Distribution of plant diversity used for identifying the green infrastructure in Grand Genève in the context of global changes

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UNIVERSITÉ DE GENÈVE FACULTÉ DES SCIENCES

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Section des Sciences de la Terre et de l'environnement
Département F.-A. Forel
Professeur A. Lehmann

DISTRIBUTION OF PLANT DIVERSITY USED FOR IDENTIFYING THE GREEN INFRASTRUCTURE IN GRAND GENEVE IN THE CONTEXT OF GLOBAL CHANGES

THÈSE

présentée aux Facultés de médecine et des sciences de l'Université de Genève
pour obtenir le grade de Docteur ès sciences en sciences de la vie,
mention Ecologie et évolution

par

Arthur SANGUET

de

Chambéry (France)

Thèse N° 181

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LIFE SCIENCES
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DOCTORAT ÈS SCIENCES EN SCIENCES DE LA VIE DES FACULTÉS DE MÉDECINE ET DES SCIENCES MENTION ECOLOGIE ET ÉVOLUTION

Thèse de M. Arthur SANGUET

Intitulée :

« Distribution of Plant Diversity Used for Identifying the Green Infrastructure in Grand Genève in the Context of Global Changes »

Les Facultés de médecine et des sciences, sur le préavis de Madame Michelle PRICE, Professeure titulaire et directrice de thèse (Département de botanique et biologie végétale), Monsieur Anthony LEHMANN, Professeur associé et co-directeur de thèse (Département F.-A. Forel des sciences de l'environnement et de l'eau) , Monsieur Nicolas WYLER, Docteur et co-directeur de thèse (Département de la culture et de la transition numérique, Conservatoire et Jardin botaniques de Genève), Monsieur Antoine ADDE, Docteur (Faculté des géosciences et de l'environnement, IDYST, Université de Lausanne, Lausanne), Madame Ramona MAGGINI, Docteure (Agroscope Cadenazzo, Plant Protection, Neobiotes, Cadenazzo) autorisent l'impression de la présente thèse, sans exprimer d'opinion sur les propositions qui y sont énoncées.

Genève, le 6 septembre 2022

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FACULTÉ DE MÉDECINE
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UNIVERSITÉ DE GENÈVE

« Nous ne défendons pas la Nature, nous sommes la Nature qui se défend… »

« We are not defending Nature, we are Nature defending itself »

- Militants à la ZAD de Notre-Dame-des-Landes (2012)

Me at the end of the summer 1995 close to my grandmother's chalet near the protected national park of "La Vanoise" in the French Alps. I would spend hours looking at insects and plants in these subalpine managed meadows, without knowing that wild carnivorous plants were growing a few hundred meters from the rock I am sitting on!

Abstract

English version

Biodiversity loss and global environmental changes are some of the most urgent challenges of our time. Biodiversity is declining worldwide, and we fail at bending the curve of extinctions, despite many efforts devoted to protecting species and ecosystems. In Switzerland, changes in land-use, the fragmentation of natural habitats, climate change and the spread of exotic invasive species are among the most important threats to local biodiversity. The aim of this work is to study the distribution of plant diversity through assessing the effects of climate and land-use changes on species distribution, and evaluating their associated vulnerability and conservation level in the cross-border territory of the Grand Genève (France/Switzerland).

New methods for protecting biodiversity are gaining attention and among them the identification of a Green Infrastructure (GI). GI is promoted at the national and cantonal levels in Switzerland with the aim of protecting core areas with high ecological value and links between them allowing spatial connectivity. However, the term "Green Infrastructure" has been widely used for various contexts and there is no consensus on how to identify and implement GI. Using a systematic review of articles, the first chapter of the PhD summarizes and evaluates commonly used methods for GI identification, providing key insights on the "three pillars approach" based on the separate assessment of biodiversity (composition), ecosystem services and landscape connectivity. Five theoretical levels toward a more complex, reliable and integrative approach to identify GI networks were also proposed and discussed.

One way of assessing the biodiversity pillar is to produce species distribution maps using habitat suitability models and a performant set of predictors. Thus, the distributions of 72 plants species from various ecological groups were modelled with several sets of high-resolution raster predictors (25m) including topo-climatic and biotic explanatory variables – based on the distribution of natural habitats with various levels of complexity – as well as remote sensing images. The results showed that a set of eight moderately complex biotic predictors combined with eight topo-climatic predictors produced the highest performances. On the contrary, models using remote sensing images were less performant on average. Models' performances and the associated set of predictors varied according to the species' ecological group emphasizing the fact that knowing the ecology of species is fundamental to create performant models.

The third part of this thesis explores the consequences of climate and Land-Use-Land-Cover (LULC) changes on plant distribution and examines species vulnerability to global changes according to their native and red list statuses. Hence, the distributions of 1692 plant species were modelled in the study area in 2050 for various future scenarios of climate and LULC changes using around 22 million occurrences from the Global Biodiversity Information Facility (GBIF) as well as Swiss and French local monitoring programmes. Two methods were tested to combine a continental scale climatic model to a regional bio-topographic (biotopo) one since no general methodological agreement emerges in the literature. By measuring several indicators of species distribution change between current and future conditions, a vulnerability index was calculated. It was found that indigenous species were more vulnerable to global changes than exotic ones which are even expected to benefit from them. The results did not show any relations between the red list status and the vulnerability index, indicating that the current health of species' populations and the level of threats they are currently facing are not good indicators for the conservation challenges ahead.

Finally, the last chapter of this work aims at using the previous results to evaluate the relevance of Conservation Areas (CA) for current and future conditions and to propose a network of areas of high ecological interest for the plant diversity conservation, named the Biodiversity Pillar (BP), in order to participate in the elaboration of the GI in Grand Genève. The relevance of CA was evaluated by measuring the proportion of species' distributions integrated into them for current and future conditions. The BP was then created using the most valuable areas from the distribution of suitability hotspots and from the ranking maps resulted from a prioritization process (priority areas). It was found that although CA are not very effective in conserving hotspots and priority areas, they will not lose effectiveness in the future compared to the current situation. Areas with high conservation interests composing the BP could be used by local authorities to expand current CA surface and ameliorate their effectiveness in conserving long-term plant diversity.

