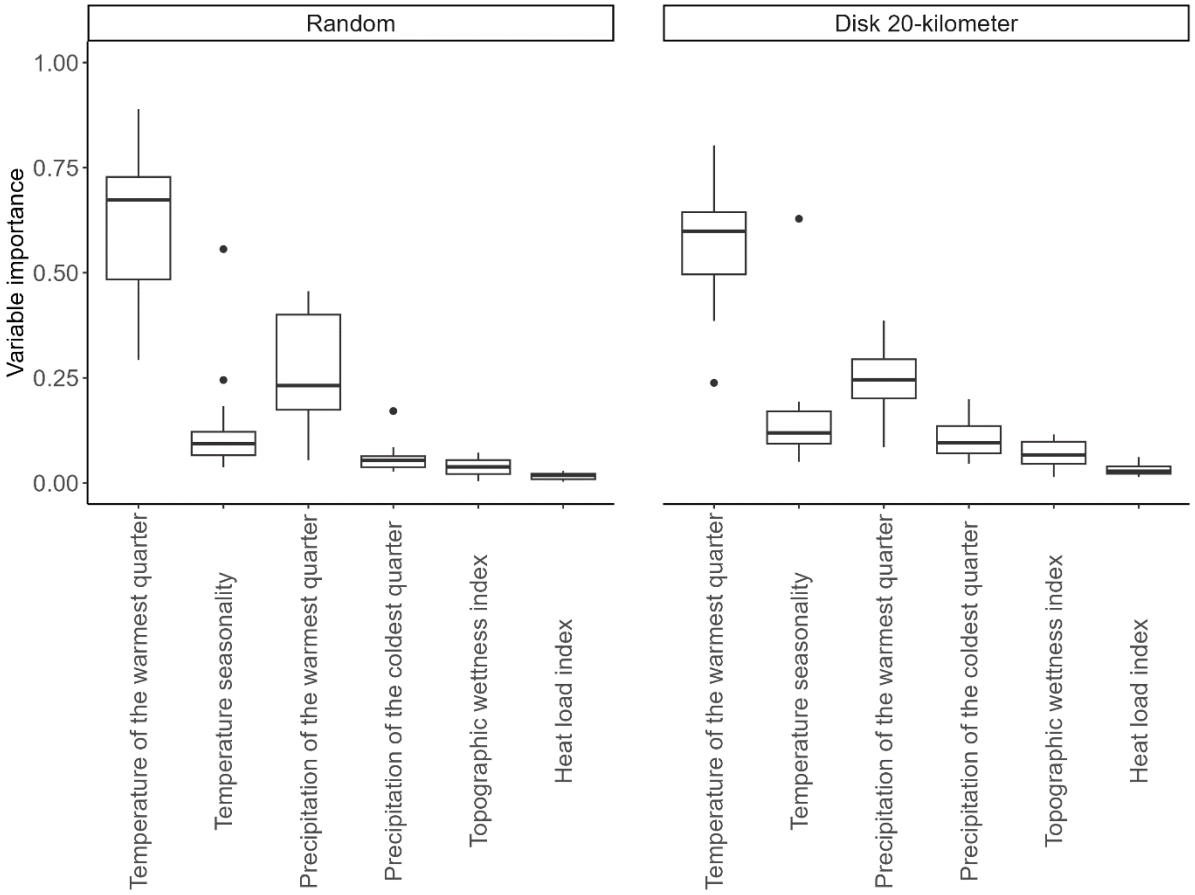

Figure 1: Mean importance of predictor variables for all 16 species in 45 single model runs (5 pseudo-absence draws x 3 modeling techniques x 3 replicates) for both approaches of pseudo-absence selection.

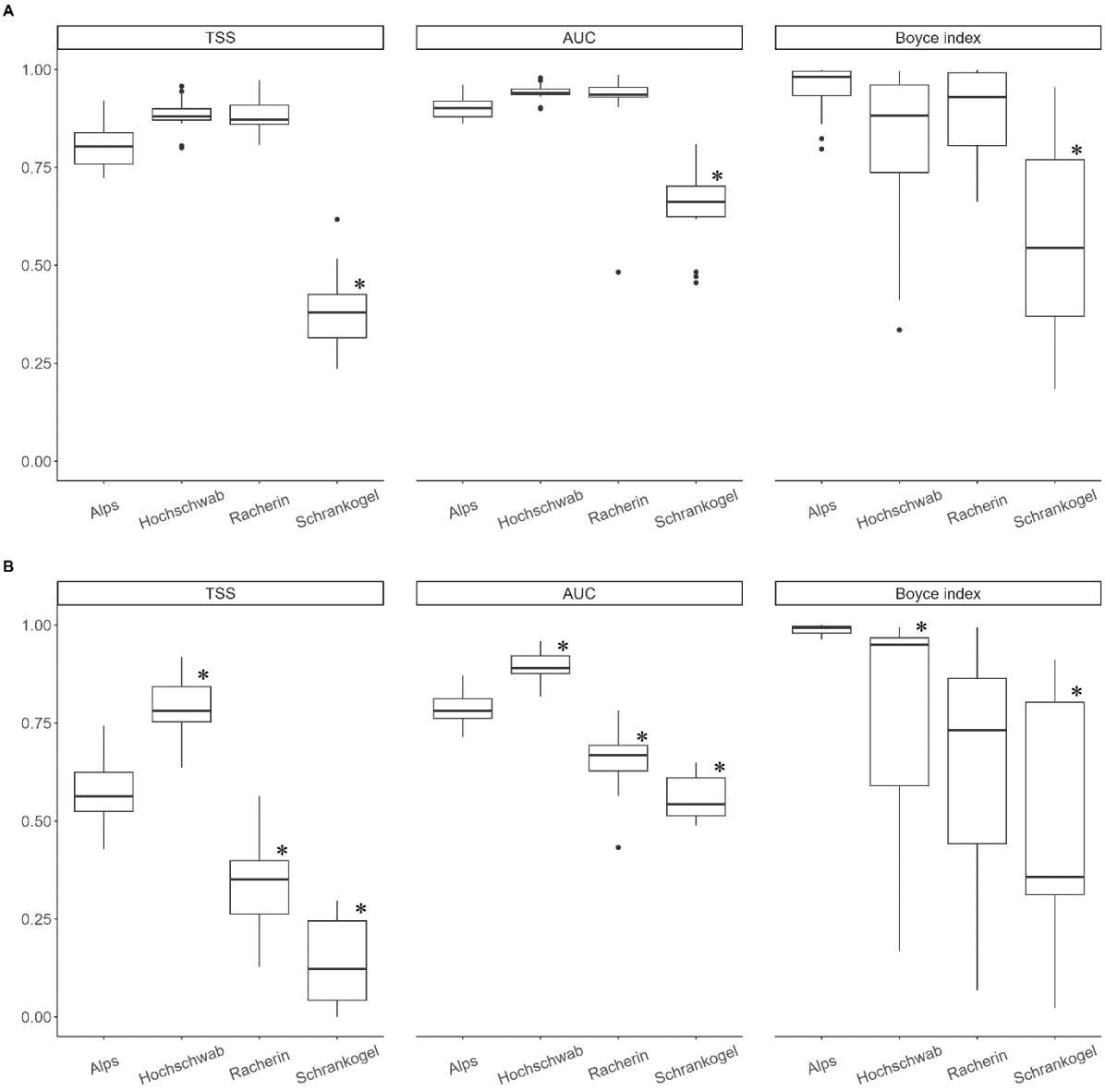

Figure 2: The accuracy of model projections, measured by TSS, AUC and Boyce index, at the extent of the Alps and the three mountains Hochschwab, Racherin and Schrankogel. Asterisks indicate a significant difference in model accuracy between the extent of the Alps and an individual mountain. A) shows the evaluation of SDMs calibrated with random pseudo-absence selection within the Alps including a 20 km buffer. B) shows the evaluation of SDMs calibrated with pseudo-absence selection within a 20km buffer around the species presences. For readability, values below zero are not displayed.

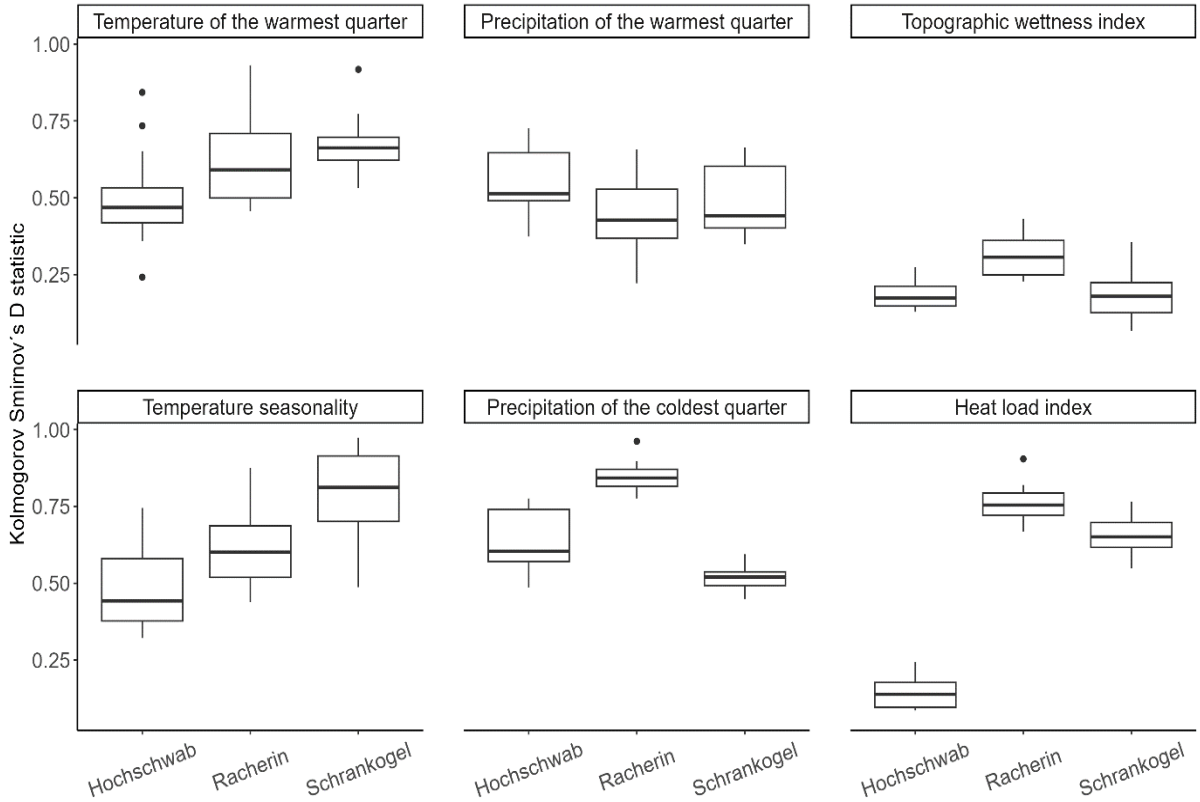

Figure 3: Kolmogorov-Smirnov distance D as a measure of dissimilarity between the distribution of the 16 species across the Alps and on each mountain (Hochschwab, Racherin, Schrankogel) along gradients of the six predictors used in model fitting.

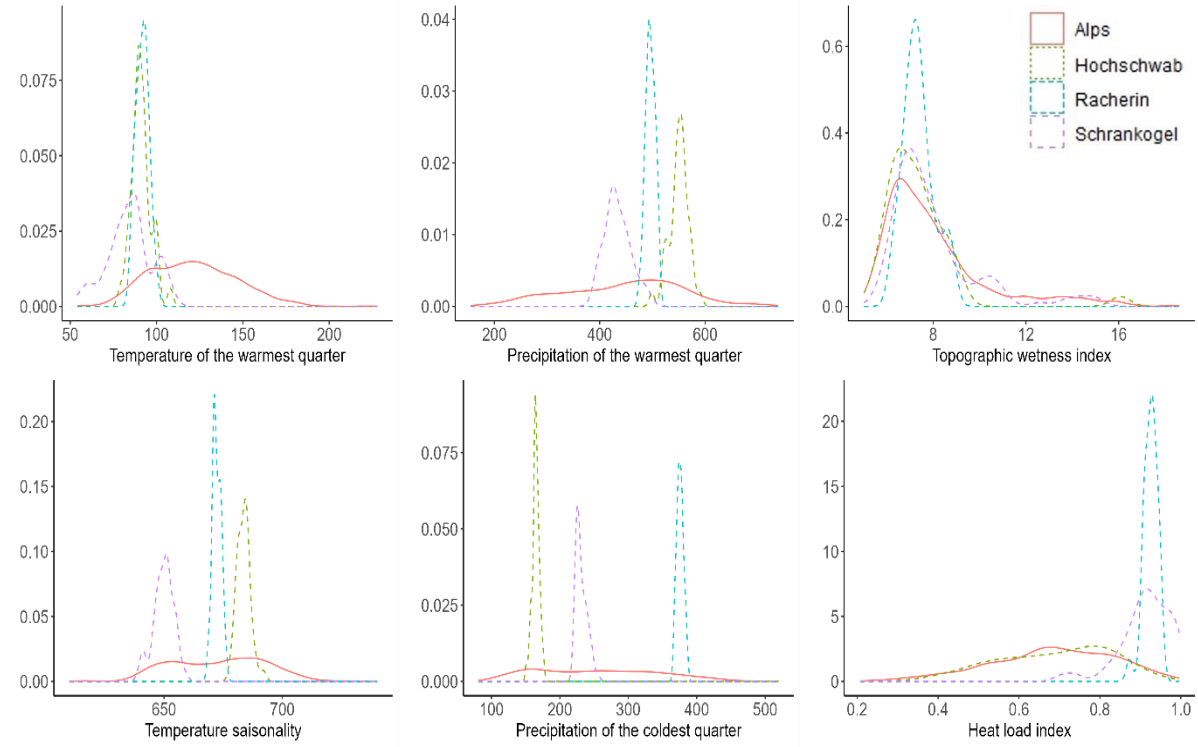

Figure 4: Density distribution of predictor variables of the presence observations of all 16 species across the Alps and each mountain.

Table 1: Results of the linear regression models, relating the difference in projection accuracy between the Alps and each mountain to the dissimilarity in species distributions along gradients of the six predictors used in model fitting, separately for each evaluation metric, predictor variable and pseudo-absence selection strategy. For reasons of readability, the predictor variables were renamed as followed: Bio4 = Temperature seasonality, Bio10 = Temperature of the warmest quarter, Bio18 = Precipitation of the warmest quarter, Bio19 = Precipitation of the coldest quarter, TWI = Topographical wetness index, HLI = Heat load index.

Pseudo-absence selection approach	Evaluation metric	Predictor variable	Intercept	Estimate	P-value	R-squared
Random	TSS	Bio4	-0.681	1.301	<0.001	0.518
Random	TSS	Bio10	-0.519	1.116	0.001	0.273
Random	TSS	Bio18	0.006	0.267	1	0.009
Random	TSS	Bio19	0.763	-0.94	0.013	0.197
Random	TSS	TWI	0.246	-0.485	1	0.019
Random	TSS	HLI	-0.077	0.412	0.081	0.134
Random	AUC	Bio4	-0.34	0.65	<0.001	0.518
Random	AUC	Bio10	-0.26	0.558	0.001	0.273
Random	AUC	Bio18	0.003	0.133	1	0.009
Random	AUC	Bio19	0.382	-0.47	0.013	0.197
Random	AUC	TWI	0.123	-0.243	1	0.019
Random	AUC	HLI	-0.038	0.206	0.081	0.134
Random	BOYCE	Bio4	-0.532	1.258	0.001	0.282
Random	BOYCE	Bio10	-0.426	1.166	0.027	0.173
Random	BOYCE	Bio18	0.042	0.442	1	0.015
Random	BOYCE	Bio19	0.574	-0.472	1	0.029
Random	BOYCE	TWI	0.278	-0.08	1	0
Random	BOYCE	HLI	0.151	0.209	1	0.02

Pseudo-absence selection approach	Evaluation metric	Predictor variable	Intercept	Estimate	P-value	R-squared
Disk20	TSS	Bio4	-0.481	1.04	<0.001	0.353
Disk20	TSS	Bio10	-0.417	1.004	0.004	0.235
Disk20	TSS	Bio18	0.461	-0.583	0.886	0.048
Disk20	TSS	Bio19	0.335	-0.242	1	0.014
Disk20	TSS	TWI	-0.003	0.791	0.756	0.054
Disk20	TSS	HLI	-0.286	0.884	<0.001	0.655
Disk20	AUC	Bio4	-0.24	0.52	<0.001	0.353
Disk20	AUC	Bio10	-0.208	0.502	0.004	0.235
Disk20	AUC	Bio18	0.231	-0.291	0.887	0.048
Disk20	AUC	Bio19	0.168	-0.121	1	0.014
Disk20	AUC	TWI	-0.001	0.396	0.756	0.054
Disk20	AUC	HLI	-0.143	0.442	<0.001	0.655
Disk20	BOYCE	Bio4	-0.429	1.47	0.001	0.277
Disk20	BOYCE	Bio10	-0.441	1.592	0.005	0.232
Disk20	BOYCE	Bio18	0.188	0.625	1	0.022
Disk20	BOYCE	Bio19	0.691	-0.293	1	0.008
Disk20	BOYCE	TWI	0.439	0.256	1	0.002
Disk20	BOYCE	HLI	0.177	0.613	0.107	0.124

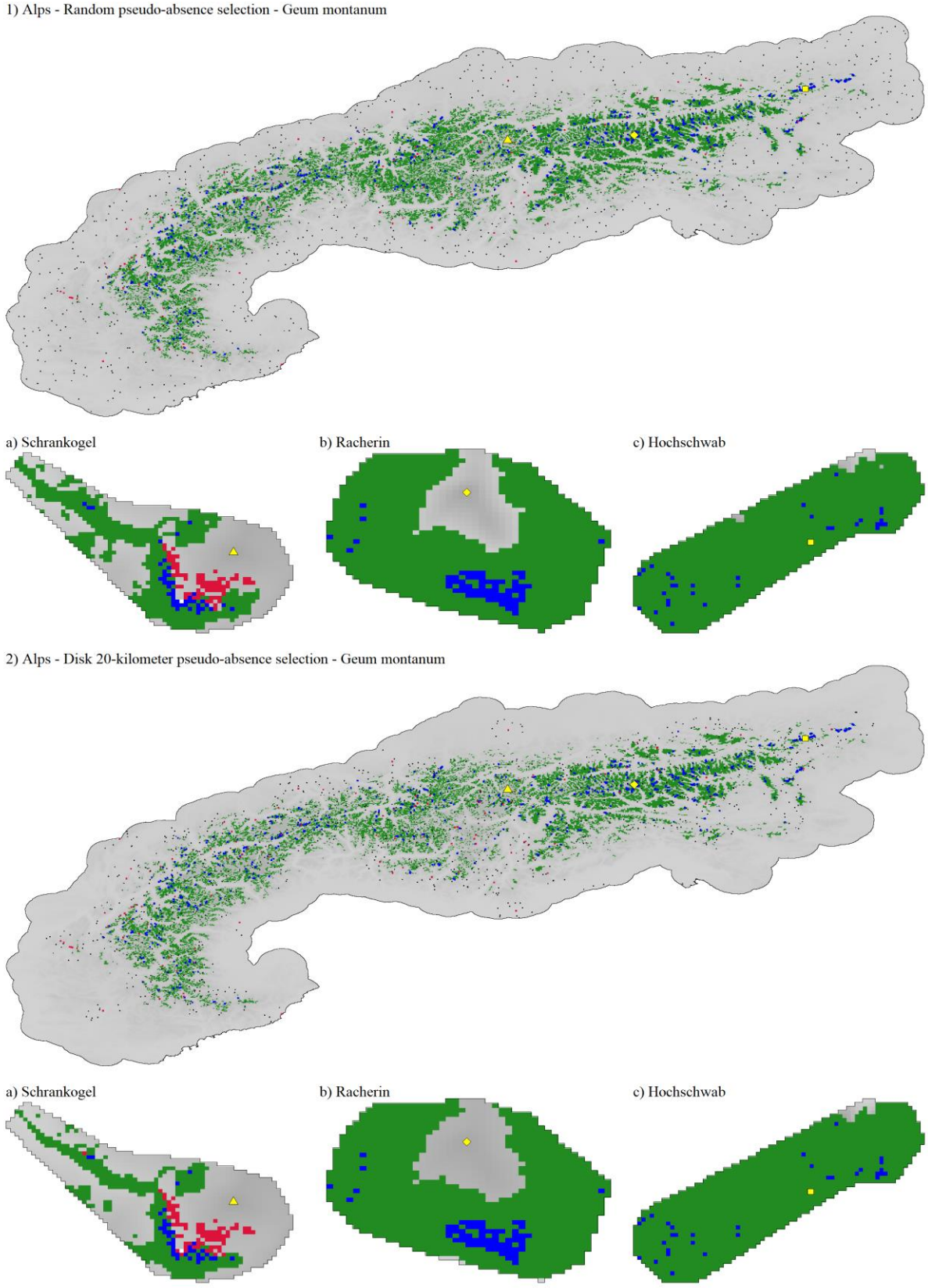

Figure 5: Binary predictions of Geum montanum at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