The global discussion following the above-presented results is articulated in three sections. First, the relevance of the use of models to determine species distribution is discussed and while these models are essential tools to understand the future impacts of global changes on the local plant diversity, they also have inherent limits that are presented. Second, a thorough focus is made on the territory of the study area, showing that this work has brought important findings for local conservation practices by highlighting ecologically rich areas and crucial trends regarding the evolution of species distributions and plant diversity, especially for mountain species and exotic plants. Finally, as an opening for this thesis, some key ideas derived from this work are discussed at the global scale and a particular emphasis is made on how to limit our impacts on the natural world and how to manage natural ecosystems in order to favour a global biodiversity rebound.

This thesis provides new insights and key elements to the understanding of the distribution and expected evolution of plant diversity in Grand Genève. By exploring how several scenarios of global changes will impact the distribution of plant species according to their ecology and conservation level, this project participated in identifying the ecological trends forecast for in the near future and proposed several possible responses. The outputs of this work reveal new data for local conservation authorities through a fine description of the territory's natural diversity, which ultimately helps in anticipating the impacts of global changes and contributed to bridging the gap between academic science and on-the-ground conservation actions for better shared practices.

Version française

La perte en biodiversité et les changements environnementaux représentent des défis parmi les plus urgents que nous ayons à relever. La biodiversité périclite partout sur la planète et nous ne parvenons pas à inverser ce phénomène malgré tous les efforts mis en place pour protéger les espèces et les écosystèmes. En Suisse, le changement d'utilisation des sols, la fragmentation des habitats naturels, le changement climatique et les espèces exotiques invasives sont parmi les menaces les plus importantes pour la biodiversité locale. L'objectif de ce travail est d'étudier la distribution et l'évolution de la diversité de la flore sur le territoire du Grand Genève, en évaluant les impacts des changements climatiques et d'utilisation du sol sur la distribution des espèces ainsi que leur vulnérabilité et leur niveau de conservation.

De nouveaux outils de protection de la biodiversité gagnent en visibilité et parmi eux, l'identification d'une infrastructure écologique. Elle est aujourd'hui promue à l'échelle nationale et cantonale en Suisse avec comme objectif de protéger des aires nodales avec une forte valeur écologique et des corridors assurant leur connectivité structurelle et fonctionnelle. En revanche, même si le terme « infrastructure écologique » a été largement employé dans la littérature et dans de nombreux contextes, il n'y a pas encore de consensus sur la méthode à appliquer pour l'identifier et correctement l'implémenter. En se basant sur une revue de la littérature, le premier chapitre de ce travail résume et évalue les méthodes habituellement utilisées pour identifier une infrastructure écologique et apporte les éléments clés d'une nouvelle approche basée sur l'étude séparée de trois piliers, à savoir la biodiversité (composition en espèces), les services écosystémiques et la connectivité des milieux. Enfin, cinq niveaux ont été proposés afin d'évaluer la qualité des méthodes utilisées pour identifier une infrastructure écologique de manière pertinente en utilisant l'approche des trois piliers.

Afin d'étudier la distribution de la biodiversité, il faut d'abord être en mesure de produire des cartes de distribution des différentes espèces qui la composent en utilisant des modélisations et des variables explicatives performantes. Pour cela, les distributions de 72 espèces de plantes appartenant à différents groupes écologiques ont été modélisées grâce à plusieurs associations de prédicteurs à résolution fine (25m), comprenant des variables topo-climatiques, biotiques – basés sur des classes plus ou moins complexes représentant la distribution des habitats naturels – ainsi que des images satellites. Les résultats ont montré que l'utilisation de huit prédicteurs biotiques, de complexité moyenne, combinés à huit prédicteurs topo-climatiques produisent les modèles avec les performances les plus élevées. En revanche, les modèles utilisant les images satellites étaient moins performants en moyenne. Les résultats montrent que les espèces alpines avec une distribution large ont de meilleures performances que les espèces dépendant d'habitats spécifiques dont la distribution est fragmentée (i.e. les milieux humides). En revanche, ces dernières ont de meilleures performances avec des prédicteurs biotiques représentant des classes d'habitats très précises, ce qui démontre la nécessité de connaître l'écologie des espèces pour créer des modèles pertinents.

Le troisième volet de ce travail explore les conséquences des changements climatiques et d'utilisation du sol sur la distribution des plantes ainsi que leur vulnérabilité à ces changements en fonction de leur indigénat et de leur statut de menace. Les distributions de 1692 espèces de plantes ont été modélisées dans l'aire d'étude pour 2050 en utilisant plusieurs scenarios de changements climatiques et d'utilisation du sol. Comme il n'existe pas de méthodologie claire pour intégrer un modèle climatique produit à l'échelle européenne et un modèle bio-topographique produit à l'échelle régionale, deux méthodes combinant les prédictions de ces deux types de modèle ont été testées. Finalement, la vulnérabilité des espèces a été calculée en mesurant plusieurs indices décrivant des changements associés à leur distribution dans les futures conditions. Les résultats montrent que les espèces indigènes sont plus

vulnérables aux changements globaux que les espèces exotiques qui pourraient même en tirer un avantage. En revanche, les résultats ne montrent aucun lien évident entre le statut de menace et la vulnérabilité aux changements globaux, ce qui suggère que les niveaux actuels de menaces qui pèsent sur les espèces et la santé de leurs populations ne sont pas des indicateurs pertinents pour les défis de conservation à venir.

Le dernier volet de ce travail a pour objectif d'utiliser les résultats produits précédemment afin d'évaluer la pertinence des aires protégées du Grand Genève dans les futures conditions environnementales, puis de proposer un « réseau biodiversité » composé d'aires particulièrement intéressantes pour la conservation de la diversité de la flore. La pertinence des aires protégées actuelles pour la diversité floristique est évaluée en mesurant la proportion de la distribution des espèces actuelles et futures qui leur sont intégrées. Le réseau biodiversité a été créé à partir des zones les plus intéressantes pour la richesse spécifique, et des aires prioritaires selon une carte de priorisation. Les résultats montrent que les aires protégées n'intègrent que très peu les zones prioritaires et celles riches en espèces, mais qu'elles ne perdent pas en efficacité dans le futur. Les zones particulièrement intéressantes identifiées par le réseau biodiversité pourront servir pour l'identification de l'infrastructure écologique, mais aussi pour agrandir la surface d'aires protégées et améliorer leur efficacité pour la conservation de la diversité floristique sur le long terme.

La discussion globale est articulée en 3 principaux axes. Tout d'abord, l'intérêt et la pertinence de l'utilisation de modèles de distribution d'espèces dans la conservation de la biodiversité sont discutés. En effet, ces modélisations sont essentielles pour comprendre les impacts futurs des changements globaux et l'évolution de la distribution des espèces, mais elles possèdent aussi des limites inhérentes aux méthodologies utilisées. La seconde partie se concentre sur la conservation de la diversité floristique sur le territoire d'étude en montrant l'intérêt et les utilisations possibles des résultats de ce travail par les autorités locales de protection de la nature. En particulier, les grandes tendances de changement de distribution des espèces subalpines et des néophytes sont discutées, ainsi que les caractéristiques des aires pertinentes à intégrer dans un système de protection renforcée. Enfin, et comme ouverture de cette thèse de doctorat, les concepts importants liés à la conservation de la biodiversité abordés durant ce travail sont discutés à l'échelle globale en insistant sur les techniques qui permettent de limiter notre impact sur la nature et sur les méthodes de gestion des espaces naturels qui favorisent un maintien, voire un retour global de la biodiversité.

Cette thèse de doctorat fournit de nouveaux éléments dans la compréhension et l'évolution de la distribution des espèces végétales et de la diversité de la flore actuelle et future dans le Grand Genève. En explorant les conséquences des changements globaux sur la distribution des espèces selon plusieurs scénarios et en considérant les caractéristiques écologiques et de conservation des plantes étudiées, ce projet participe à la compréhension des grandes tendances écologiques prédites dans un futur proche et propose quelques réponses. Les résultats de ce travail permettent une meilleure anticipation des conséquences des changements globaux sur la diversité végétale du territoire et représentent de nouvelles données utilisables par les autorités locales de gestion de la nature permettant au monde académique et aux acteurs de la conservation de travailler ensemble pour une meilleure protection de la biodiversité.

Table of Contents

Abstract 5
Table of Contents 9
Abbreviations and acronyms 13
Acknowledgements... 14
Chapter 1 – INTRODUCTION 17
1.1. Defining biodiversity and understanding its decline.. 18
1.1.1. Global threats 18
1.1.1.1. Changes in land and sea-uses 20
1.1.1.2. Climate change 20
1.1.1.3. Invasive exotic species... 21
1.1.1.4. Other global threats... 22
1.2. Methods to protect biodiversity.. 23
1.2.1. Why does protecting biodiversity matter? 24
1.2.2. How to protect biodiversity?.. 25
1.2.2.1. Green infrastructure 26
1.3. Assessing biodiversity’s distribution.. 29
1.3.1. Overview of SDM theory and methods 29
1.3.1.1. Methodological approaches.. 30
1.3.1.2. Predictors 32
1.3.1.3. Occurrences and spatial bias 32
1.3.1.4. Evaluating performances.. 33
1.3.2. Predicting species distributions under climate change 33
1.4. Local context and research questions... 35
1.4.1. Context and study area.. 35
1.4.2. Local threats and protection systems.. 36
1.4.3. Structure, objectives and research questions.. 37
RESULTS 40
Chapter 2 – Methods for identifying Green Infrastructure 41
2.1. Context.. 42
2.2. Introduction 44
2.2.1. Context.. 44
2.2.2. The concept of Green Infrastructure... 44
2.2.3. Objectives 46
2.3. Methods... 46

- 2.3.1. Articles selection 46
- 2.3.2. Evaluation methods 46
- 2.4. Results 47
  - 2.4.1. Bibliographic search 47
  - 2.4.2. Approaches to GI mapping 50
    - 2.4.2.1. Pillars assessment methods and dimensions of a holistic GI 50
    - 2.4.2.2. Overall GI identification approaches 52
- 2.5. Discussion and Conclusion 54
- 2.6. Bibliography 56
- 2.7. Appendix 1 62

Chapter 3 – Beyond topo-climatic predictors: does habitats distribution and remote sensing information improve predictions of species distribution models? 72

- 3.1. Context 73
- 3.2. Introduction 75
- 3.3. Data and methods 77
  - 3.3.1. Study area 77
  - 3.3.2. Species Data 77
  - 3.3.3. Predictors 78
  - 3.3.4. SDM and evaluation 79
- 3.4. Results 81
  - 3.4.1. Models' performances 81
  - 3.4.2. Remote sensing predictors 82
  - 3.4.3. The influence of species' ecology 85
- 3.5. Discussion 86
  - 3.5.1. Predictors' selection and limits 86
  - 3.5.2. Performances of ecological groups and insights for conservation 87
- 3.6. Conclusion 88
- 3.7. References 90
- 3.8. Appendix 2 97

Chapter 4 – Effects of climate and land-use changes on plant distributions and vulnerability index assessment 114

- 4.1. Context 115
- 4.2. Methods 115
  - 4.2.1. Data 115
    - 4.2.1.1. Predictor selection 115
    - 4.2.1.2. Species occurrences 117
  - 4.2.2. Modelling methods 118
  - 4.2.3. Vulnerability index 121

4.3. Results.....123
4.3.1. Modelling methods.....123
4.3.2. Impacts of global changes on plant distribution.....126
4.3.3. Vulnerability index.....127
4.4. Discussion.....130
4.4.1. Modelling method.....130
4.4.2. Plant distributions.....131
4.4.3. Plant species vulnerability.....132
4.5. Conclusion.....133
Chapter 5 – Assessment and improvement of conservation areas effectiveness under climate and land-use changes.....134
5.1. Context.....135
5.2. Methods.....135
5.2.1. Data.....135
5.2.2. Spatial Conservation Prioritization.....136
5.2.3. Relevance of CA and biodiversity pillar assessment.....137
5.3. Results.....139
5.3.1. Priority areas and suitability hotspots distribution.....139
5.3.2. Effectiveness and relevance of CA.....142
5.3.3. Biodiversity pillar characteristics and comparison with CA.....142
5.4. Discussion.....143
5.4.1. Spatial distribution of plant diversity.....143
5.4.2. Relevance of CA and biodiversity pillar.....146
5.5. Conclusion and perspectives.....148
Chapitre 6 – DISCUSSION & CONCLUSIONS.....149
6.1. Foreword.....150
6.2. About the use of models in conservation.....150
6.2.1. Biases and quality of predictions.....150
6.2.2. Difficulties of modelling species distribution under global changes.....152
6.3. Insights for local conservation planning.....153
6.3.1. Species migration.....154
6.3.2. The case of mountain species.....156
6.3.3. The spread of exotic species.....158
6.3.4. Species' vulnerability index.....162
6.4. Insights about biodiversity conservation.....162
6.4.1. Systematic conservation planning.....162
6.4.2. Rewilding anthropogenic systems.....163

6.4.3. Outlooks for global biodiversity conservation 164
6.5. Conclusions and perspectives 166
6.5.1. Main contributions 166
6.5.2. Perspectives and ameliorations 167
6.5.3. Concluding words 168
REFERENCES 169
APPENDICES 203
6.6. Appendix 3 204
6.7. Appendix 4 207

Abbreviations and acronyms

Biotopo	Biotic-Topographic-Edaphic
BP	Biodiversity Pillar
CA	Conservation Areas
CMIP	Coupled Model Intercomparison Project
GBIF	Global Biodiversity Information Facility
GI	Green Infrastructure
LULC	Land-Use-Land-Cover
RCP	Representative Concentration Pathway
RSI	Remote Sensing Images
SCP	Systematic Conservation Planning
SDM	Species Distribution Models

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The iconic temperate greenhouse of the CJB in mid-February when all the vegetation comes back to life.