Discussion

The selection of environmental predictors is a crucial step in SDMs (Fourcade et al. 2018) and should be guided by the environmental requirements of the species (Guisan et al. 1998, Austin 2002, Guisan et al. 2017). Thereby, climatic and topographical predictors are the most commonly used predictors in SDMs (Miller 2010). However, it is well recognized, that the distribution of species is influenced by various factors that operate with varying intensities at different spatial scales (Wiens 1989, Levin 1992). Although climate is the primary driver of species distribution at a large spatial scale (Woodward et al. 1990), the fine scale distribution of alpine plants is shaped by additional factors such as topography, geology, soil type, land use, or biotic interactions (Körner 2003). Understanding how the extent and resolution of an investigation influence the importance of predictor variables remains a critical challenge in SDMs (Araújo and Guisan 2006). In this study, the predictor variable with the greatest influence on SDMs was the mean temperature of the warmest quarter, followed by the precipitation of the warmest quarter. In contrast, topographical predictors such as the heat load index and the topographic wetness index showed the lowest variable importance regardless of the approach of pseudo-absence selection. Given that this study focuses on alpine plant species, and that these species are found in environments characterized by extreme climates (Araújo and Guisan 2006), the high importance of climatic predictors for modelling the species distribution is not surprising. Although fine-scale predictors can improve the predictive accuracy of SDMs calibrated at large extents (Austin and Van Niel 2011), the topographical variables showed a low variable importance. This is clearly demonstrated by projections onto individual mountains which, by and large, distinguish suitable from unsuitable elevational bands without or with little further topographical differentiation. This result appears at odds with the strong effect that topography may have on the fine-scale species distribution in alpine environments (Scherrer and Körner 2011). However, first, the 100 x 100 meters resolution of the models is probably too coarse to detect these topographical patterns, and second, despite microclimatic variation at each elevation, there is a clear frequency distribution with typical climates being much more frequent than extreme ones at each elevation (Scherrer and Körner 2011). The frequency distribution of microclimates affects the distribution of species which are hence most likely to occur where their preferred climates are most frequent. As a corollary, SDM calibrated over a large extent, mainly capture the response of species to the frequency distribution of climates across the landscape. This finding fits the assumption that SDMs calibrated over a large extent mainly identify the general pattern of species distribution, because fine-scale deviations from these coarse patterns are too infrequent to cause a strong imprint on the modelled niche. This is particularly likely with presence-only data because the model cannot use additional information from topographically driven absences to refine projections.

For SDMs with random pseudo-absence selection, the accuracy of the model predictions was high at the extents of the Alps, Hochschwab and Rachering, but significantly lower at Schrankogel for all evaluation metrics. Since the pseudo-absences for the model evaluation with TSS and AUC were

selected randomly over the entire study area for all extents, the commission error should be similar at all spatial extents. Therefore, the low model accuracy at Schrankogel can be ascribed to omission errors with certainty. For SDMs with pseudo-absence selection within a 20-kilometer disk around the species observations the accuracy of the model predictions significantly increased from the Alps to Hochschwab, but significantly decreased from the Alps to Racherin and Schrankogel according to TSS and AUC. Further, the accuracy of the model predictions declined from the Alps to Racherin and significantly declined from the Alps to Hochschwab and Schrankogel according to the Boyce index. Since the pseudo-absences were selected within a 20-kilometer disk around the species presence observations, the commission errors differed for the spatial extent of the Alps and each of the individual mountains. Therefore, it remains uncertain whether the low model accuracy at Racherin and Schrankogel according to TSS and AUC is due to errors of omission or commission. Regarding the Boyce index, I found that the distribution of presences was more consistent with the model predictions across the Alps than at Hochschwab, Racherin and Schrankogel regardless of the approach of pseudo-absence selection. The reason for this is that the predicted probabilities at the individual mountains are less variable than in the Alps. Therefore, only a small range of similar probabilities are predicted on the individual mountains, which is why the Boyce index decreases.

In mountainous areas, environmental gradients occur over short distances and available area decreases with increasing elevation (Beniston 2006). Firstly, this leads to a decrease in species presence observations with increasing elevation, which might be reinforced by decreased sampling effort. Secondly, pseudo-absences are more frequently selected at low compared to high elevations. Therefore, the species response to the environment may not be sufficiently captured at higher elevations, while at lower elevations, the increased number of pseudo-absences may lead to a misspecification of the species niche. For SDMs investigating the distribution of alpine species, this could result in an increase in omission errors towards the lower and upper range margins in general. Compared to SDMs with a random pseudo-absence selection approach, SDMs with a pseudo-absence selection approach within a 20-kilometer buffer around the species observations obtain pseudo-absences with more similar environmental conditions to those of the species presence observations. This can make it more difficult to correctly predict presences, but it also increases the probability that pseudo-absences are selected in suitable habitats. Consequently, this leads to an increase in commission and omission errors, resulting in a lower overall accuracy for SDMs when there is a higher similarity between presences and pseudo-absences. By presenting the results of SDMs with the two different approaches of pseudo-absence selection, I demonstrated once again that the approach of pseudo-absence selection can influence the model output (Chefaoui and Lobo 2008, VanDerWal et al. 2009, Wisz and Guisan 2009, Lobo et al. 2010, Barbet-Massin et al. 2012, Hanberry et al. 2012). Indeed, this applies not only to model calibration, but also to model evaluation when SDMs are evaluated using pseudo-absences instead of true absences in the case of TSS and AUC. Therefore, I reiterate the criticism on the use of presence-

absence evaluation metrics when SDMs are evaluated based on presence and pseudo-absence observations (Jiménez-Valverde 2012, Leroy et al. 2018). Instead, I recommend the use of presence only metrics. In addition to the sensitivity of the model accuracy to the approach of pseudo-absence selection and the used evaluation metric, the results suggest that the accuracy can differ with the spatial extent of model evaluation. However, since this change is not linear, I must reject the hypothesis that model accuracy generally decreases when evaluating models at extents smaller than those on which they were fitted.

The accuracy of the model predictions therefore seems to depend not necessarily on the spatial extent, but on specific characteristics of the individual mountains. Among the three individual mountains, Hochschwab is the lowest and the easternmost, Schrankogel is the highest and the westernmost and Racherin is intermediate in height and located between the other two mountains. Therefore, each species experiences different environmental conditions on each of the individual mountains, which may match those the species experiences across its alpine distribution to a different degree. At range margins, populations may occupy habitats with environmental conditions distinct from those they experience at the core of their distribution (Braunisch et al. 2008). This may apply not only to geographical but also to environmental range margins. Thus, the difference in model accuracy between the extent of the Alps and the individual mountains could be related to the difference in environmental conditions a species experiences across the Alps, compared to those it experiences at each of the individual mountains. For both approaches of pseudo-absence selection, the results indeed show a significant relationship between the difference in model accuracy and the similarity of environmental conditions the species is exposed to with respect to both temperature seasonality and the temperature of the warmest quarter for all evaluation metrics. In general, species occur under conditions most similar to those found in the Alps on Hochschwab, less similar on Racherin, and least similar on Schrankogel. Put differently, on Schrankogel species occur under conditions which are rather extreme as compared to the overall Alpine distribution. In the case of geographical range margins it has been shown that the regional models appear to outperform global models (Vale et al. 2014), and I assume that I observe a similar effect here, i.e. that the environmentally marginal situation of Schrankogel results in the general drop of projection accuracy there. I see this as a clear confirmation of the hypothesis that models will lose accuracy at smaller extents the more dissimilar the local conditions are from the average across larger areas. I assume this to be true even if the similarity in the most important predictor, temperature of the warmest quarter, was not consistently the one correlated closest to the change in model accuracy between the Alps and the individual mountains.

For applicability in nature conservation, SDMs should be able to distinguish between suitable and unsuitable habitat, have a fine spatial resolution and be applicable at local extents (Oliveira et al. 2021). In this study I show that SDMs calibrated at large spatial extents do not necessarily fit the distribution at smaller spatial extents, such as nature conservation areas. This raises the question of the appropriate

spatial extent for model calibration. It has been shown that calibrating SDMs at the regional extent is a valid approach if the aim is to predict the local distribution at the current point in time (Lyet et al. 2013). Additionally, it has been suggested that models calibrated at large spatial extents are less accurate in capturing the fine scale distribution of species compared to models calibrated at smaller extents (Mateo et al. 2019). Thus, if the aim of SDMs is to guide protected area design one might argue they should probably be calibrated at smaller spatial extents, offering more detailed insight into the fine-scale distribution of a species (Gogol-Prokurat 2011, Vale et al. 2014, Oliveira et al. 2021). However, SDMs calibrated over a restricted geographical extent are less easily applied to future environmental conditions (Guisan et al. 2017), because they are less likely to cover the entire range of both current and future conditions. In a changing climate, selecting model extents for conservation purposes must hence consider this trade-off between covering a broad array of conditions, or long gradients, and the model's ability to sufficiently resolve the habitat suitability on a regional extent.

Overall, I show that the accuracy of SDMs calibrated over large geographical extents can substantially differ when making projections on smaller subsets of the larger extent. This seems to be particularly likely where the distribution of species in these subsets is restricted to rather marginal parts of the predictor ranges, which they occupy across the large extent. Moreover, I demonstrate once again that the approach of pseudo-absence selection can have a tremendous effect on SDMs during both calibration and evaluation. Therefore, I recommend an evaluation using presence-only evaluation metrics. For designing nature conservation areas or for studying the fine scale distribution of species, I recommend that the evaluation of model predictions over a large spatial extent should be treated with caution as they do not necessarily reflect the model accuracy on smaller extents. If the aim is to predict local species distribution to designate nature conservation areas at the current point in time, I propose that SDMs should be calibrated at regional extents with high spatial resolution.

Schlussfolgerungen

In Anbetracht der bevorstehenden Biodiversitätskriese (Pereira et al. 2010) können Verbreitungsmodelle ein wirksames Instrument im Naturschutz darstellen (Guisan et al. 2013), indem sie zur Einrichtung von geeigneten Naturschutzgebieten beitragen (Tulloch et al. 2016). Obwohl Verbreitungsmodelle bereits starke Verbesserung in ihrer Methodik erfahren haben (Guisan and Thuiller 2005) und zunehmend Anwendung finden (Lobo et al. 2010, Guisan et al. 2013), bleiben methodische Herausforderungen bestehen (Austin 2007). Eine grundlegende Annahme von Verbreitungsmodellen ist, dass die Artvorkommen die Umweltansprüche einer Art umfassend widerspiegeln (Guisan et al. 2017). In der Realität ist dies jedoch nicht immer der Fall, insbesondere dann wenn die Artvorkommen aus Datenbanken stammen (Graham et al. 2004). Aufgrund einer opportunistischen Datenaufnahme kann es dazu kommen, dass Umweltgradienten nicht umfassend beprobt werden. Somit kann es notwendig sein, zusätzliche Daten über Artvorkommen an den Extremen von Umweltgradienten zu erheben (Mohler 1983). In dieser Studie haben wir Verbreitungsmodelle auf der Basis von Artvorkommen aus GBIF (GBIF.org 2024) und der österreichischen Vegetationsdatenbank (Willner et al. 2012) kalibriert. Die Artvorkommen aus GBIF umfassen dabei die gesamten Alpen, während die Artvorkommen aus der österreichischen Vegetationsdatenbank auf Österreich beschränkt sind. Dadurch kam es zu räumlicher Autokorrelation, was zu einer erhöhten prädizierten Vorkommenswahrscheinlichkeit in den Ostalpen geführt hat. Aus diesem Grund ist es wichtig, die räumliche Autokorrelation der Artvorkommen zu korrigieren (Araújo and Guisan 2006). Des Weiteren sollten Modelprädiktionen anhand von unabhängigen Artbeobachtungen evaluiert werden (Guisan et al. 2017). Während die Artbeobachtungen auf den einzelnen Bergen diesem Kriterium entsprachen, wurden die Modellprädiktionen auf der räumlichen Ebene der Alpen anhand der Artbeobachtungen evaluiert, welche bereits zum Kalibrieren der Verbreitungsmodelle verwendet wurden. Dies könnte zu einer ungleichen Bewertung der verschiedenen räumlichen Ebenen geführt, und somit zu einer vergleichsweise schlechteren Bewertung auf den einzelnen Berge beigetragen haben. In dieser Studie konnte gezeigt werden, dass die Modellgenauigkeit vom Ansatz der Pseudo-Absenzauswahl und den verschiedenen Evaluierungsmetriken abhängt. Pseudo-Absenzen suggerieren etwas zu sein was sie nicht sind, nämlich wahre Absenzen (Barry and Elith 2006). Da wahre Absenzen nur sehr schwer zu beobachten sind, werden Verbreitungsmodelle weiterhin oft mithilfe von Pseudo-Absenzen kalibriert und evaluiert werden. Es ist jedoch wichtig zu hinterfragen, in welchem Gebiet Pseudo-Absenzen ausgewählt werden und welche Konsequenzen dies für die Kalibrierung und Evaluierung von Verbreitungsmodellen hat. Die Modellqualität sinkt im Allgemeinen, je ähnlicher die Umweltbedingungen von Präsenzen und Pseudo-Absenzen sind (Chefaoui and Lobo 2008). Um eine Vergleichbarkeit zwischen Verbreitungsmodellen zu gewährleisten, könnte beispielsweise die Ähnlichkeit zwischen Präsenzen und Pseudo-Absenzen bei der Evaluation berücksichtigt werden. Weiterhin könnte untersucht werden, ob großräumige oder kleinräumige Verbreitungsmodelle genauere

Vorhersagen für kleinräumige Gebiete liefern. Hierfür könnten Verbreitungsmodelle mit unterschiedlichem räumlichen Ausmaß kalibriert und auf demselben kleinräumigen Gebiet evaluiert werden.

Literature

Afkhami, M. E., P. J. McIntyre, and S. Y. Strauss. 2014. Mutualist-mediated effects on species' range limits across large geographic scales. Ecology Letters **17**:1265-1273.

Allouche, O., A. Tsoar, and R. Kadmon. 2006. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology **43**:1223-1232.

Anderson, R. P., A. T. Peterson, and M. Gómez-Laverde. 2002. Using niche-based GIS modeling to test geographic predictions of competitive exclusion and competitive release in South American pocket mice. Oikos **98**:3-16.

Araújo, M. B., and A. Guisan. 2006. Five (or so) challenges for species distribution modelling. Journal of Biogeography **33**:1677-1688.

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography **16**:743-753.

Austin, M. 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. Ecological modelling **200**:1-19.

Austin, M. P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecological modelling **157**:101-118.

Austin, M. P., and I. Noy-Meir. 1971. The Problem of Non-Linearity in Ordination: Experiments with Two-Gradient Models. The Journal of Ecology **59**:763.

Austin, M. P., and K. P. Van Niel. 2011. Impact of landscape predictors on climate change modelling of species distributions: a case study with Eucalyptus fastigata in southern New South Wales, Australia. Journal of Biogeography **38**:9-19.

Barbet-Massin, M., F. Jiguet, C. H. Albert, and W. Thuiller. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? Methods in Ecology and Evolution **3**:327-338.

Barry, S., and J. Elith. 2006. Error and uncertainty in habitat models. Journal of Applied Ecology **43**:413-423.

Barve, N., V. Barve, A. Jiménez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberón, and F. Villalobos. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological modelling **222**:1810-1819.

Beniston, M. 2006. Mountain Weather and Climate: A General Overview and a Focus on Climatic Change in the Alps. Hydrobiologia **562**:3-16.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological modelling **157**:281-300.

Braunisch, V., K. Bollmann, R. F. Graf, and A. H. Hirzel. 2008. Living on the edge—modelling habitat suitability for species at the edge of their fundamental niche. Ecological modelling **214**:153-167.

Brown, J. H., and M. V. Lomolino. 1998. Biogeography. Sinuer Associates Publishers.

Ceballos, G., P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, and T. M. Palmer. 2015. Accelerated modern human–induced species losses: Entering the sixth mass extinction. Science advances **1**:e1400253.

Chamberlain, S., K. Ram, V. Barve, D. Mcglinn, and M. S. Chamberlain. 2017. Package 'rgbif'. Interface to the Global Biodiversity Information Facility 'API **5**:0.9.

Charbonnel, A., P. Lambert, G. Lassalle, E. Quinton, A. Guisan, L. Mas, G. Paquignon, M. Lecomte, and M.-L. Acolas. 2023. Developing species distribution models for critically endangered species using participatory data: The European sturgeon marine habitat suitability. Estuarine, Coastal and Shelf Science **280**:108136.

Chase, J. M., and M. A. Leibold. 2009. Ecological niches: linking classical and contemporary approaches. University of Chicago Press.

Chefaoui, R. M., and J. M. Lobo. 2008. Assessing the effects of pseudo-absences on predictive distribution model performance. Ecological modelling **210**:478-486.

Conrad, O., B. Bechtel, M. Bock, H. Dietrich, E. Fischer, L. Gerlitz, J. Wehberg, V. Wichmann, and J. Böhner. 2015. System for Automated Geoscientific Analyses (SAGA) v. 2.1.4. Geoscientific Model Development **8**:1991-2007.

D'Amen, M., H. K. Mod, N. J. Gotelli, and A. Guisan. 2018. Disentangling biotic interactions, environmental filters, and dispersal limitation as drivers of species co-occurrence. Ecography **41**:1233-1244.

Di Cola, V., O. Broennimann, B. Petitpierre, F. T. Breiner, M. D'Amen, C. Randin, R. Engler, J. Pottier, D. Pio, A. Dubuis, L. Pellissier, R. G. Mateo, W. Hordijk, N. Salamin, and A. Guisan. 2017. ecospat: an R package to support spatial analyses and modeling of species niches and distributions. Ecography **40**:774-787.

Dullinger, S., A. Gattringer, W. Thuiller, D. Moser, N. E. Zimmermann, A. Guisan, W. Willner, C. Plutzar, M. Leitner, T. Mang, M. Caccianiga, T. Dirnböck, S. Ertl, A. Fischer, J. Lenoir, J.-C. Svenning, A. Psomas, D. R. Schmatz, U. Silc, P. Vittoz, and K. Hülber. 2012. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature Climate Change **2**:619-622.

Elith, J. 2009. Unknown article.

Elith, J., C. H. Graham, R. P. Anderson, M. Dudík, S. Ferrier, A. Guisan, R. J. Hijmans, F. Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G. Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. McC. M. Overton, A. Townsend Peterson, S. J. Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberón, S. Williams, M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography **29**:129-151.

Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics **40**:677-697.

Ellenberg, H. 1974. Zeigerwerte der Gefasspflanzen Mitteleuropas= Indicator values of vascular plants in Central Europe.

Engler, R., A. Guisan, and L. Rechsteiner. 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. Journal of Applied Ecology **41**:263-274.

Esselman, P. C., and J. D. Allan. 2011. Application of species distribution models and conservation planning software to the design of a reserve network for the riverine fishes of northeastern Mesoamerica. Freshwater Biology **56**:71-88.

Evans, J. S., and K. Ram. 2015. Package 'spatialEco'. R Packag.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation **24**:38-49.

Fourcade, Y., A. G. Besnard, and J. Secondi. 2018. Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. Global Ecology and Biogeography **27**:245-256.

GBIF.org. 2024. Derived dataset GBIF.org (19 January 2024) Filtered export of GBIF occurrence data https://doi.org/10.15468/dd.aavkzx.

Gogol-Prokurat, M. 2011. Predicting habitat suitability for rare plants at local spatial scales using a species distribution model. Ecological Applications **21**:33-47.

Goldberg, D. E., and A. M. Barton. 1992. Patterns and Consequences of Interspecific Competition in Natural Communities: A Review of Field Experiments with Plants. The American Naturalist **139**:771-801.

Graham, C. H., S. Ferrier, F. Huettman, C. Moritz, and A. T. Peterson. 2004. New developments in museum-based informatics and applications in biodiversity analysis. Trends in ecology & evolution **19**:497-503.

Guisan, A., J.-P. Theurillat, and F. Kienast. 1998. Predicting the potential distribution of plant species in an alpine environment. Journal of Vegetation Science **9**:65-74.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters **8**:993-1009.

Guisan, A., W. Thuiller, and N. E. Zimmermann. 2017. Habitat suitability and distribution models: with applications in R. Cambridge University Press.

Guisan, A., R. Tingley, J. B. Baumgartner, I. Naujokaitis-Lewis, P. R. Sutcliffe, A. I. T. Tulloch, T. J. Regan, L. Brotons, E. McDonald-Madden, C. Mantyka-Pringle, T. G. Martin, J. R. Rhodes, R. Maggini, S. A. Setterfield, J. Elith, M. W. Schwartz, B. A. Wintle, O. Broennimann, M. Austin, S. Ferrier, M. R. Kearney, H. P. Possingham, and Y. M. Buckley. 2013. Predicting species distributions for conservation decisions. Ecology Letters **16**:1424-1435.

Guisan, A., and N. E. Zimmermann. 2000. Predictive habitat distribution models in ecology. Ecological modelling **135**:147-186.

Hamner, B., M. Frasco, and E. LeDell. 2018. Package 'Metrics'. R Foundation for Statistical Computing.

Hanberry, B. B., H. S. He, and B. J. Palik. 2012. Pseudoabsence Generation Strategies for Species Distribution Models. PLoS ONE **7**:e44486.

Hector, A., S. Von Felten, Y. Hautier, M. Weilenmann, and H. Bruelheide. 2012. Effects of Dominance and Diversity on Productivity along Ellenberg's Experimental Water Table Gradients. PLoS ONE **7**:e43358.

Hernandez, P. A., C. H. Graham, L. L. Master, and D. L. Albert. 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography **29**:773-785.

Hirzel, A. H., G. Le Lay, V. Helfer, C. Randin, and A. Guisan. 2006. Evaluating the ability of habitat suitability models to predict species presences. Ecological modelling **199**:142-152.

Hutchinson, G. E. 1957. Cold spring harbor symposia on quantitative biology. (No Title) **22**:415.

Jiménez-Valverde, A. 2012. Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. Global Ecology and Biogeography **21**:498-507.

Karger, D. N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-Auza, N. E. Zimmermann, H. P. Linder, and M. Kessler. 2017. Climatologies at high resolution for the earth's land surface areas. Scientific Data **4**:170122.

Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters **12**:334-350.

Körner, C. 2003. Alpine Plant Life.

Landolt, E., B. Bäumler, A. Ehrhardt, O. Hegg, F. Klötzli, W. Lämmler, M. Nobis, K. Rudmann-Maurer, F. Schweingruber, and J. Theurillat. 2010. Flora indicativa: Okologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. Haupt.

Leathwick, J. R., and M. P. Austin. 2001. COMPETITIVE INTERACTIONS BETWEEN TREE SPECIES IN NEW ZEALAND'S OLD-GROWTH INDIGENOUS FORESTS. Ecology **82**:2560-2573.

Leroy, B., R. Delsol, B. Hugueny, C. N. Meynard, C. Barhoumi, M. Barbet-Massin, and C. Bellard. 2018. Without quality presence-absence data, discrimination metrics such as TSS can be misleading measures of model performance. Journal of Biogeography **45**:1994-2002.

Levin, S. A. 1992. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. Ecology **73**:1943-1967.

Liu, C., M. White, and G. Newell. 2013. Selecting thresholds for the prediction of species occurrence with presence-only data. Journal of Biogeography **40**:778-789.

Lobo, J. M., A. Jiménez-Valverde, and J. Hortal. 2010. The uncertain nature of absences and their importance in species distribution modelling. Ecography **33**:103-114.

Lobo, J. M., A. Jiménez-Valverde, and R. Real. 2008. AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography **17**:145-151.

Lyet, A., W. Thuiller, M. Cheylan, and A. Besnard. 2013. Fine-scale regional distribution modelling of rare and threatened species: bridging GIS Tools and conservation in practice. Diversity and Distributions **19**:651-663.

Mackey, B. G., and D. B. Lindenmayer. 2001. Towards a hierarchical framework for modelling the spatial distribution of animals. Journal of Biogeography **28**:1147-1166.

Mateo, R. G., A. Gastón, M. J. Aroca-Fernández, O. Broennimann, A. Guisan, S. Saura, and J. I. García-Viñas. 2019. Hierarchical species distribution models in support of vegetation conservation at the landscape scale. Journal of Vegetation Science **30**:386-396.

Mayr, E. 1996. What is a Species, and What is Not? Philosophy of Science **63**:262-277.

Miller, J. 2010. Species distribution modeling. Geography Compass **4**:490-509.

Mohler, C. 1983. Effect of sampling pattern on estimation of species distributions along gradients. Vegetatio **54**:97-102.

Oliveira, M., W. Tomas, N. Guedes, A. Peterson, J. Szabo, A. S. Júnior, A. Camilo, C. Padovani, and L. Garcia. 2021. The relationship between scale and predictor variables in species distribution models applied to conservation. Biodiversity and Conservation **30**:1971-1990.

Pearman, P. B., A. Guisan, O. Broennimann, and C. F. Randin. 2008. Niche dynamics in space and time. Trends in ecology & evolution **23**:149-158.

Pellissier, L., K. Anne Bråthen, J. Pottier, C. F. Randin, P. Vittoz, A. Dubuis, N. G. Yoccoz, T. Alm, N. E. Zimmermann, and A. Guisan. 2010. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. Ecography **33**:1004-1014.

Pereira, H. M., P. W. Leadley, V. Proença, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarrés, M. B. Araújo, P. Balvanera, R. Biggs, W. W. L. Cheung, L. Chini, H. D. Cooper, E. L. Gilman, S. Guénette, G. C. Hurtt, H. P. Huntington, G. M. Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U. R. Sumaila, and M. Walpole. 2010. Scenarios for Global Biodiversity in the 21st Century. Science **330**:1496-1501.

Pulliam, H. R. 2000. On the relationship between niche and distribution. Ecology Letters **3**:349-361.

Pyšek, P., P. E. Hulme, D. Simberloff, S. Bacher, T. M. Blackburn, J. T. Carlton, W. Dawson, F. Essl, L. C. Foxcroft, P. Genovesi, J. M. Jeschke, I. Kühn, A. M. Liebhold, N. E. Mandrak, L. A. Meyerson, A. Pauchard, J. Pergl, H. E. Roy, H. Seebens, M. Van Kleunen, M. Vilà, M. J. Wingfield, and D. M. Richardson. 2020. Scientists' warning on invasive alien species. Biological Reviews **95**:1511-1534.

R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www. R-project. org/.

Randin, C. F., T. Dirnböck, S. Dullinger, N. E. Zimmermann, M. Zappa, and A. Guisan. 2006. Are niche-based species distribution models transferable in space? Journal of Biogeography **33**:1689-1703.

Scherrer, D., and C. Körner. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. Journal of Biogeography **38**:406-416.

Schluter, D. 2001. Ecology and the origin of species. Trends in ecology & evolution **16**:372-380.

Soberon, J., and A. T. Peterson. 2005. Interpretation of Models of Fundamental Ecological Niches and Species' Distributional Areas. Biodiversity Informatics **2**.

Thuiller, W., D. Georges, R. Engler, F. Breiner, M. D. Georges, and C. W. Thuiller. 2016. Package 'biomod2'. Species distribution modeling within an ensemble forecasting framework.

Tulloch, A. I., P. Sutcliffe, I. Naujokaitis-Lewis, R. Tingley, L. Brotons, K. M. P. Ferraz, H. Possingham, A. Guisan, and J. R. Rhodes. 2016. Conservation planners tend to ignore improved accuracy of modelled species distributions to focus on multiple threats and ecological processes. Biological conservation **199**:157-171.

Vale, C. G., P. Tarroso, and J. C. Brito. 2014. Predicting species distribution at range margins: testing the effects of study area extent, resolution and threshold selection in the Sahara-Sahel transition zone. Diversity and Distributions **20**:20-33.

VanDerWal, J., L. P. Shoo, C. Graham, and S. E. Williams. 2009. Selecting pseudo-absence data for presence-only distribution modeling: how far should you stray from what you know? Ecological modelling **220**:589-594.

Wessely, J., A. Gattringer, F. Guillaume, K. Hülber, G. Klonner, D. Moser, and S. Dullinger. 2022. Climate warming may increase the frequency of cold-adapted haplotypes in alpine plants. Nature Climate Change **12**:77-82.

Wiens, J. A. 1989. Spatial Scaling in Ecology. Functional Ecology **3**:385.

Willner, W., C. Berg, and P. Heiselmayer. 2012. Austrian vegetation database. Biodiversity & Ecology **4**:10.7809.

Willner, W., R. Di Pietro, and E. Bergmeier. 2009. Phytogeographical evidence for post-glacial dispersal limitation of European beech forest species. Ecography **32**:1011-1018.

Wisz, M. S., and A. Guisan. 2009. Do pseudo-absence selection strategies influence species distribution models and their predictions? An information-theoretic approach based on simulated data. BMC Ecology **9**:8.

Woodward, F. I., G. E. Fogg, and U. Heber. 1990. The impact of low temperatures in controlling the geographical distribution of plants. Philosophical Transactions of the Royal Society of London. B, Biological Sciences **326**:585-593.

Zizka, A., D. Silvestro, T. Andermann, J. Azevedo, C. Duarte Ritter, D. Edler, H. Farooq, A. Herdean, M. Ariza, R. Scharn, S. Svantesson, N. Wengström, V. Zizka, and A. Antonelli. 2019. <scp>CoordinateCleaner</scp> : Standardized cleaning of occurrence records from biological collection databases. Methods in Ecology and Evolution **10**:744-751.

Appendix

List of tables

List of figures

Table 2: Number of observations at the spatial scale of the Alps, Hochschwab, Racherin and Schrankogel for each species.

Species	Alps	Hochschwab	Racherin	Schrankogel
Agrostis alpina	427	70	22	141
Anthoxanthum alpinum	639	49	66	229
Bartsia alpina	1495	62	53	62
Campanula scheuchzeri	1472	83	61	211
Carex sempervirens	862	92	41	125
Geum montanum	1102	32	64	118
Homogyne alpina	1387	24	29	157
Leontodon hispidus	2963	32	40	104
Mutellina adonidifolia	392	50	23	138
Myosotis alpestris	632	42	43	114
Persicaria vivipara	1252	120	63	188
Poa alpina	1221	92	39	223
Potentilla aurea	1160	56	63	192
Selaginella selaginoides	742	82	23	68
Thymus praecox subsp. polytrichus	531	42	40	52
Vaccinium vitis idaea	1622	41	30	106

Table 3: Maximum intercorrelation between the predictors for all species in SDMs with both pseudo-absence approaches.

	Bio 10	Bio 18	Bio 19	HLI	TWI
Bio 4	0,615	0,465	0,618	0,092	0,231
Bio 10		0,831	0,478	0,124	0,537
Bio 18			0,663	0,137	0,467
Bio 19				0,141	0,221
HLI					0,106

Table 4: Results of the TukeyHSD tests showing differences in model accuracy between the spatial extent of the Alps and each individual mountain for both approaches of pseudo-absence selection and every evaluation metric separately.

	Pseudo-absence selection approach	Evaluation Metric	Difference in mean	Adjusted P-value
Hochschwab	Random	TSS	0.076	0.985
Racherin	Random	TSS	0.020	0.529
Schrankogel	Random	TSS	-0.510	> 0.001
Hochschwab	Random	AUC	0.038	0.985
Racherin	Random	AUC	0.010	0.529
Schrankogel	Random	AUC	-0.255	> 0.001
Hochschwab	Random	Boyce index	-0.226	0.633
Racherin	Random	Boyce index	-0.139	0.222
Schrankogel	Random	Boyce index	-0.563	> 0.001

	Pseudo-absence selection approach	Evaluation Metric	Difference in mean	Adjusted P-value
Hochschwab	Disk 20-kilometer	TSS	0.221	> 0.001
Racherin	Disk 20-kilometer	TSS	-0.257	> 0.001
Schrankogel	Disk 20-kilometer	TSS	-0.454	> 0.001
Hochschwab	Disk 20-kilometer	AUC	0.110	> 0.001
Racherin	Disk 20-kilometer	AUC	-0.129	> 0.001
Schrankogel	Disk 20-kilometer	AUC	-0.227	> 0.001
Hochschwab	Disk 20-kilometer	Boyce index	-0.280	0.008
Racherin	Disk 20-kilometer	Boyce index	-0.447	0.174
Schrankogel	Disk 20-kilometer	Boyce index	-0.837	> 0.001

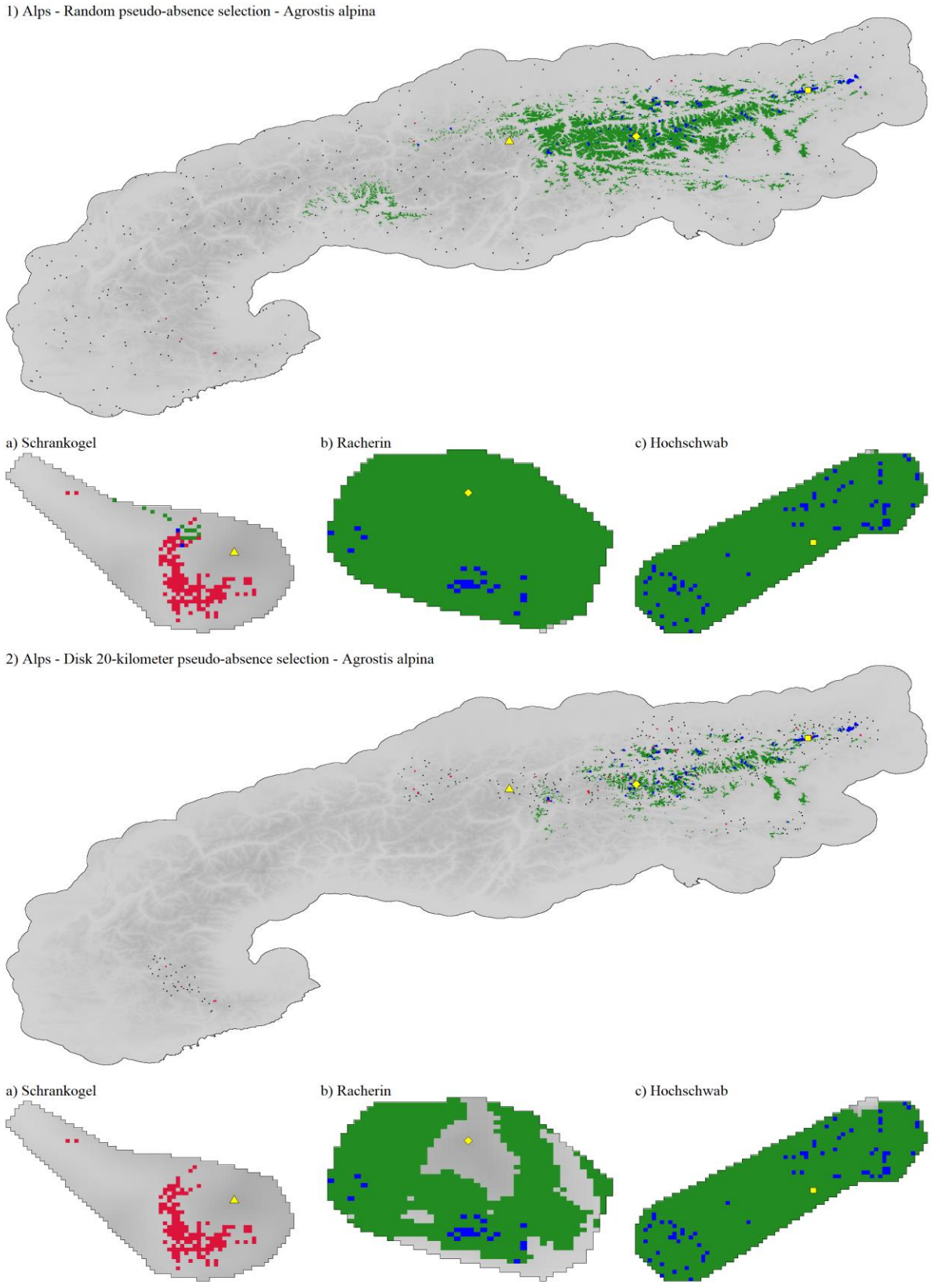

Figure 6: Binary predictions of Agrostis alpina at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

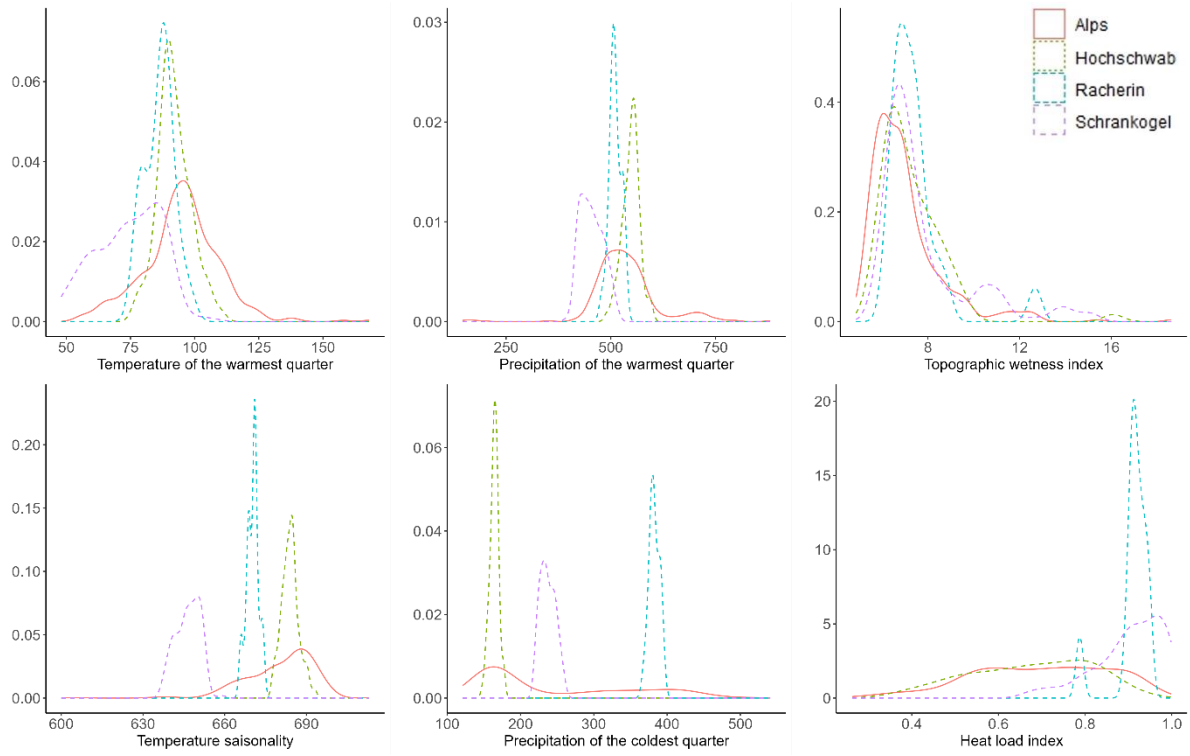

Figure 7: Density distribution of predictor variables of the presence observations of Agrostis alpina across the Alps and each mountain.