Chapter 1

Introduction

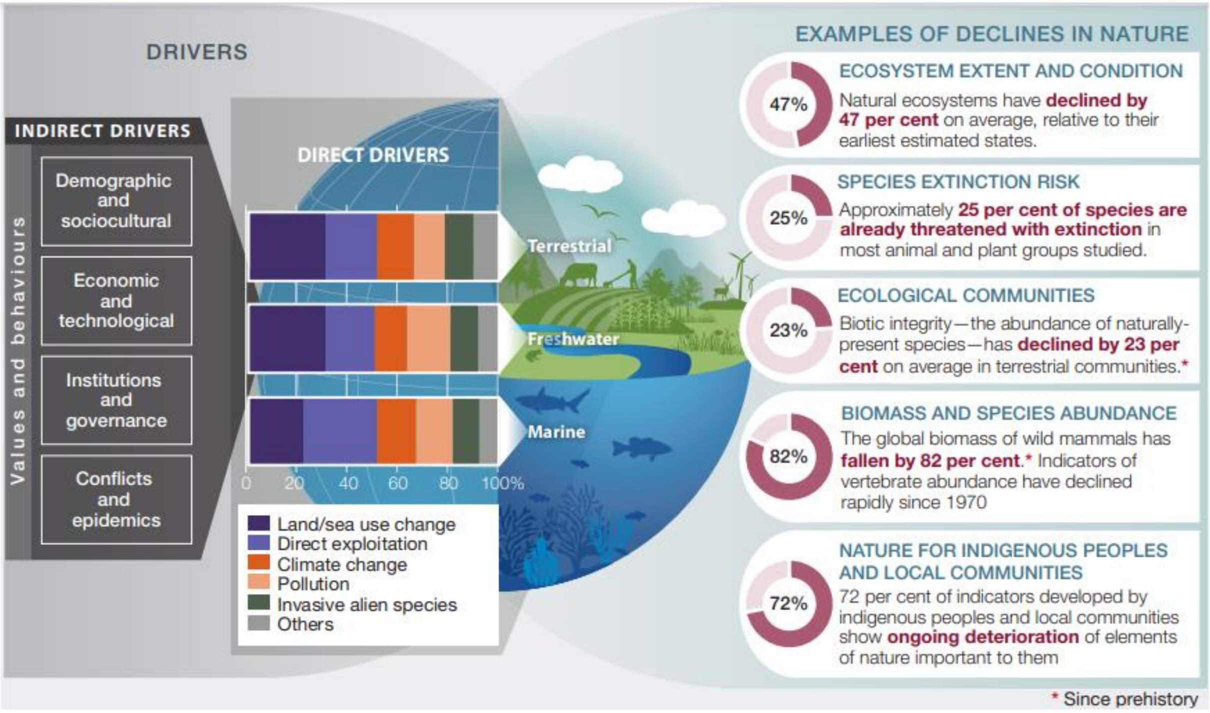
« Si la militance se décorrèle de la compétence, ça fait des militants fragiles. »

« If militancy is uncorrelated with competence, it creates week activists »

- Etienne Klein, conférence de clôture des rencontres Philosophia St Emilion 2020, 25 Octobre 2020.

1.1. Defining biodiversity and understanding its decline

The term “biodiversity” gained in popularity after the “United Nations Conference on Environment and Development’ (UNCED)” in 1992, also known as the Rio Summit on Biological Diversity, although the concept of “species diversity”, “species richness” or “biological diversity” were already used in the scientific community (Boudouresque, 2014; Dasmann, 1968; Whittaker, 1972). Nowadays, biodiversity encompasses the whole variety and complexity of life at various scales, from the genes to species, ecosystems and functional roles within ecosystems, even though it is complicated to give an exact definition to this concept (Swingland, 2001). It is often seen by the public community as the variety of species or the number of taxa that could be found in an area (species richness or alpha-diversity), popularized by the concept of “hotspots” (Myers, 1988, 1990) or the extinction of species (Proença & Pereira, 2017).



Natural ecosystems have **declined by 47 per cent** on average, relative to their earliest estimated states.

Approximately **25 per cent of species are already threatened with extinction** in most animal and plant groups studied.

Biotic integrity—the abundance of naturally-present species—has **declined by 23 per cent** on average in terrestrial communities.*

The global biomass of wild mammals has **fallen by 82 per cent.*** Indicators of vertebrate abundance have declined rapidly since 1970

72 per cent of indicators developed by indigenous peoples and local communities show **ongoing deterioration** of elements of nature important to them

* Since prehistory

Figure 1. Examples of declines in nature that have been caused by human direct and indirect drivers, from IPBES, 2019.