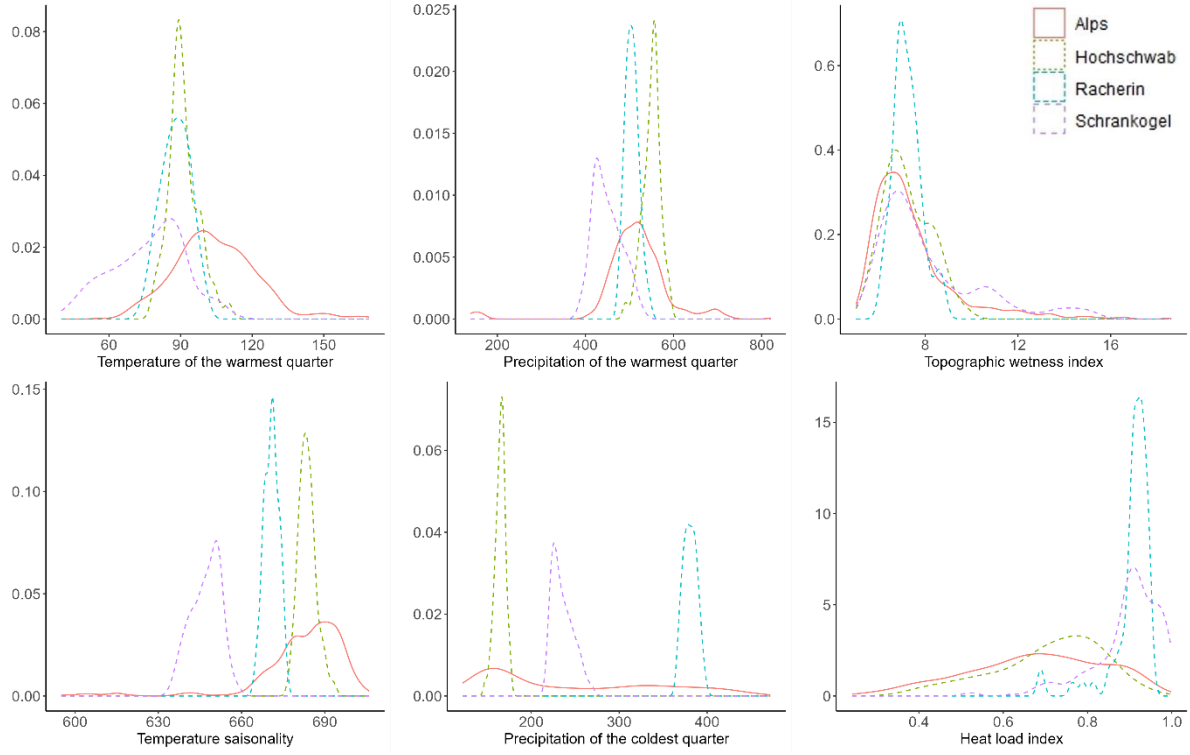

Figure 8: Density distribution of predictor variables of the presence observations of Anthoxanthum alpinum across the Alps and each mountain.

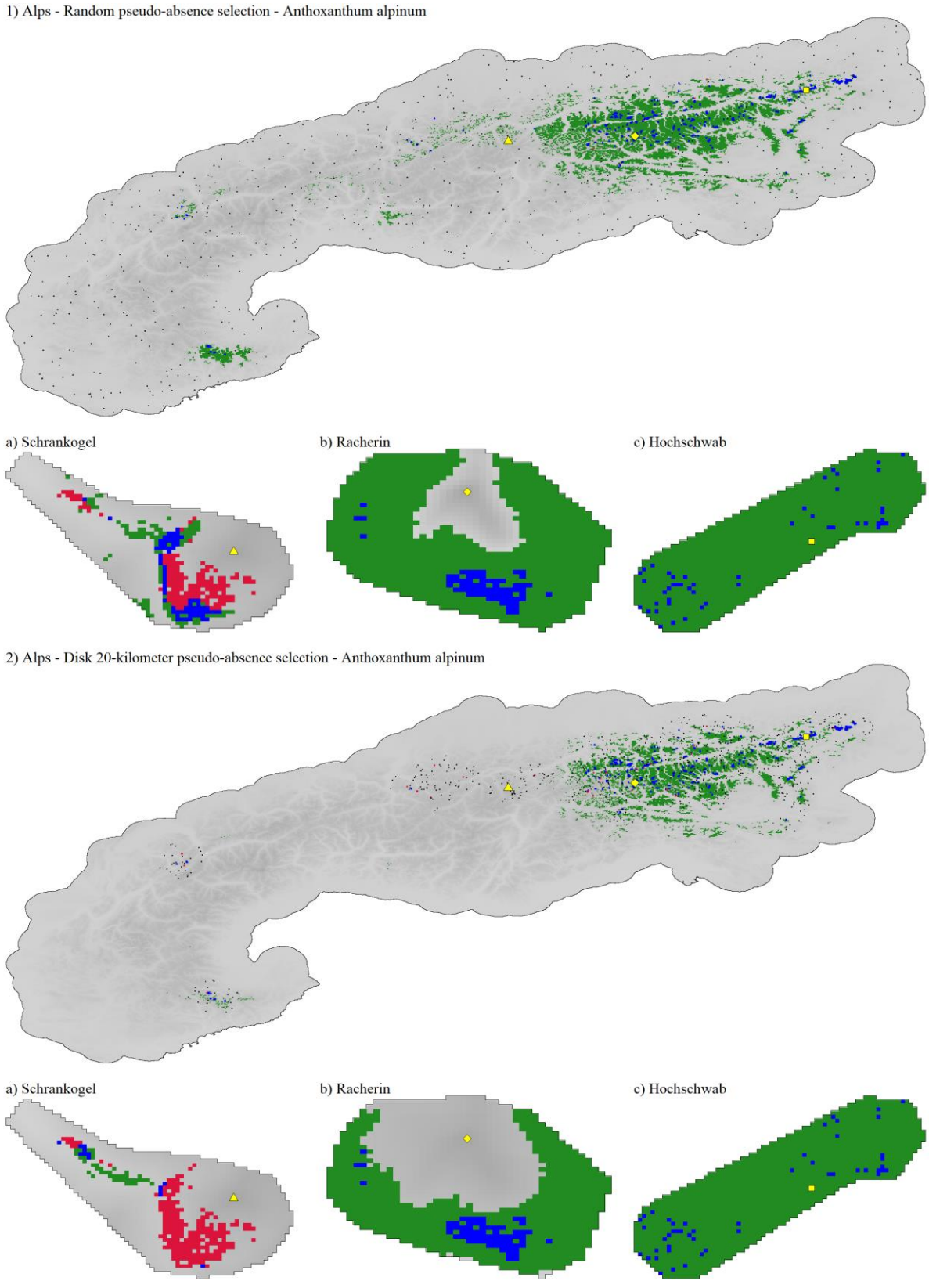

Figure 9: Binary predictions of Anthoxanthum alpinum at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

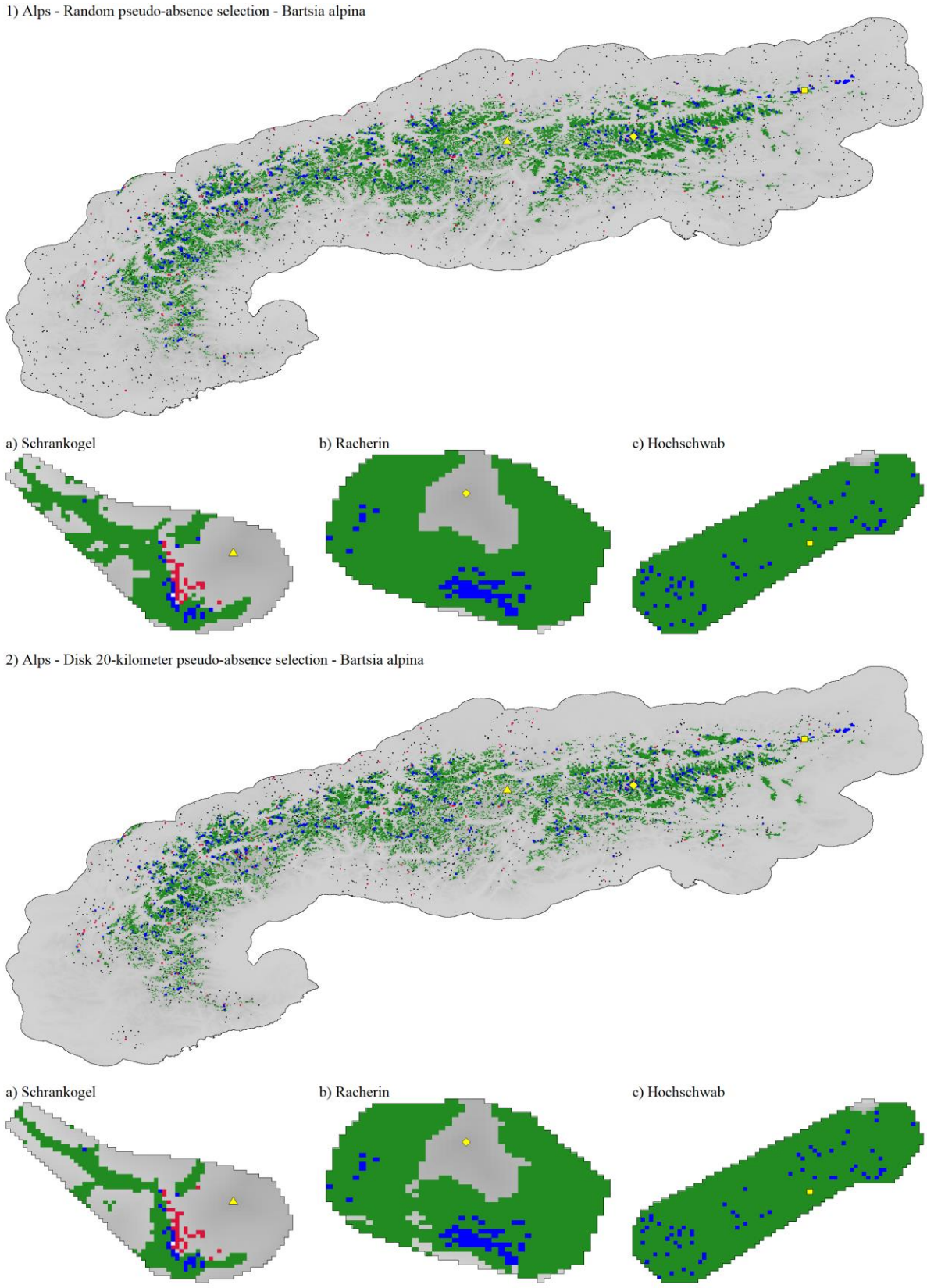

Figure 10: Binary predictions of Bartsia alpina at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

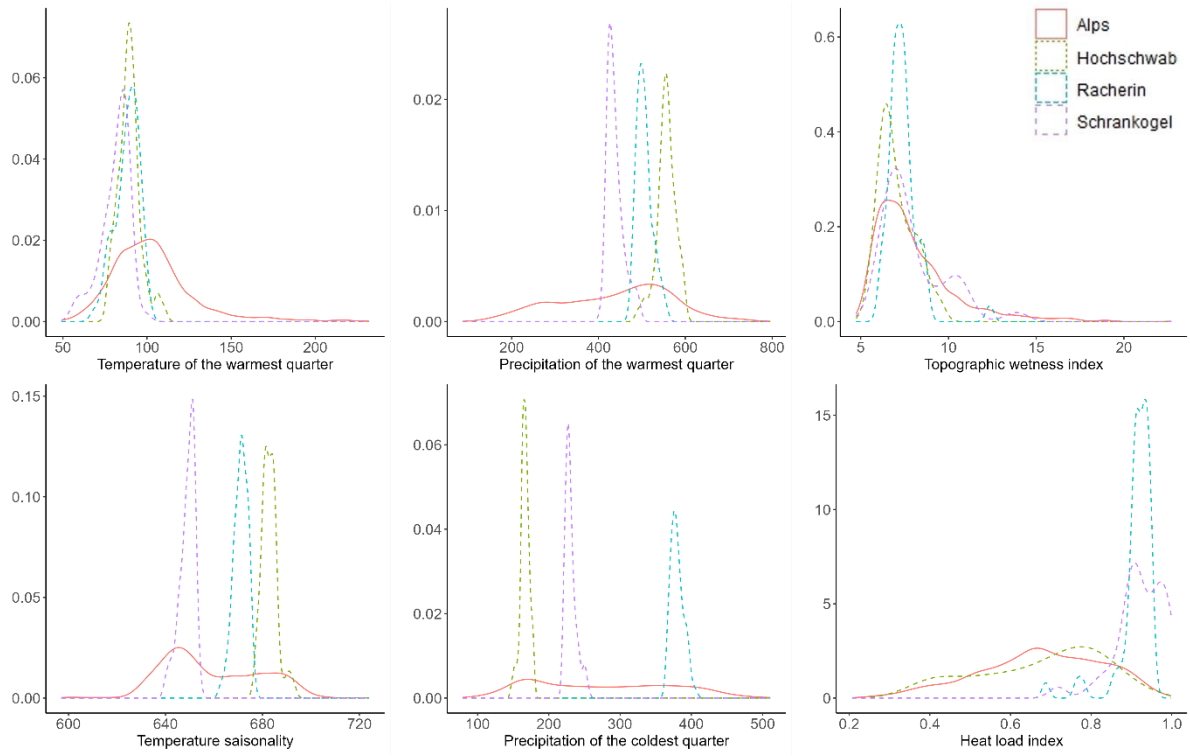

Figure 11: Density distribution of predictor variables of the presence observations of Bartsia alpina across the Alps and each mountain.

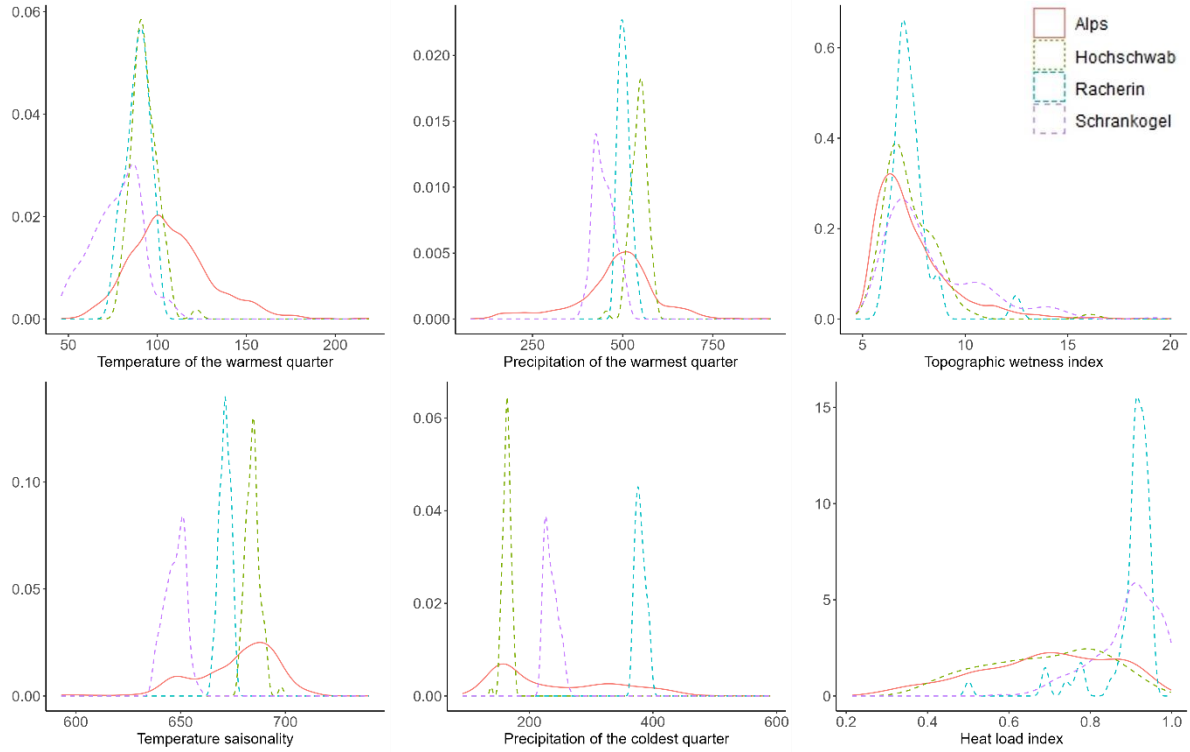

Figure 12: Density distribution of predictor variables of the presence observations of Campanula scheuchzeri across the Alps and each mountain.

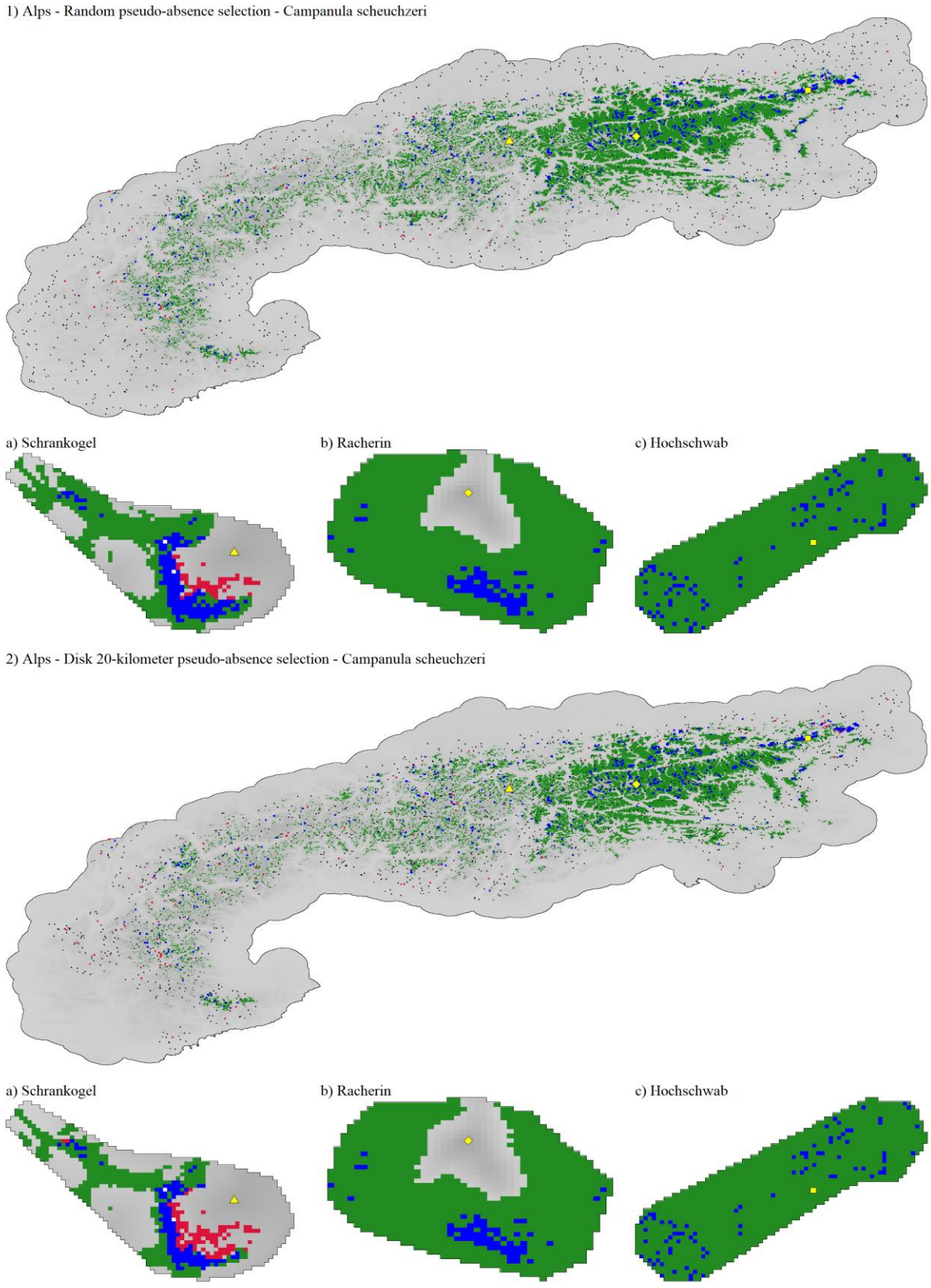

Figure 13: Binary predictions of Campanula scheuchzeri at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

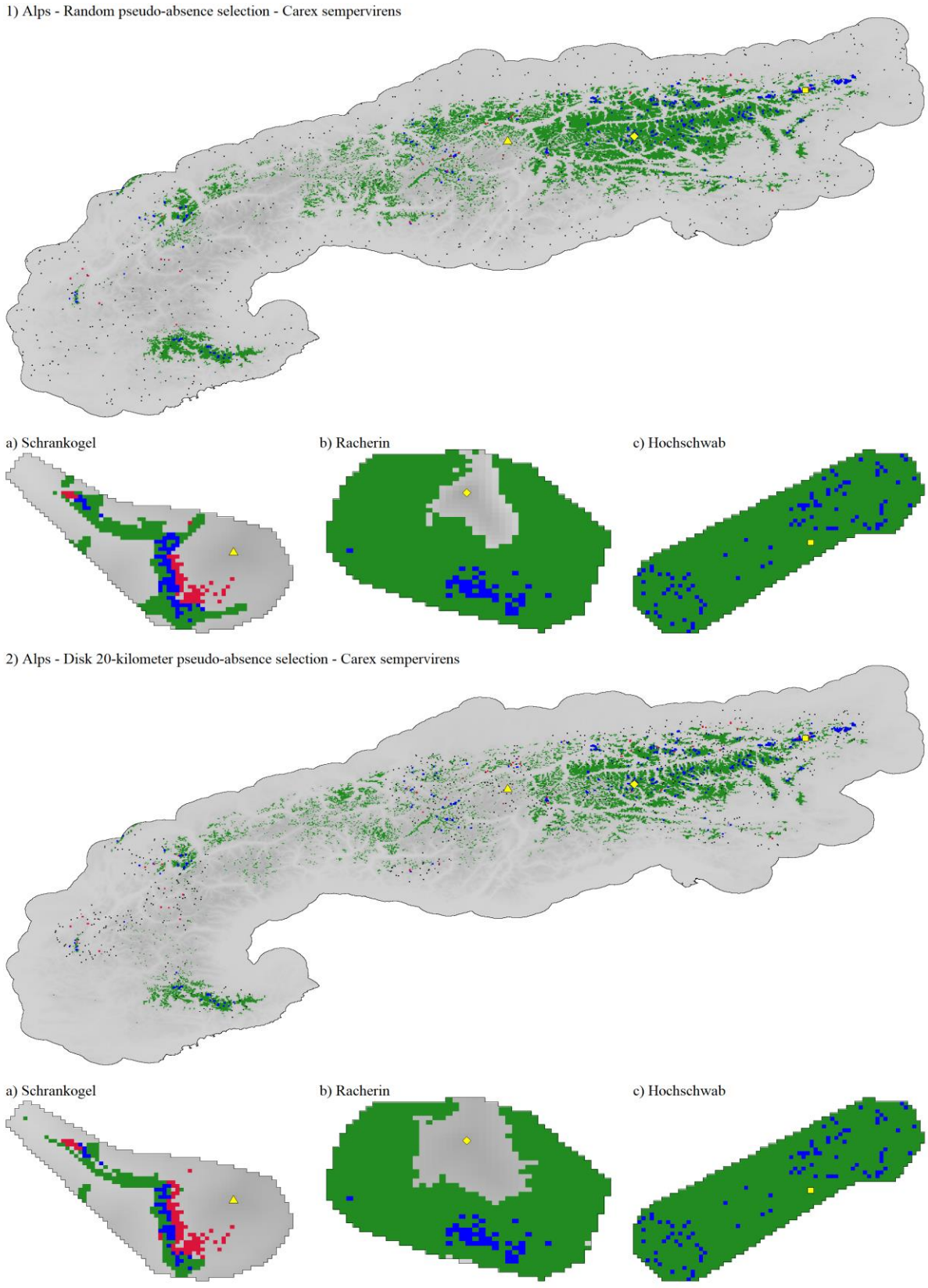

Figure 14: Binary predictions of Carex sempervirens at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

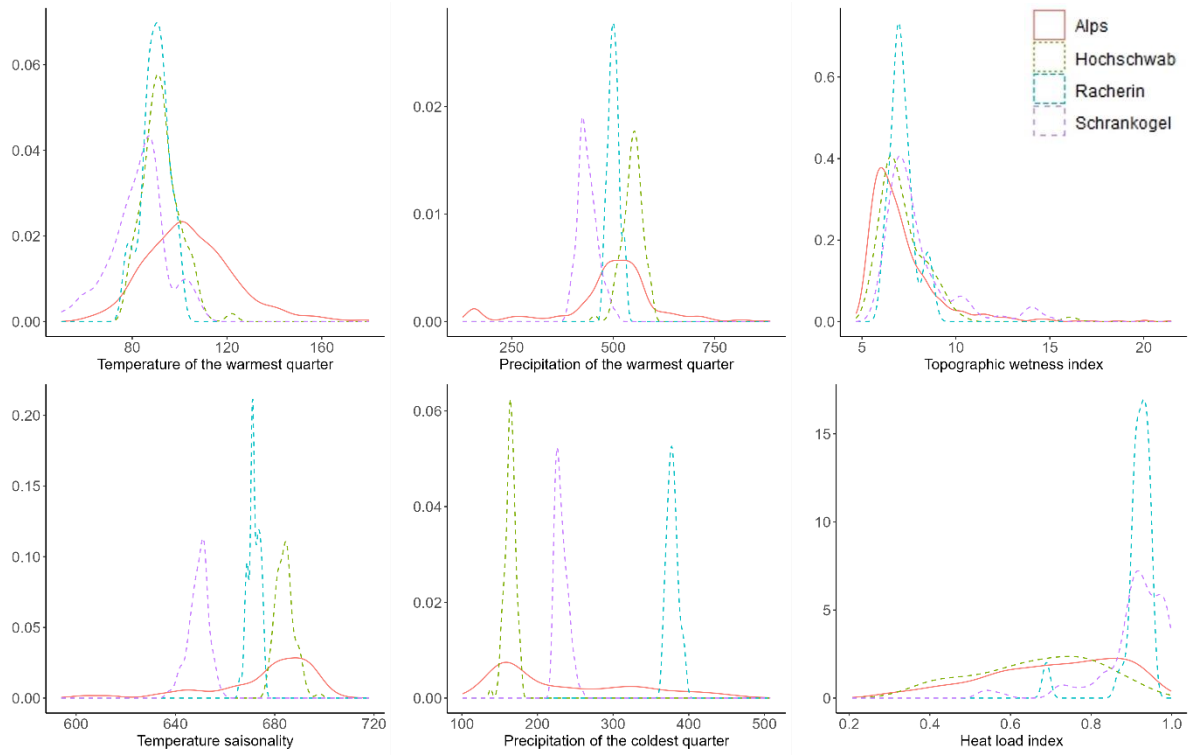

Figure 15: Density distribution of predictor variables of the presence observations of Carex sempervirens across the Alps and each mountain.

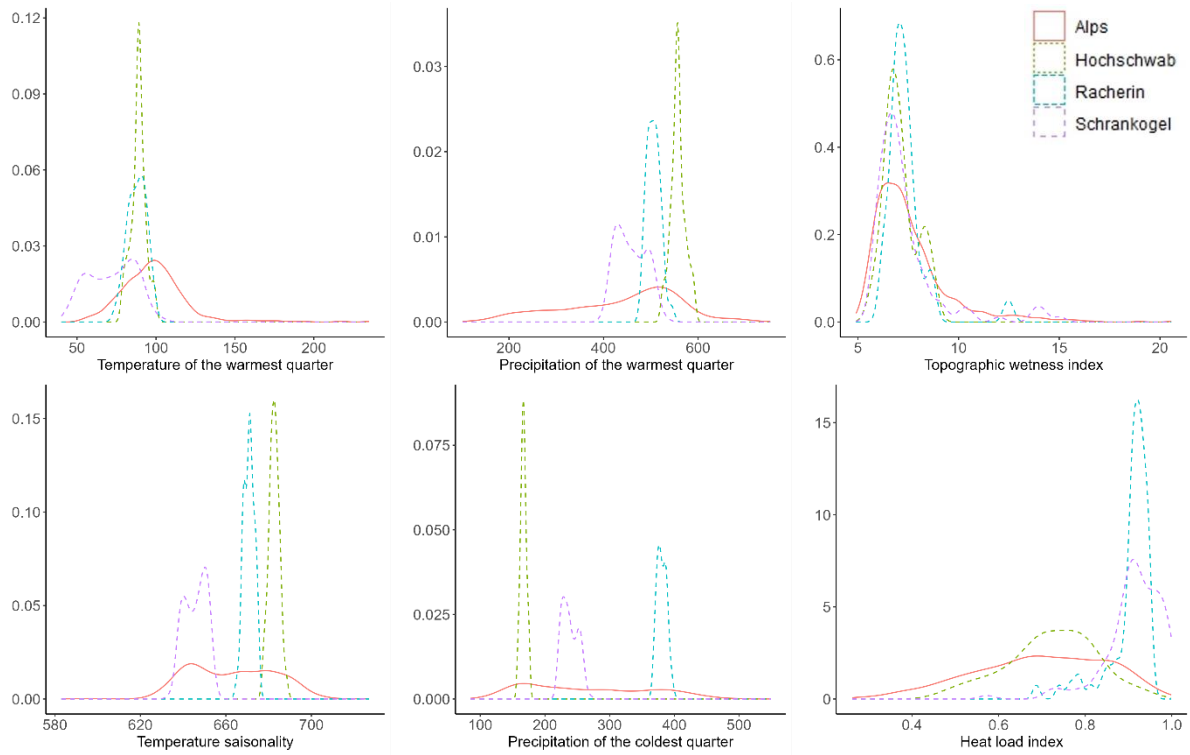

Figure 16: Density distribution of predictor variables of the presence observations of Geum montanum across the Alps and each mountain.

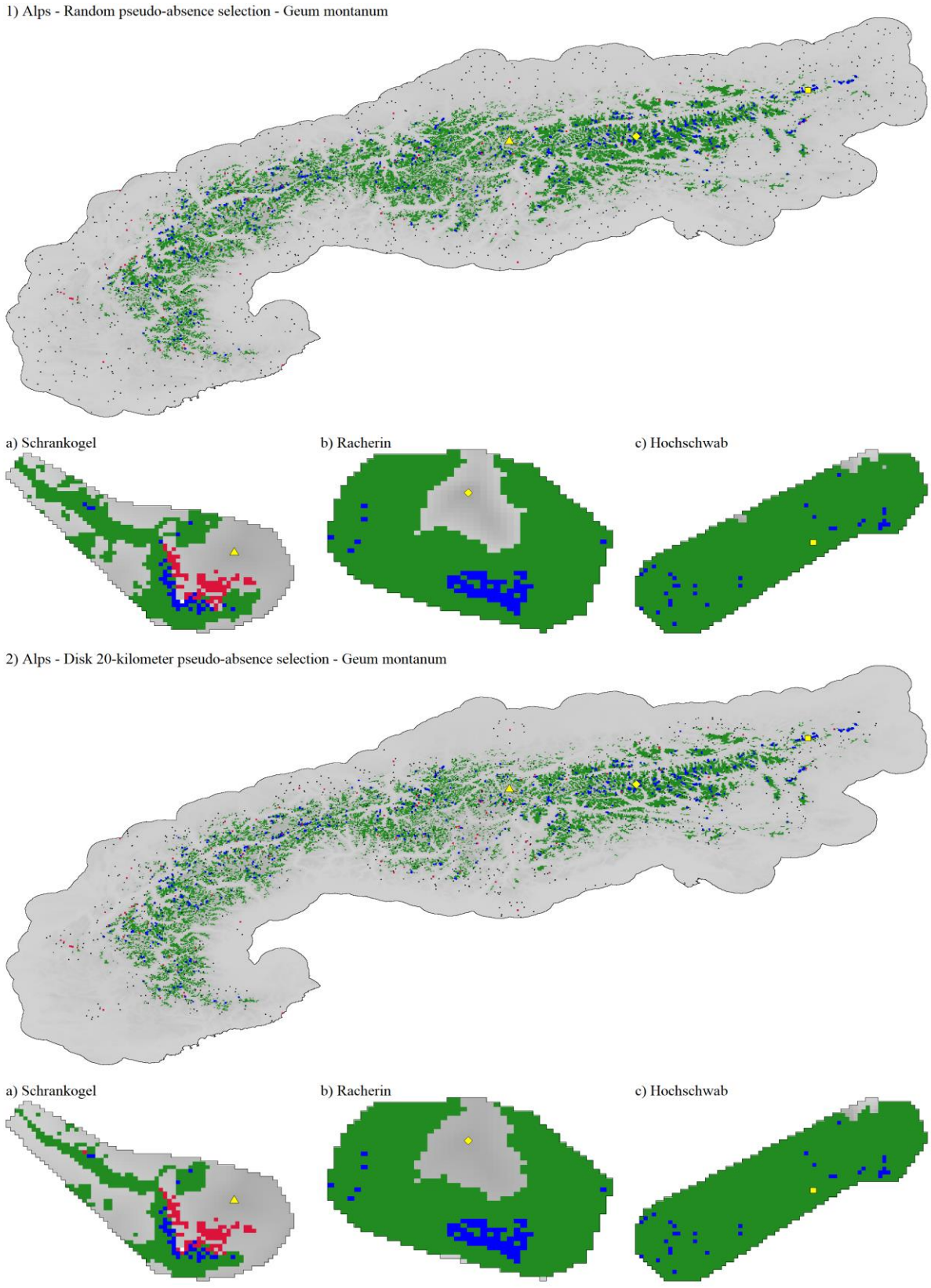

Figure 17: Binary predictions of Geum montanum at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

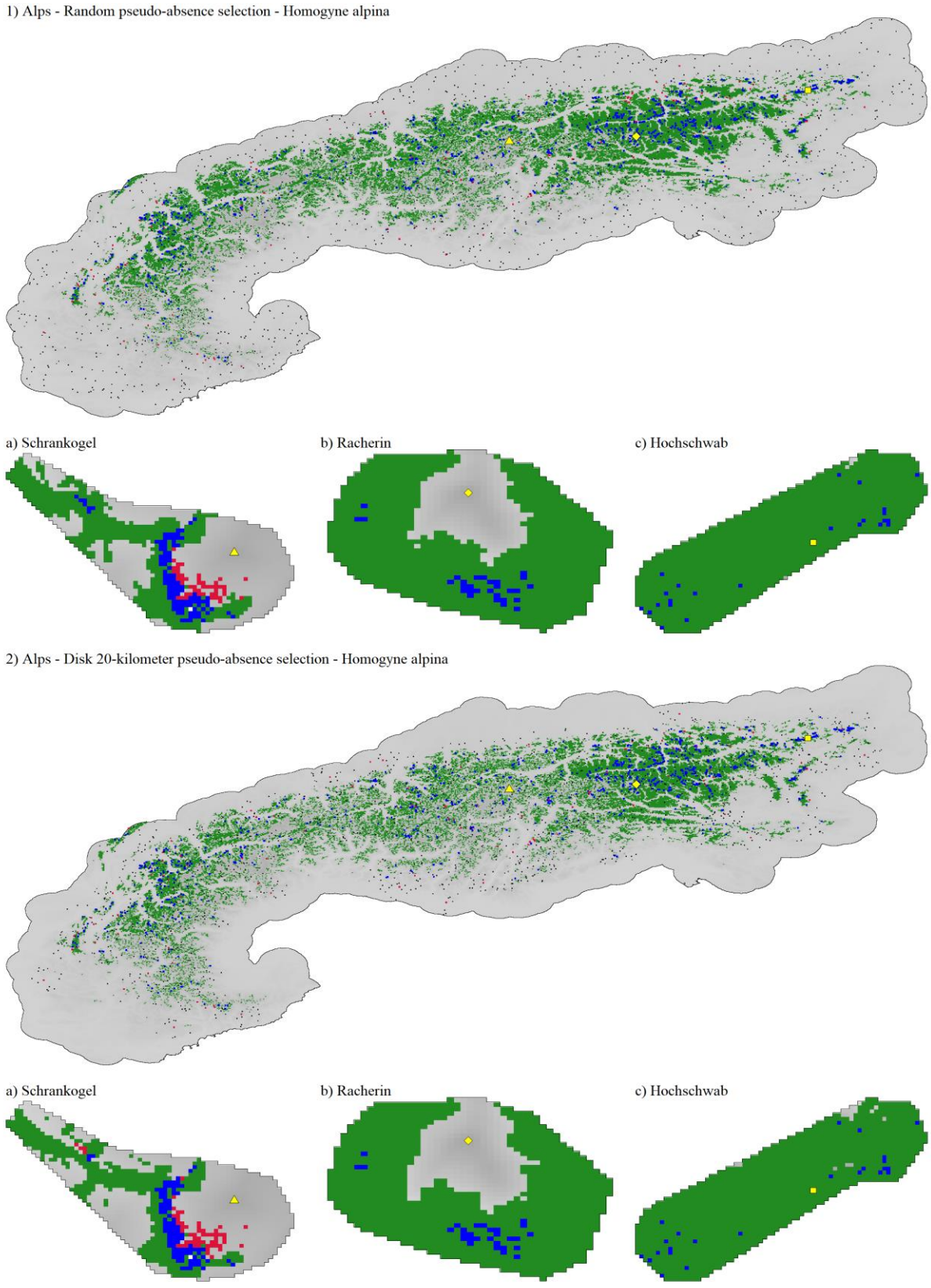

Figure 18: Binary predictions of Homogyne alpina at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

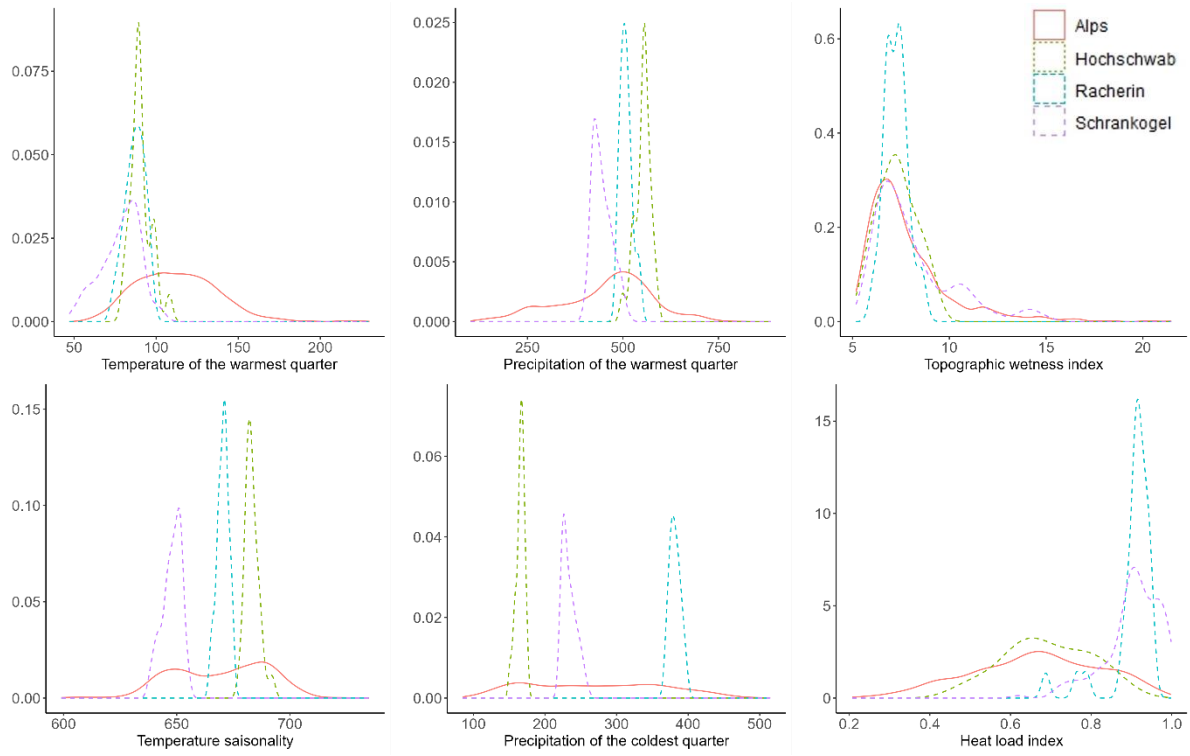

Figure 19: Density distribution of predictor variables of the presence observations of Homogyne alpina across the Alps and each mountain.