1.1.1. Global threats

Biodiversity at all levels is in a systematic crisis and is declining worldwide at an unprecedented rate as concluded by the Intergovernmental Platform on Biodiversity and Ecosystem Services reports (Fig. 1; IPBES, 2018a, 2019). It has been reported a 58% decline in vertebrate populations between 1970 and 2012 (McRae, *et al.*, 2017), insects biomass has declined up to 76.7% in 27 years in Germany and their abundance has dropped by 47% in a few decades in Europe and Algeria (Hallmann *et al.*, 2017; Møller, 2020), species are going extinct at a rate 100 to 10’000 higher than the background extinction rate which might be comparable to the one measured during past mass extinction events (Proença & Pereira, 2017), even at local terrestrial scale species richness has drop by 13.6% on average (Newbold *et al.*, 2015), one out of seven described species is endangered reaching 1 million plants and animals facing extinction (IPBES, 2019) and 40% of world’s insect species could be led to extinction in the next few decades (Sánchez-Bayo & Wyckhuys, 2019). Global trends and precise information are more difficult to find for plant species, however, according to the International Union for Conservation of Nature (IUCN) it is estimated that 63% of cycads, 34% of conifers and around 39% of dicots are endangered with extinction, although the dicots selected for this estimation only represent a portion of all dicot species (IUCN, 2022, Fig. 2). The IUCN Red List includes 58’000 plant species which represents a small fraction of all described plant species (374’000 or only about 15.5%; Christenhusz & Byng, 2016; IUCN, 2022) and even a smaller fraction of all existing plants not known to science yet (Corlett, 2016a). It is estimated that plants have a comparable level of extinction risk to mammals and a higher one than birds, although this is highly overlooked (Brummitt *et al.*, 2015). As examples, it has been demonstrated that 31% of all cacti are currently under threat (Goettsch *et al.*, 2015), 46.9% of assessed orchids are endangered but the proportion of species that have been studied only represents around 6.5% of all members of the Orchidaceae (1’855 out of 28’000)(IUCN, 2022; Fay, 2018) and around one quarter of all carnivorous plants are currently endangered with this number is expected to rise in the coming decades (Cross *et al.*, 2020; Fitzpatrick *et al.*, 2018).

Main threats to biodiversity are composed of: changes in land and sea uses, the direct overexploitation of organisms, climate change, various forms of pollution and alien invasive species (IPBES, 2019; Newbold *et al.*, 2015; Pacifici *et al.*, 2015; Sage, 2020). These drivers of change have accelerated during the last 50 years due to production and consumption patterns, human population dynamics and trends as well as global trade and technological innovations that could be considered as “indirect drivers of change” (Crenna & Sala, 2019; Benton *et al.*, 2021; IPBES, 2019). Worldwide decline in biodiversity levels is so interlinked with the development of our societies and the growth of our activities that we globally failed to tackle biodiversity loss in 2010 and in 2020 by not fully meeting even one of the 20 Aichi target (Global Biodiversity Outlook 5, 2020; Mace *et al.*, 2018; Xu *et al.*, 2021). If no concrete actions are taken, it is expected that population abundance will continue to decrease while species extinction risk will increase in the near future (Bellard *et al.*, 2012; Visconti *et al.*, 2016). We here develop an overview of main biodiversity’s threats at the global scale and will focus on local threats in the last part of this introduction.

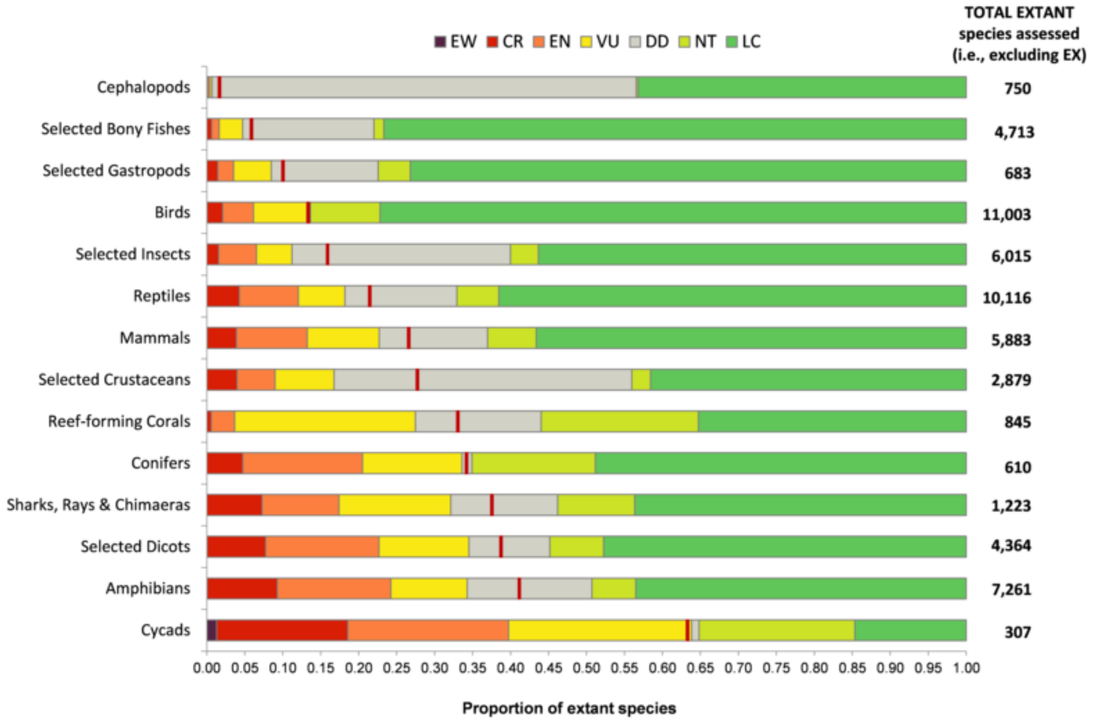


Figure 2. Proportion of each category of the IUCN red list for all assessed groups of species (IUCN, 2022).

1.1.1.1. Changes in land and sea-uses

Changes in land and sea use are recognized as the main threat to biodiversity and encompass all kind of degradation, fragmentation or destruction of natural habitats for the implementation of another surface less likely to host similar levels of biological diversity (Haines-Young, 2009; IPBES, 2019). On lands, it includes deforestation for logging or food production, urban sprawl, extraction of natural resources, the expansion of agriculture or human activities, and the development of communication infrastructures. The main drivers of change in the Land-Use-Land-Cover (LULC) are the high consumption lifestyles of developed countries and rising consumption in emerging economies (IPBES, 2018b).

It is estimated that 55% of the ocean is dedicated to industrial-scale harvest of fishes, more than three quarters of all land's surface is altered by human activities, especially for agricultural purposes and grazing, leaving only 23.2% of remaining wilderness (IPBES, 2018b, 2019; Kroodsma *et al*., 2018; McCauley *et al*., 2016). These numbers are expected to increase as the world's population and demands are rising (Nkonya *et al*., 2016). However, it has been shown that 56% of the terrestrial surface (minus permanent ice and snow), has low human impact, despite being heavily fragmented (Jacobson *et al*., 2019). The majority of forest landscapes have been drastically reduced in area and structural biodiversity due to human influence in boreal, temperate and tropical regions (Hansen *et al*., 2013; Moen *et al*., 2014). Nowadays, the majority of deforestation happens in the tropics and is mainly due to agricultural expansion, timber and wood extraction, the spread of fires, landscape fragmentation, new species and pathogen invasions as well as climate change (Malhi *et al.*, 2014). Built-up areas have increased 17% in 10 years, mostly in Asia and sub-Saharan Africa (Angel *et al*., 2016; Potere *et al*., 2009). It has been modelled that world cropland will be 10 to 25% larger than today in a scenario where food production will increase by 43 to 99% in 2050 (von Lampe *et al*., 2014; Schmitz *et al*., 2014).