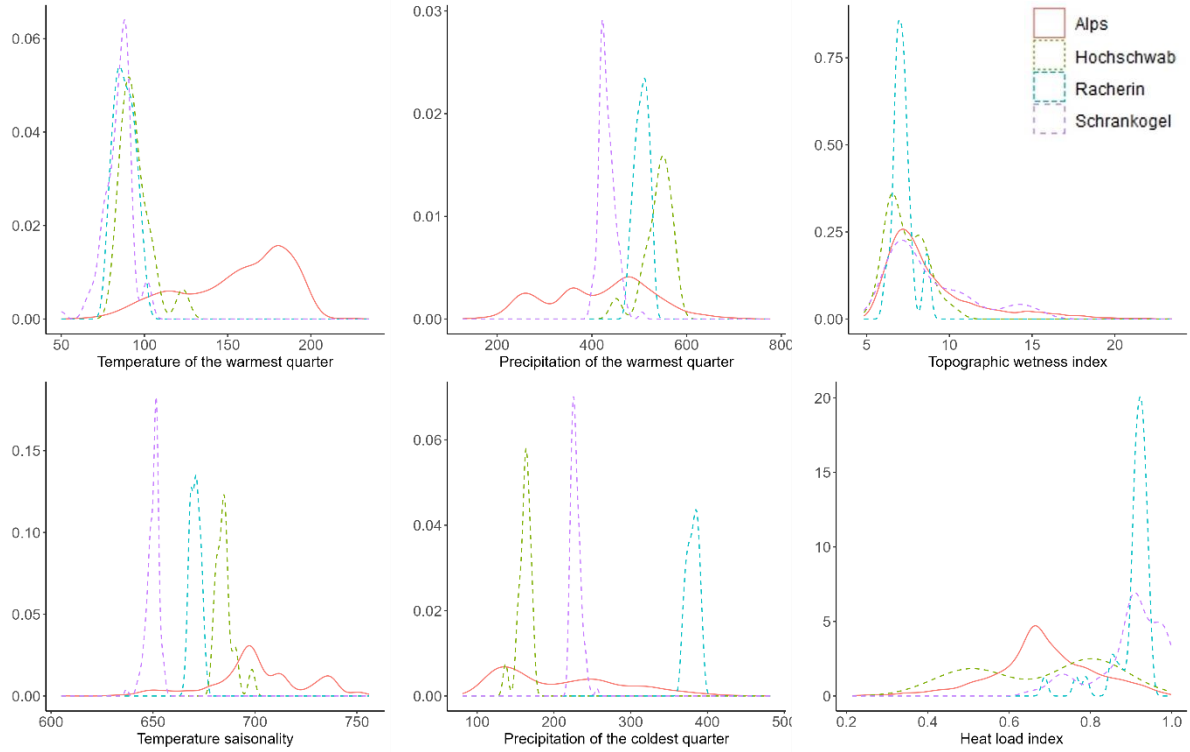

Figure 20: Density distribution of predictor variables of the presence observations of Leontodon hispidus across the Alps and each mountain.

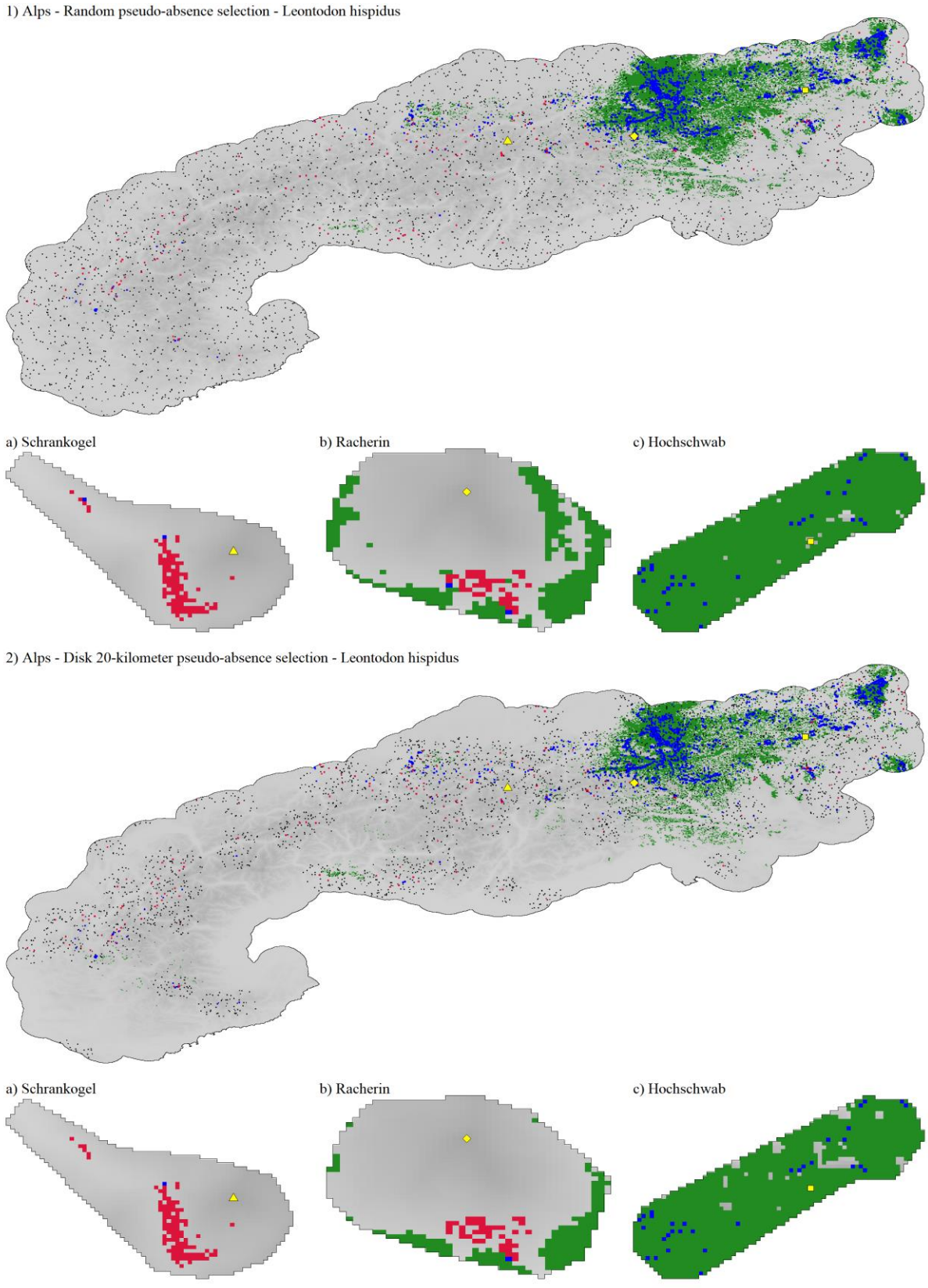

Figure 21: Binary predictions of Leontodon hispidus at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

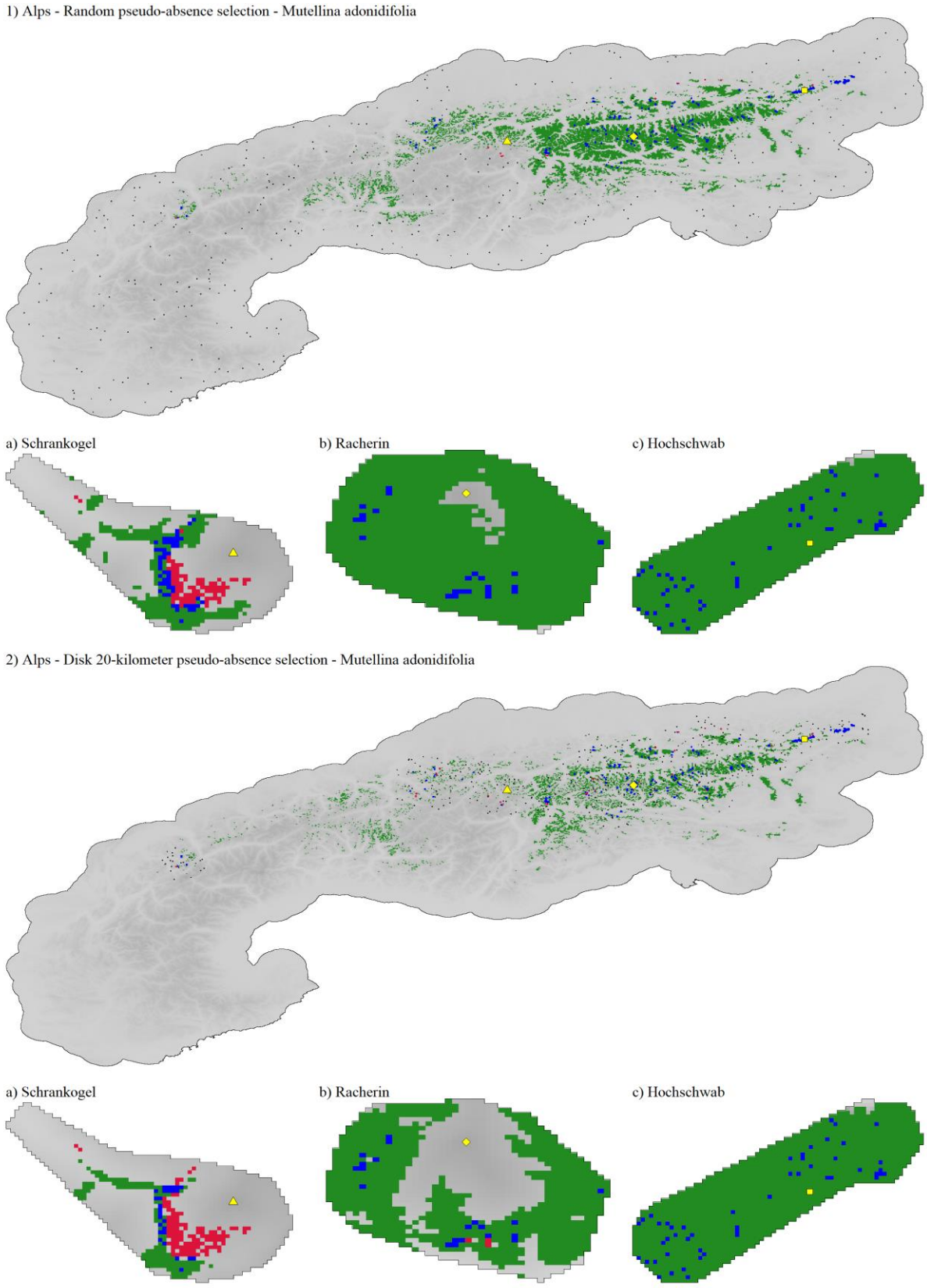

Figure 22: Binary predictions of Mutellina adonidifolia at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

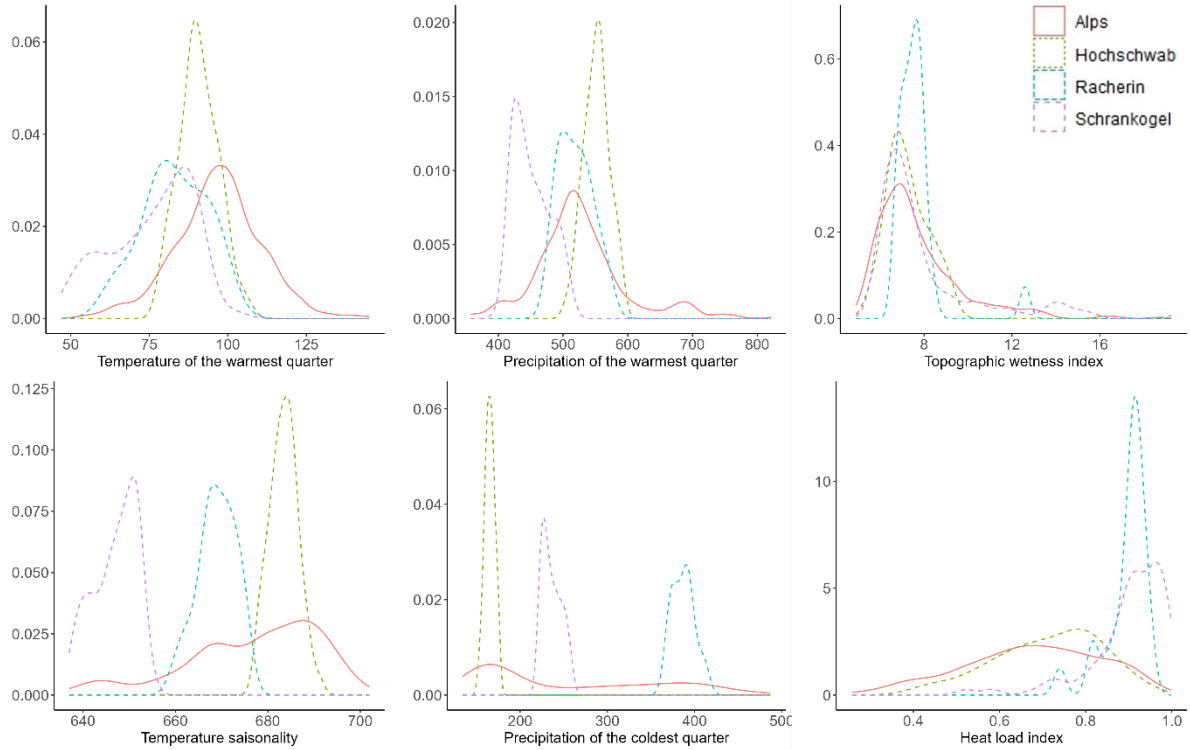

Figure 23: Density distribution of predictor variables of the presence observations of Mutellina adonidifoila across the Alps and each mountain.

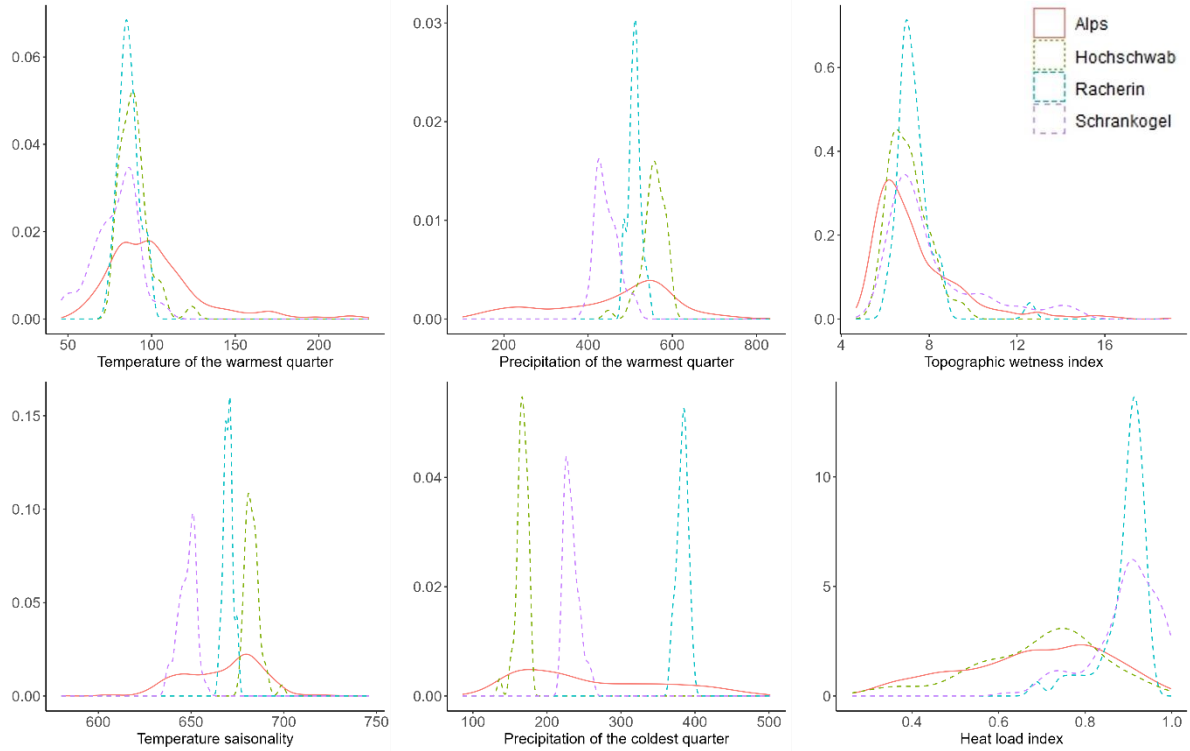

Figure 24: Density distribution of predictor variables of the presence observations of Myosotis alpestris across the Alps and each mountain.

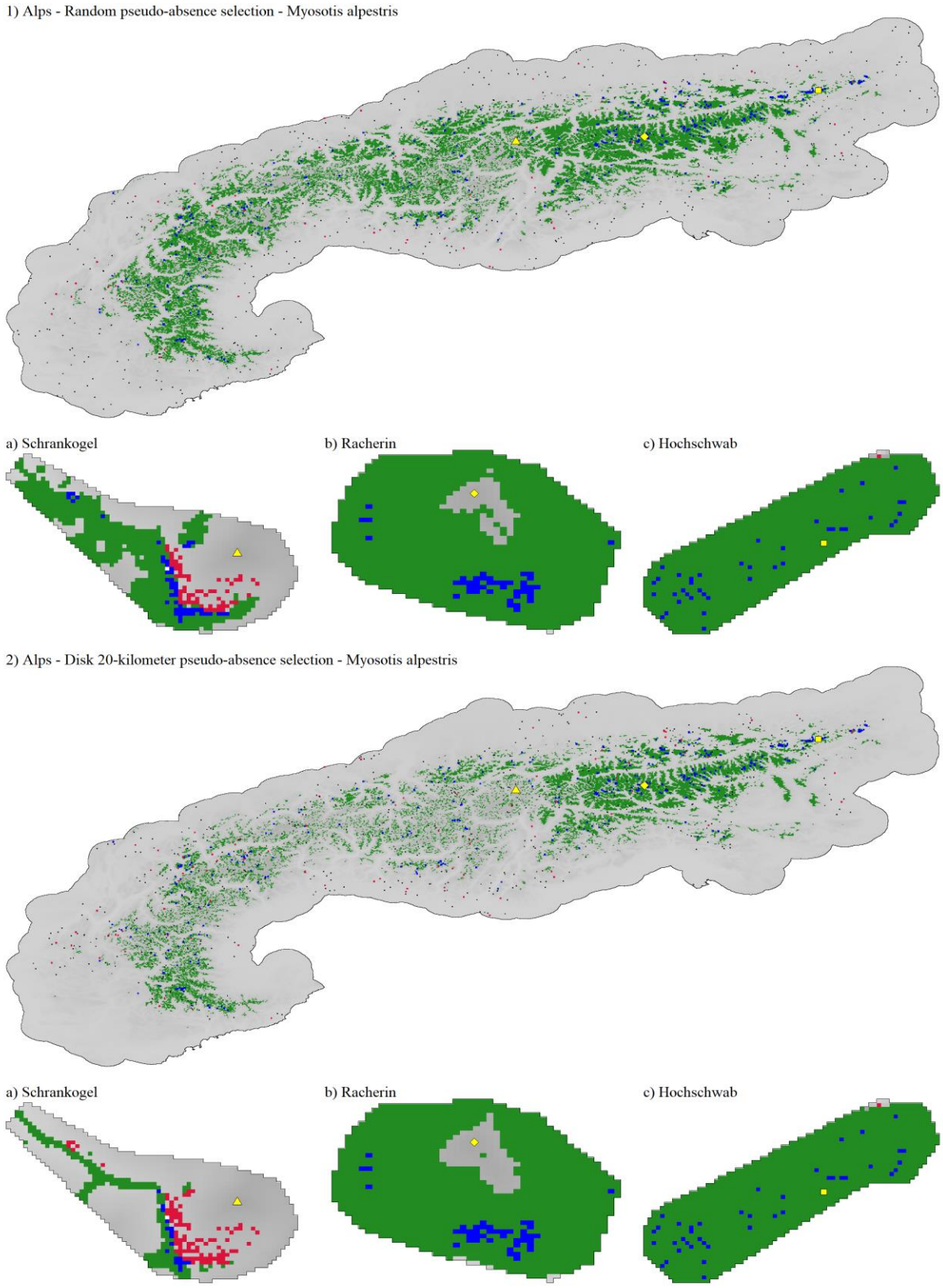

Figure 25: Binary predictions of Myosotis alpestris at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

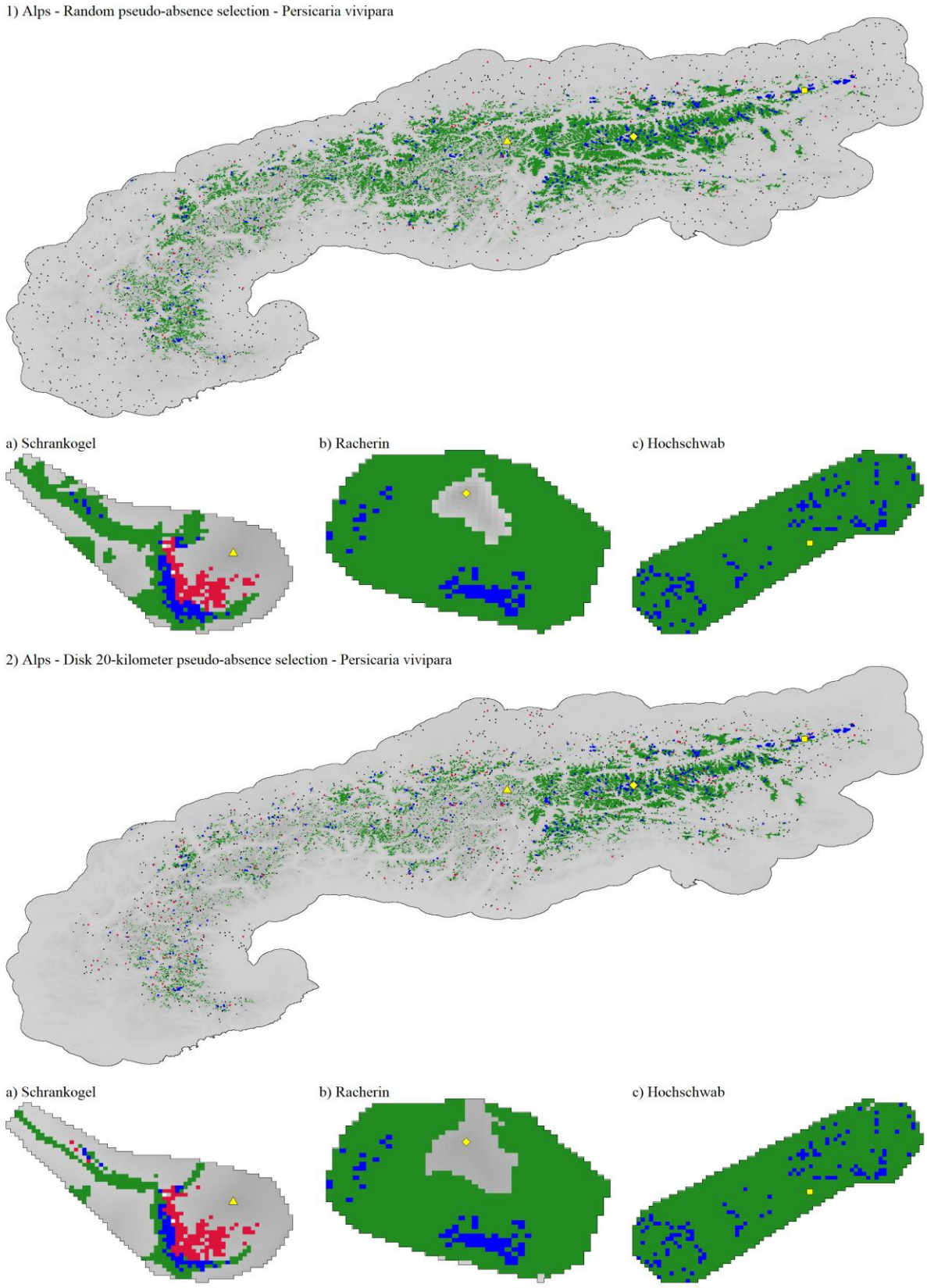

Figure 26: Binary predictions of Persicaria vivipara at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

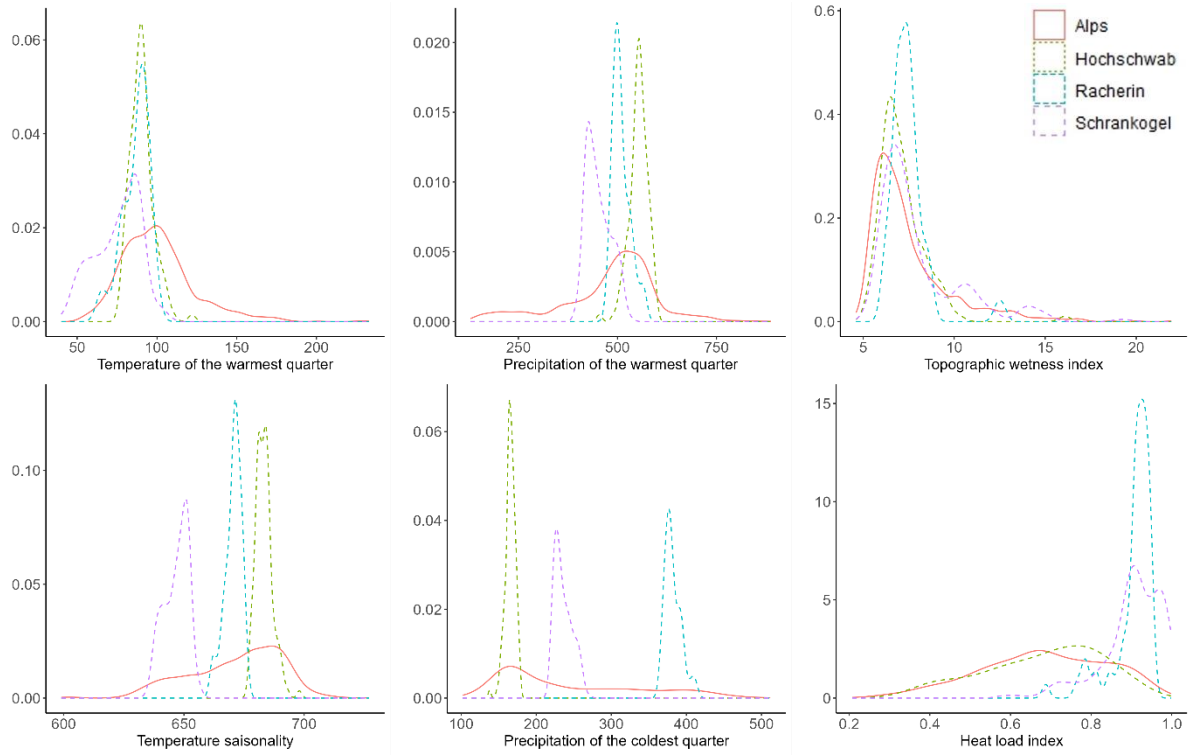

Figure 27: Density distribution of predictor variables of the presence observations of Persicaria vivipara across the Alps and each mountain.

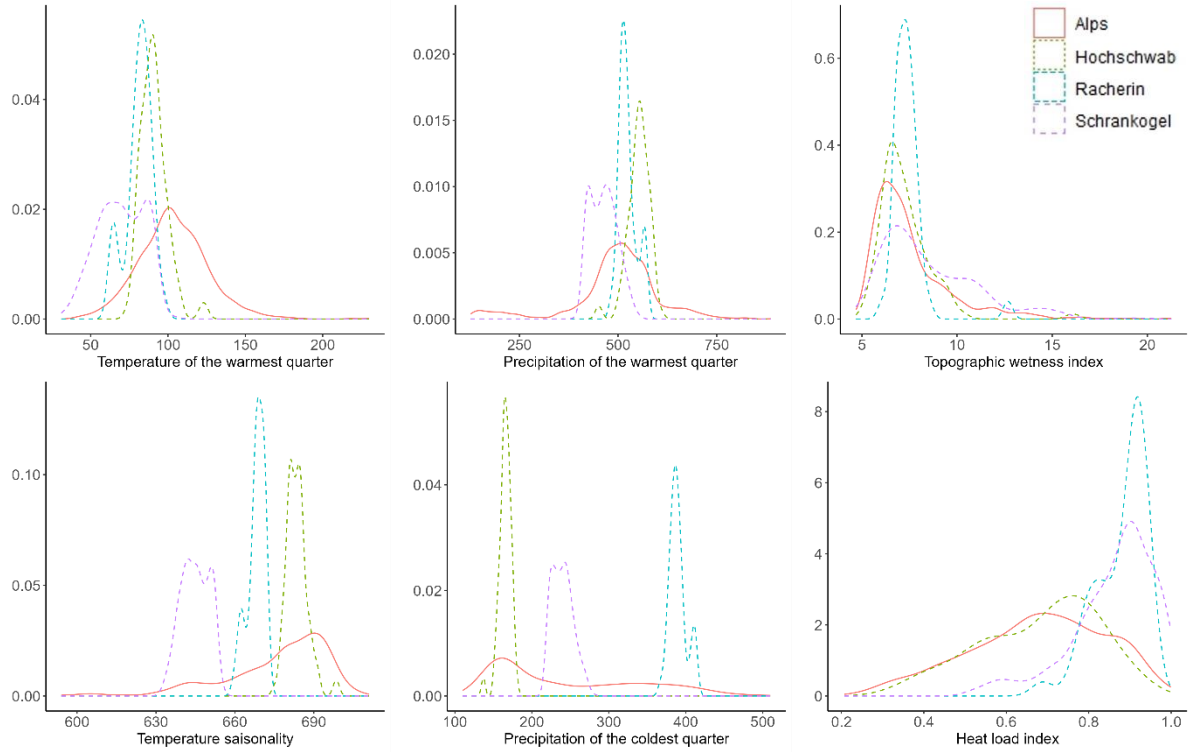

Figure 28: Density distribution of predictor variables of the presence observations of Poa alpina across the Alps and each mountain.

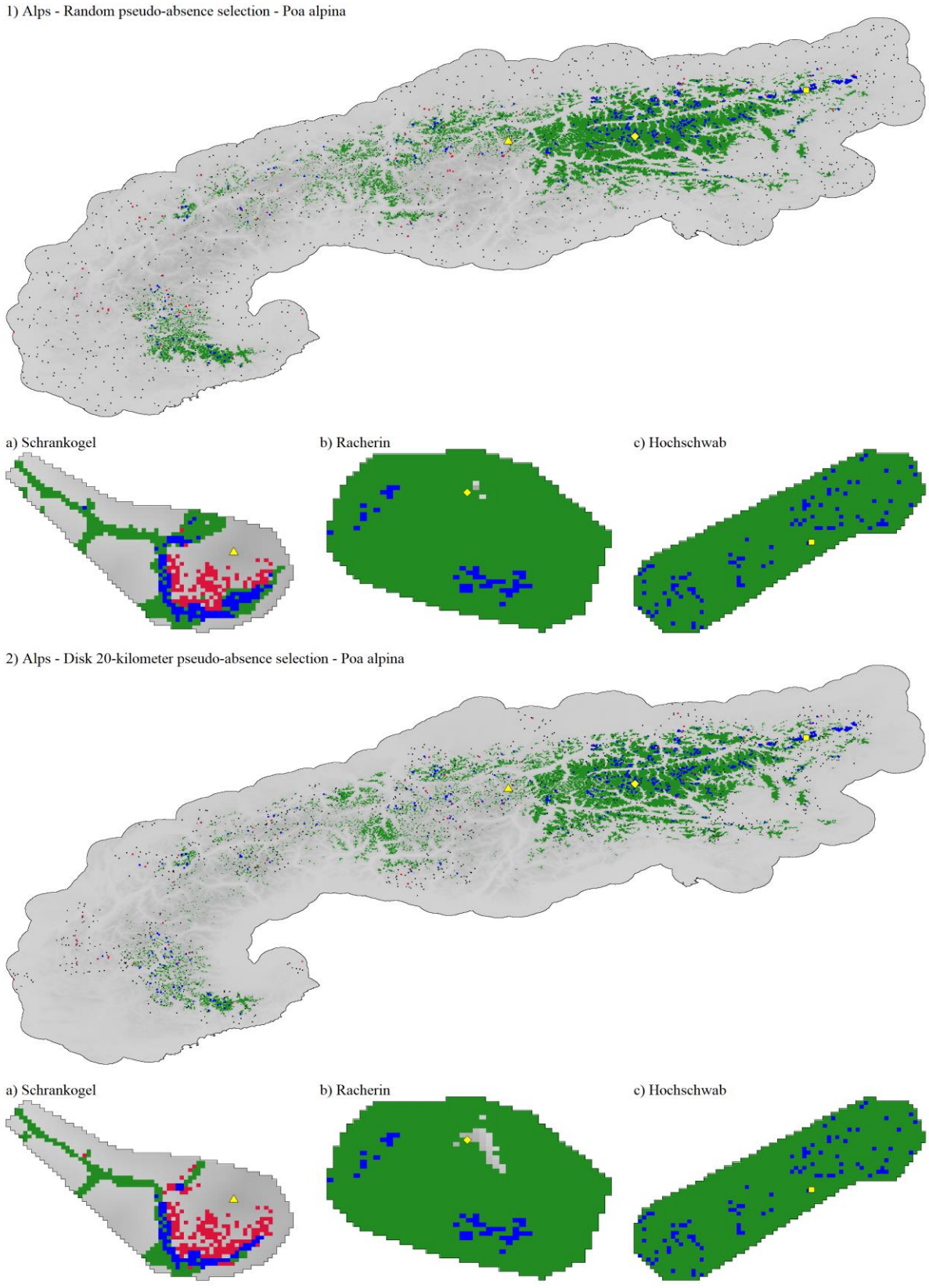

Figure 29: Binary predictions of Poa alpina at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

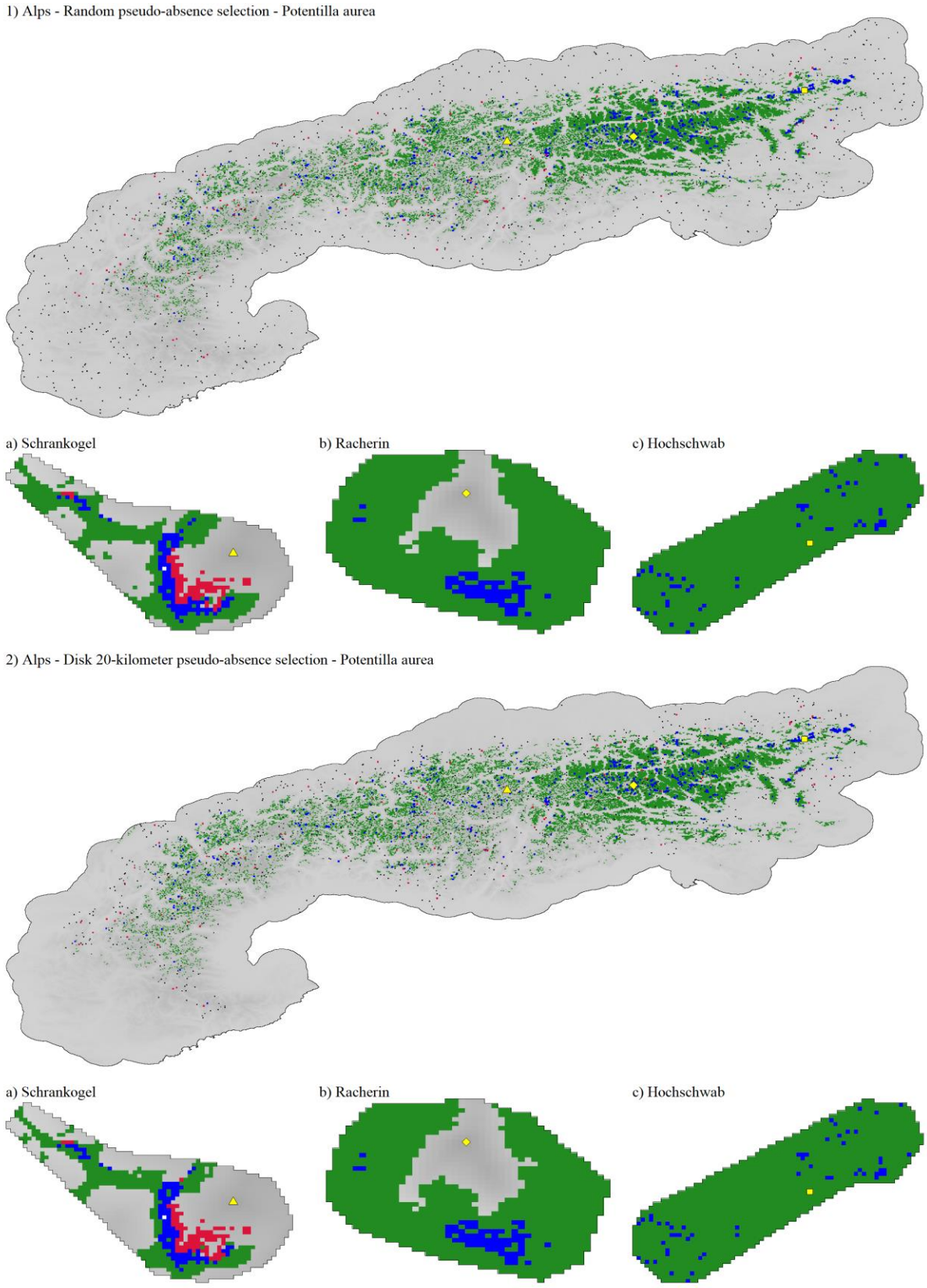

Figure 30: Binary predictions of Potentilla aurea at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

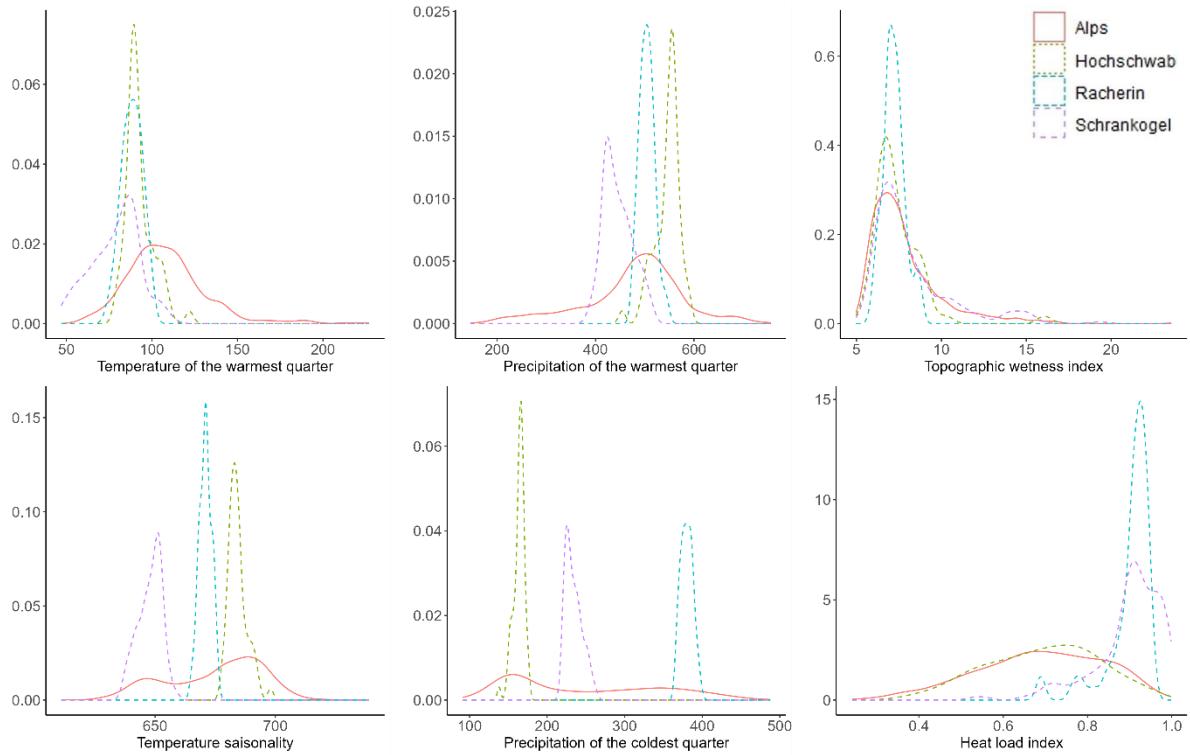

Figure 31: Density distribution of predictor variables of the presence observations of Potentilla aurea across the Alps and each mountain.