1.1.1.2. Climate change

Climate change and biodiversity decline represent the most urgent challenges of our time as written by the Intergovernmental Panel on Climate Change (IPCC) -IPBES co-sponsored workshop (Pörtner *et al*., 2021). There is now a large consensus on the fact that human activities are the cause of the observed global warming and that altered climate regimes will impact our society (IPCC, 2021, 2022a, 2022b). Temperatures are estimated to have already risen by around 1°C above pre-industrial levels and are expected to reach 1.5°C in 2030 (IPCC, 2018). According to the US National Oceanic and Atmospheric Administration (NOAA, 2022), 2021 is the sixth warmest year on record while being influenced by a cold phase El Niño Southern Oscillation, also known as "La Niña" which tends to cool global temperatures. The last eight years are the eight warmest years on record, 2021 is the 45th consecutive year with global average temperatures above the 20th century average, the increase in average temperature per decade has more than doubled since 1981 compared to the previous observations and global ocean heat content was the highest on record (NOAA, 2022). In Switzerland the last decade was by far the warmest on record (Fig. 3; MétéoSuisse, 2022). In 2022, temperatures in January, February and March are respectively ranked as the sixth, seventh and fifth hottest on record for these months and it is virtually certain that 2022 will be in the top ten of hottest years (NOAA, 2022).

Lately, climate change has received growing interest in the scientific and public communities. Although it is not responsible for the current state of biodiversity, it is expected to be a key driver – if not the leading driver – of species migration, extinction and overall decline of biodiversity in the near future (IPCC, 2018; IPBES, 2019; Nunez *et al*., 2019; Pacifici *et al*., 2015; Thomas, *et al*., 2004). It has been responsible for past global level extinctions (Alverson *et al*., 2003; Benton & Twitchett, 2003) and is already the main cause to observed changes in population size, drop in abundance and local species extinction (Deb, *et al*., 2018; Iknayan & Beissinger, 2018; Panetta *et al*., 2018; Román-Palacios & Wiens, 2020; Wan *et al*., 2019). Current changes in climatic regimes have already been shown to alter 77 of 94 core ecological processes, but also species physiology, sex-ratio, morphology, plant phenology, date of egg laying in birds, emergence of butterflies, seasonal greening of the vegetation and species migration (IPCC, 2018; Sheffers *et al*., 2016). Climate change is also expected to be a key driver of change in habitat/biome distributions, structure and dynamic (Deb *et al*., 2018). It has been modelled that an increase of 2°C could transform around 13% of terrestrial biomes and around 35% for an increase of 4°C (Warszawski *et al*., 2013). As an example, the Amazon Rainforest has been shown to be close to its climatic limits and, depending on the magnitude of future changes in dry-season length, could experience a complete dieback (Good *et al*., 2011, 2013). Finally, changes in precipitations, frequency and intensity of heatwaves, storms, wildfires and pest outbreak events are projected to increase with climate change and could also represent an additional threat to many ecosystems (IPBES, 2019).

The intensity of climate change only depends on our capacity and willingness to deeply change our way of living and consuming goods and services, especially by reducing our greenhouse gas emissions (IPCC, 2022b). It is important to emphasize that so far there is no effect of COP (Conferences Of the Parties) on the CO2 concentration in the atmosphere and the only year where global CO2 emissions have dropped sufficiently to respect the Paris agreement was in 2020 during the partial lock down of most of the occidental world (NOAA, 2022). Many models have been created according to socio-economic pathways and various greenhouse gas emissions scenarios to forecast future temperatures according to our level of action. The very last climatic models named Coupled Model Intercomparison Project Phase 6 (CMIP6) of the World Climate Research Program considers several scenarios for future greenhouse gas emissions from business-as-usual, reaching +3.3 to +5.7°C by the end of the century compared to pre-industrial temperatures, and overly optimistic models that consider the rapid development of highly effective new technologies to remove CO2 from the atmosphere where temperatures is modelled to rise from 1.0 to 1.8°C by 2100 (IPCC, 2021). It is interesting to note that temperatures are very likely to increase between 1.2°C to 3.0°C by 2050 no matter which scenario we are following. Finally, emerged lands are modelled to warm up 1.4 to 1.7 times higher than ocean (IPCC, 2021).

1.1.1.3. Invasive exotic species

Species are considered as “exotic”, or “alien”, when they are found outside of their natural range. In this work, species introduced or naturally arrived in the last 500 years will be named “exotic” (but could also be named “neophytes”) and prior to 500 years ago are called “archaeophytes”. A species is considered as “invasive” when it directly threatens the stability of native ecosystems by out-competing indigenous species (Lodge, 1993). All alien species are not “invasive” because most of them thrive in their new ecosystems without causing any harm to the native biodiversity, even increasing species richness. The number of alien species detected globally has doubled in the last 50 years, although it might be underestimated due to the lack of data in developing countries, and their introductions are directly linked with the globalization of our society, especially through worldwide trade and the transport of goods and people (IPBES, 2019; Seeben *et al*., 2017). Pests, parasites and pathogens represent an important problem for wild naive indigenous populations, but also for agriculture with a direct impact on production and associated economy (Pimentel *et al*., 2000, 2005). Invasive exotic species represent a threat to local species through competition or predation, but also through altering habitat characteristics such as nutrient cycling, fire regime or hydrology (Lodge, 1993; Mack *et al*., 2000).

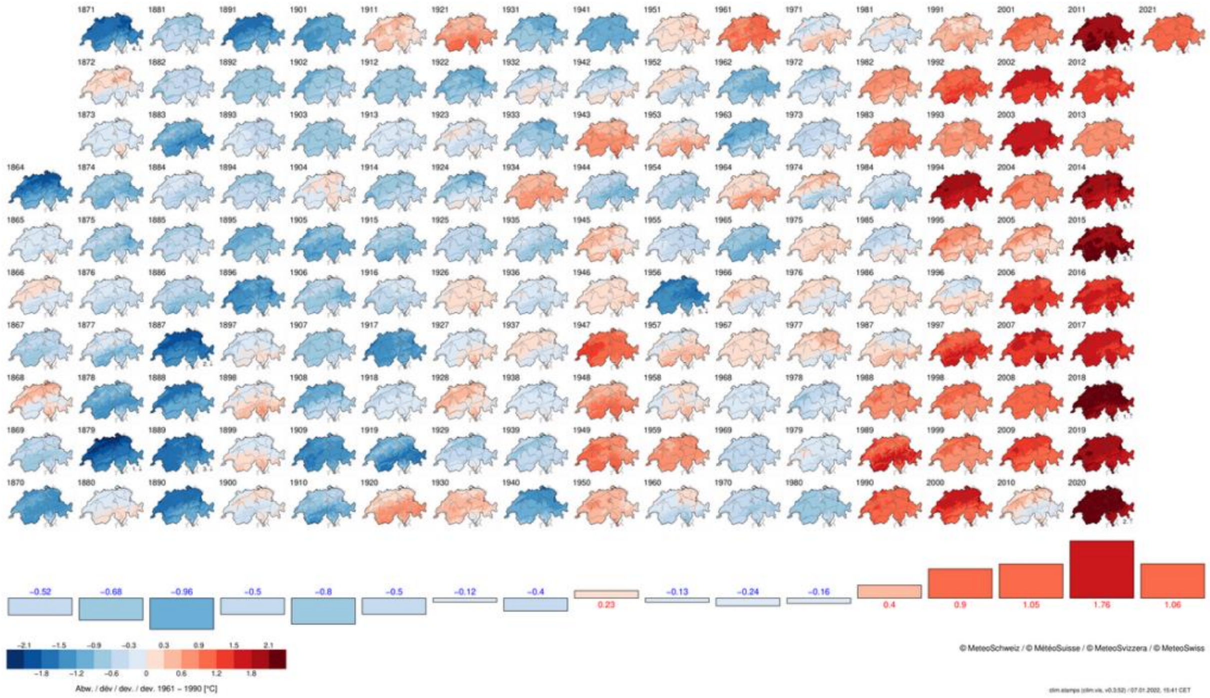


Figure 3. Temperature anomalies in Switzerland compared to the 1961-1990 average from 1864 until 2021. Years with average temperatures below average are in blue, years with temperatures above average in red (MétéoSuisse, 2022).

Exotic invasive species can have impacts on ecosystem services, human health, indigenous biodiversity both on land and in marine habitats, ecosystem functions, and on various groups of plants and animals (Çinar *et al.*, 2014; IPBES, 2019; Stout & Morales, 2009). They can have devastating impacts on local fauna and flora, which are exacerbated on island ecosystems (Russell *et al.*, 2017). In Europe, 14’000 alien species have been identified and this number is rapidly increasing, leading to a phylogenetic and taxonomic homogenization of species, especially for plants (Roy *et al.*, 2019; Seebens *et al.*, 2017; Winter *et al.*, 2009). In Switzerland, around 20% of plant taxa in the country are exotic, which represent between 500 and 600 species but only around 60 of them are considered problematic (InfoFlora, 2022). Worldwide, climate change is expected to drive biological invasions through global temperature warming, although it depends on the region and the considered species (Bellard *et al.*, 2018; Walther *et al.*, 2009). However, the effective management of invasive species is highly complex, expensive as well as being time and resource consuming (Büyüktahtakın & Haight, 2018) which suggests that limiting their introduction or spread at early stages would be beneficial.

1.1.1.4. Other global threats

Other global threats to biodiversity include the various forms of pollution. This encompasses emissions in the atmosphere (greenhouse gas and aerosols), contamination of terrestrial and aquatic habitats with chemicals and deposition of solids (plastic and wastes)(IPBES, 2019). Concentrations of CO_2, CH_4 and N_2O, which are the main greenhouse gas emitted by human activities and directly responsible for global warming, continue to increase, as well as aerosols which partially cool down greenhouse gas induced warming (IPCC, 2021). Plastic pollution has well-known dramatic impacts on marine and aquatic biodiversity that will not be further developed here (Derraik, 2002; Jambeck *et al.*, 2015; Laist, 1997). However, it has recently been shown that plastic production and release, as part of “novel entities”, is operating way beyond the planetary boundaries and could represent a high risk for our long-term survival, and that microplastic particles were literally raining down in the most isolated parts of the world (Brahney *et al*., 2020; Persson *et al*., 2022).

Agricultural inputs due to intensification represent a large part of run-off pollution into freshwater and especially nutrients from fertilizers and pesticides but also heavy metals (Huang *et al*., 2017; Quinton & Catt, 2007). Excessive quantities of nutrients, especially nitrogen and phosphorus, in rivers and lakes stimulate the growth of plants, but ultimately trigger hypoxia or oxygen depleted zones where algal blooms highly affects habitat productivity, leading to a complete shift of organisms also known as eutrophication (Schindler, 2006). In terrestrial ecosystems, it has impacts on soil quality, species community composition and plant functional traits (Erisman *et al*., 2016; Tang *et al*., 2014). Pesticides have been shown to have dramatic impacts on pollinators, birds, bats, amphibians, plants, ecosystem functions and services, and their use is still increasing worldwide (Brühl & Zaller, 2019; Chiron *et al*., 2014; Geiger *et al*., 2010; Goulson *et al*., 2015; Luzardo *et al*., 2014; Mason *et al*., 2013; Neumann *et al*., 2015; Partap & Ya, 2012; van Lexmond *et al*., 2015).

The direct exploitation of organisms through fishing, hunting, harvesting, poaching or logging, either for subsistence or trade is also a major source of threat to global biodiversity (IPBES, 2019; WWF, 2016), although this might be less important in Switzerland. However, poaching still represents a great threat to many species and is driven by increasing demands in medicinal products, luxury goods and rare species for private collections or trade (Lee *et al*., 2020). Indeed, many famous groups of plants are threatened by poaching such as orchids or carnivorous plants (Cross *et al*., 2020; Fay, 2018). A reduced number of individuals directly induces a loss of genetic diversity which ultimately increases extinction risks (Allendorf *et al*., 2008; Pinsky & Palumbi, 2014).

1.2. Methods to protect biodiversity

While biodiversity continues its decline, ecosystems are losing their resilience and functions which in turn jeopardizes our food and water security and ultimately deteriorating our health and well-being, effective conservation practices and species monitoring are crucial (Cook *et al*., 2010; Honeck* *et al*., 2020a). Efforts have been made worldwide to protect and conserve biodiversity and ecosystem services. For example, the Aichi Biodiversity Targets or the Sustainable Development Goals – also named SDGs – represent a simplified socio-economic-environmental integrated approach monitored by a list of indicators, sometimes difficult to assess (https://www.cbd.int/sp; https://sdgs.un.org).