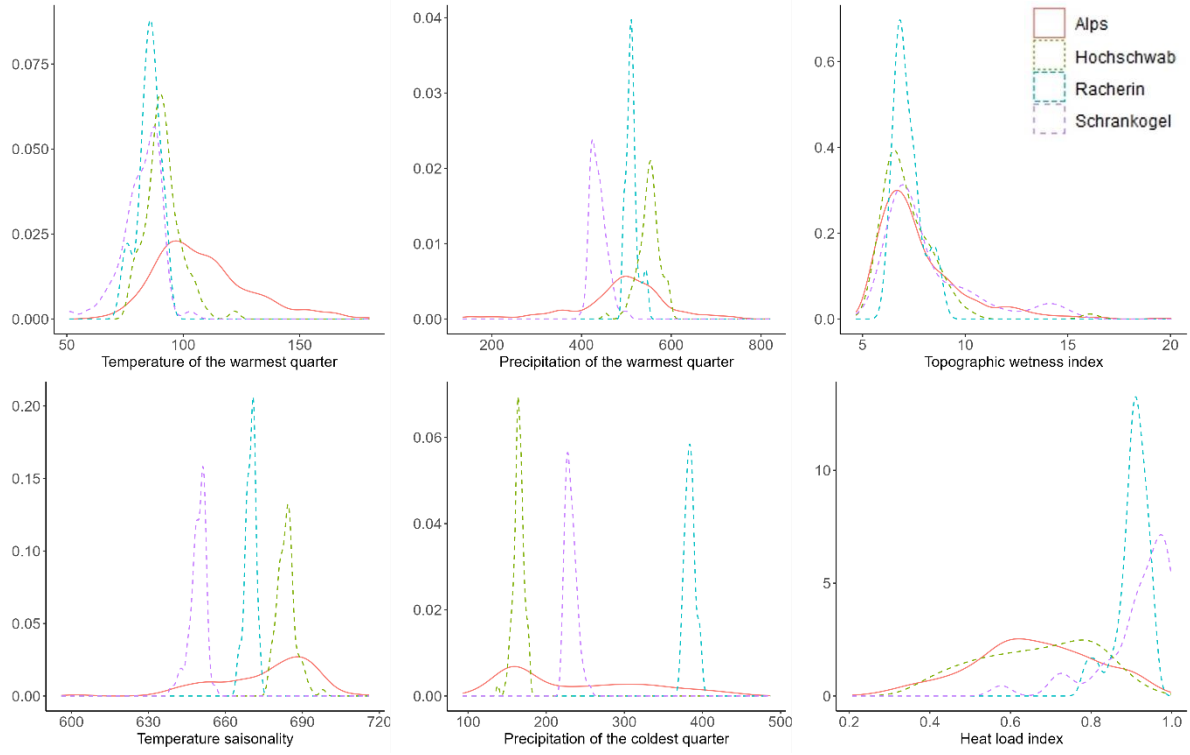

Figure 32: Density distribution of predictor variables of the presence observations of Selaginella selaginoides across the Alps and each mountain.

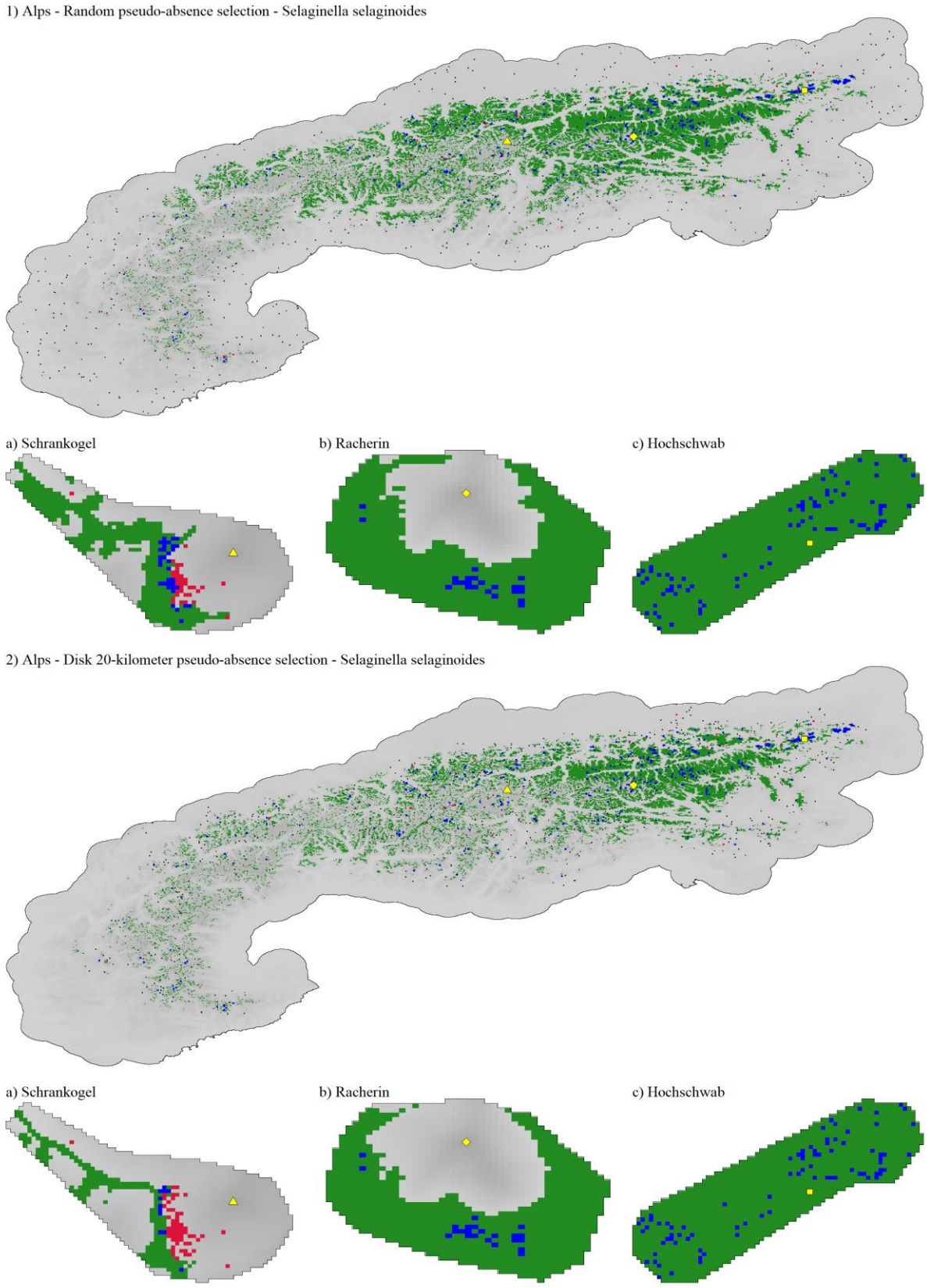

Figure 33: Binary predictions of Selaginella selaginoides at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

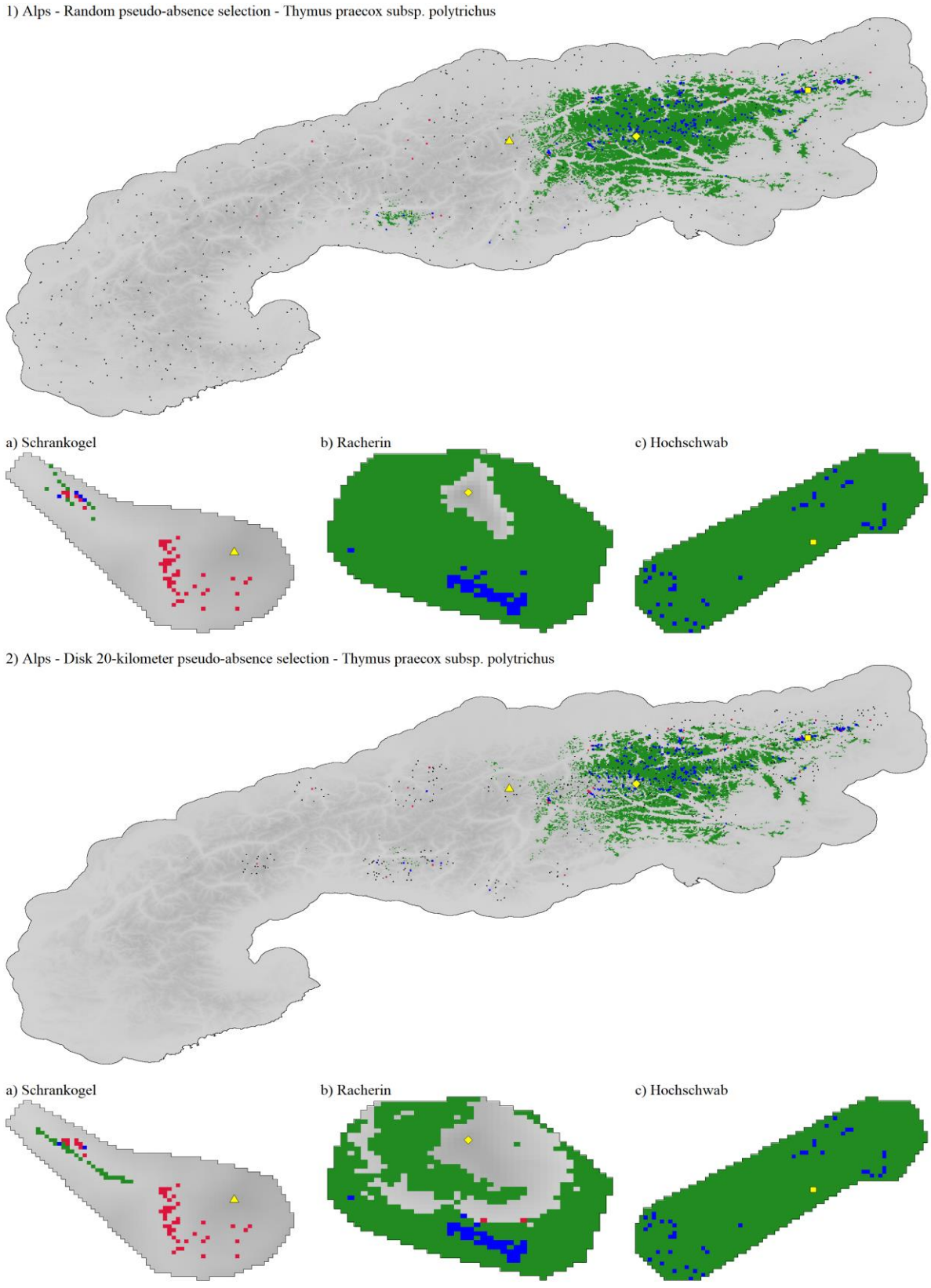

Figure 34: Binary predictions of Thymus praecox subsp. polytrichus at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.

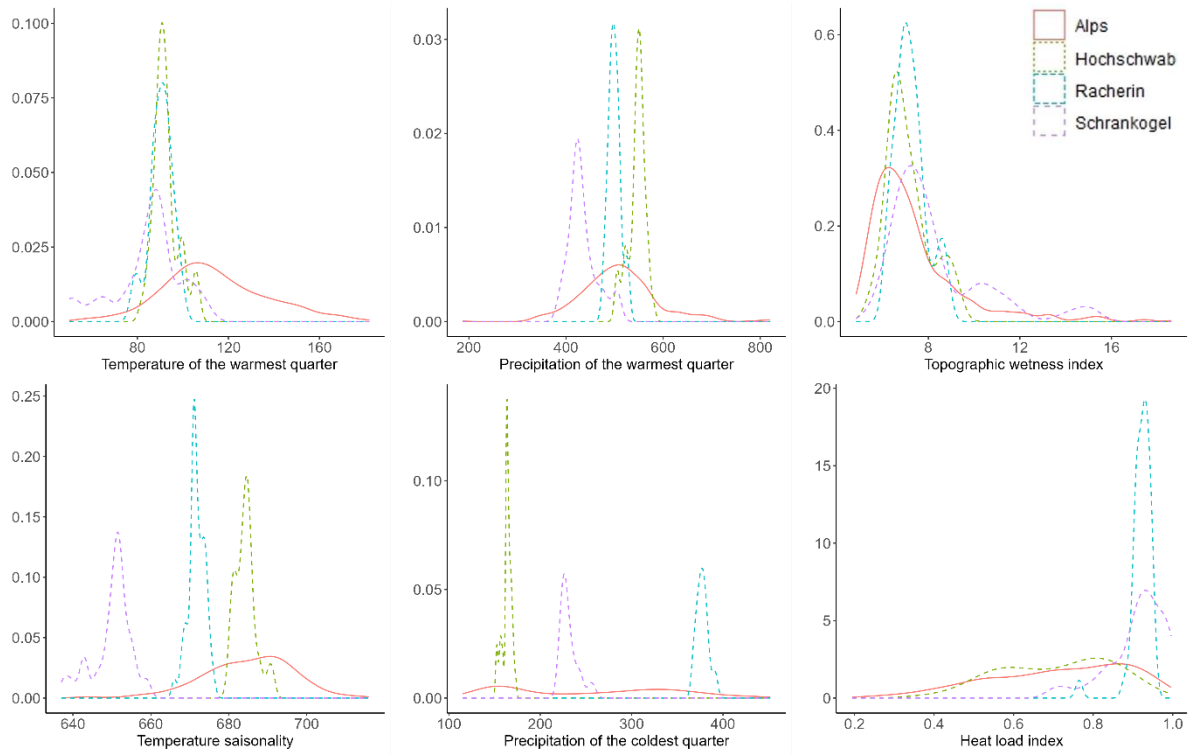

Figure 35: Density distribution of predictor variables of the presence observations of Thymus praecox subsp. polytrichus across the Alps and each mountain.

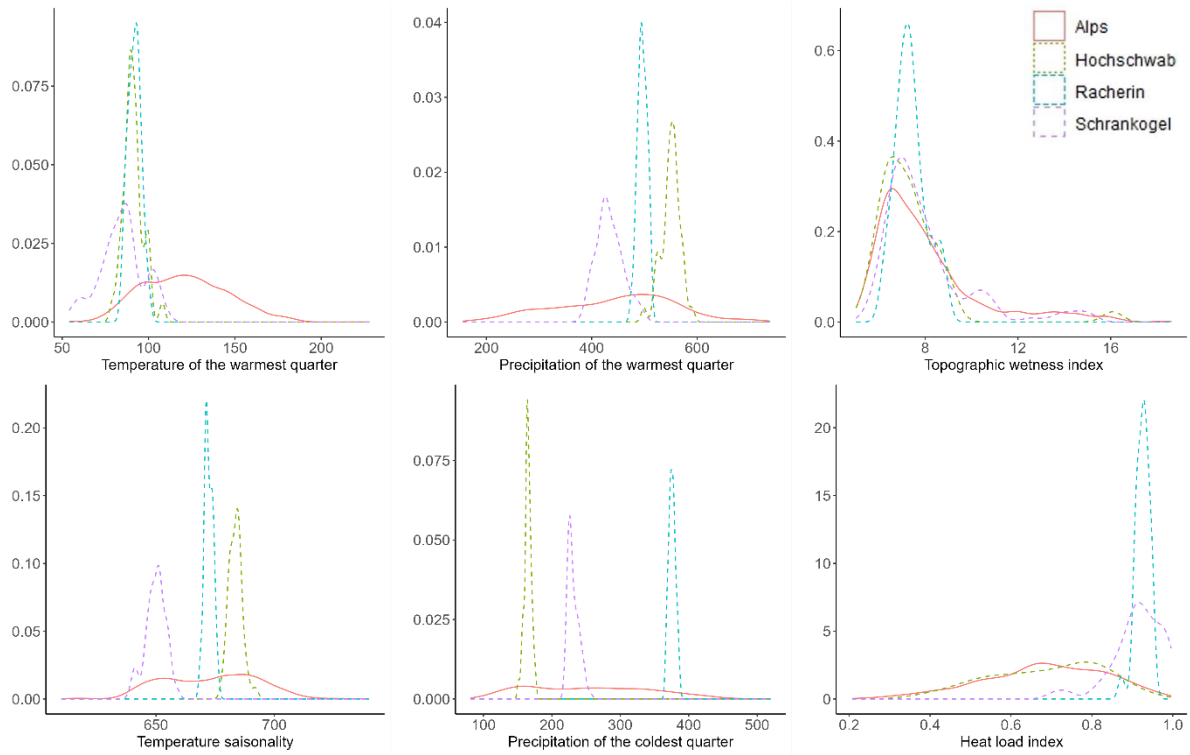

Figure 36: Density distribution of predictor variables of the presence observations of Vaccinium vitis-idaea across the Alps and each mountain.

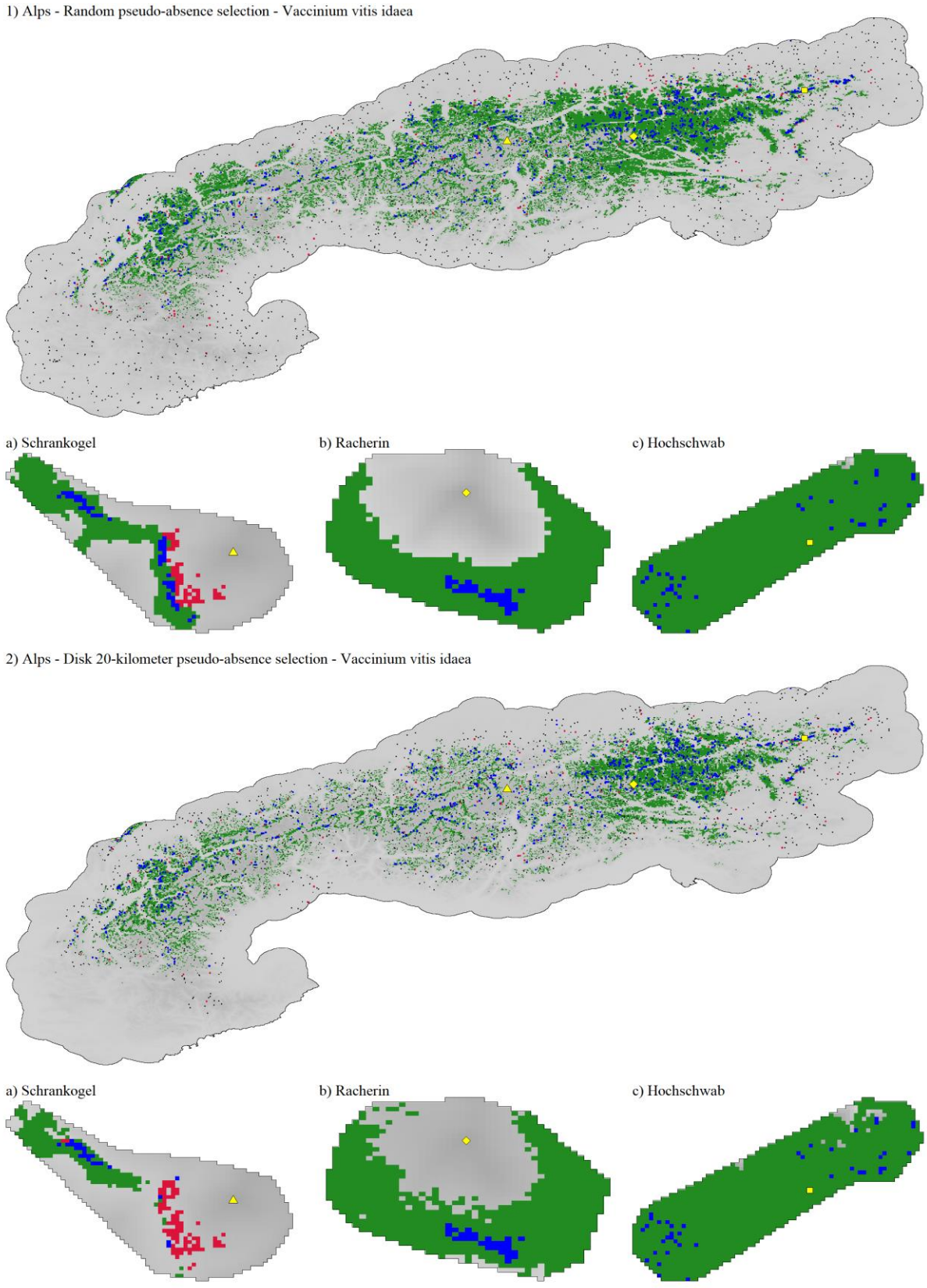

Figure 37: Binary predictions of Vaccinium vitis-idaea at the extent of the Alps and the individual mountains for both approaches of pseudo-absence selection separately. Green and grey grid cells indicate predicted presence and absence, respectively. Blue grid cells indicate where a species has been predicted and is present, whereas red grid cells display where a species has not been predicted but is present. Therefore, the sum of blue and red grid cells represents presence observations, whereas black grid cells represent pseudo-absences. For better visibility, species observations are enlarged at the extent of the Alps. Unique yellow signs symbolize the summit of each mountain.