Today, it is estimated that 16.8% of terrestrial areas and 8.01% of marine areas have protective or conservation measures for their environment according to the United Nation Environment Programme World Conservation Monitoring Centre (UNEP-WCMC & IUCN, 2021) with mixed results. Protected areas are globally increasing although there are some examples of protected area decline (Kroner *et al*., 2019; Naughton-Treves & Holland, 2019). It has been shown that protected areas reduced deforestation and forest degradation within them by 72%, with strictly protected areas showing a higher reduction than areas with a low protection level (Cazalis *et al*., 2020; Shah *et al*., 2021). However, in some areas of high development and of high economic interest, deforestation levels are similar inside and outside protected areas, questioning their effectiveness and relevance (Tesfaw *et al*., 2018). Higher levels of biodiversity have been found in protected areas compared to alternative land-uses but this result is highly dependent on the context of the studies. Nevertheless, it is also recognized that having good practices outside protected areas is essential for plants conservation (Coetzee *et al*., 2014; Heywood, 2019). The protection of species is also a great asset for biodiversity, especially for umbrella species.

For example, the improved protection of large carnivores in Europe resulted in the return of these animals, sometimes after being absent for decades (WWF, 2016).

On one hand, protected areas have important positive implications for nature, but on another hand, they are not completely devoid of human disturbances, stressing the fact that this method alone cannot fully conserve biodiversity. The same conclusions could be made for Aichi targets and SDGs and while their achievement should help bend the curve of biodiversity decline worldwide, so far we have not observed significant changes globally and we are still far from observing the beginning of its recovery (IPBES, 2019). However, some successes at the local scale are proof of the ability of biodiversity to rebound after disturbances but there are still many challenges that lie ahead if we collectively want to safeguard the survival of species and restore the ecosystems on which we depend (Mace *et al.*, 2018).

1.2.1. Why does protecting biodiversity matter?

Aside from the potential consequences that biodiversity loss could have on our own survival as a society, it is important to emphasize the ethics of our actions toward natural systems (Díaz *et al.*, 2006). Extinct species will not come back even though we take drastic initiatives to protect what's left of global biodiversity and we are currently affecting Earth's climate, geology and biosphere for thousands of years to come, at least (Mills *et al.*, 2019).

Species can influence the ecological functioning of natural habitats, and biological diversity has direct impacts on ecosystem functions such as productivity, stability and resilience, although their relation is not linear due to ecological redundancy (Hector *et al.*, 1999; Naeem *et al.*, 1994; Power *et al.*, 1996; Tilman & Downing, 1994; Tilman *et al.*, 1996; Walker, 1992). Indeed, based on a systematic review, Cardinal *et al.* (2012) developed six consensus statements regarding links between biodiversity and humanity: 1) biodiversity loss has been shown to reduce the efficiency by which ecological communities capture resources, produce biomass, decompose and recycle nutrients, ultimately altering their natural cycles; 2) biodiversity increases the stability of ecosystem functions, particularly the resource capture and biomass production; 3) the impacts of biodiversity levels on ecosystem processes are non-linear and saturating, which implies that change accelerates when biodiversity loss increases. Small variations in biodiversity levels have little to no effects on ecosystem functions, but excessive changes could have significant impacts; 4) diverse plant communities are more productive because they contain key species with high influence on the productivity but also because the presence of many functional traits in a community increases total resource capture; 5) loss of biodiversity across trophic levels has more influence on ecosystem functions than loss of biodiversity within trophic levels, meaning that weak trophic levels could lead to cascading effects on ecosystem functions; 6) key species have a major role in the relation between biological traits and ecosystem functions, signifying that the extinction of particular species has greater consequences than others.

Ecosystem functions are the ecological processes at the very base of a concept representing the benefits and well-being people obtain from nature named "ecosystem services" (ES) (Costanza *et al.*, 1997; MEA, 2005). They are also referred to as "nature's contributions to people" or "nature's benefit to people" although there might be some differences in conceptual claims (Díaz *et al.*, 2018; Kadykalo *et al.*, 2019; Pascual *et al.*, 2017). According to the Millennium Ecosystem Assessment (MEA, 2005), ES include: 1) provisioning services such as food production, water, medicinal components or constructing materials availability and resources; 2) regulating and supporting services – which are sometimes merged together – encompassing soil formation, nutrients cycling and the regulation of droughts, floods, land degradations, climate or diseases; and 3) cultural services such as recreational, spiritual, religious and other non-material benefits people could obtain from nature. In other words, the concept of ES encompasses all the values people attribute to natural landscapes as well as the direct and indirect benefits of biodiversity to their well-being and to the economy (Honeck* *et al.*, 2020a; Mace *et al.*, 2012). Indeed, areas with high species diversity provide more ES than areas with a low level of diversity and globally, natural and semi-natural areas provide more ES than cultivated lands (Balvanera *et al.*, 2016; Felipe-Lucia & Comin, 2015; Maestre *et al.*, 2012; Schwarz *et al.*, 2017). However, this link highly depends on the ES measured and the ecosystem considered so while the supply of ES implies a sufficient level of biodiversity, spatial synergies among different ES or between ES and biodiversity may be weak (Cimon-Morin *et al.*, 2013; Honeck* *et al.*, 2020a).

The biological diversity of ecosystems and the restoration of natural areas could help us mitigate the effects and intensity of global warming by improving natural carbon storage (Griscom *et al.*, 2017). Indeed, it is estimated that around 20% of anthropogenic greenhouse gas emissions are absorbed by life in terrestrial ecosystems (Le Quéré *et al.*, 2014). Re-integrating natural environments in cities (as part of nature-based solutions, Maes & Jacobs, 2017) and better protecting biodiverse ecosystems could also help with flood control or heat reduction, ultimately leading to higher mental health and improved mood/happiness (Van den Bosh & Sang, 2017). The spread of human infrastructures and populations, responsible for habitat loss and fragmentation, also creates increased exposure to novel infectious agents from wildlife, potentially leading to worldwide pandemics (Wilkinson *et al.*, 2018). This is, sadly, a hot topic with the recent propagation and spread of the COVID19 disease responsible for millions of deaths worldwide, affecting mental health and the economy with long-term consequences that are difficult to predict at the moment. It is estimated that 70% of emerging diseases and almost all known pandemics are caused by zoonoses, microbes of animal origin, and that the risk of new pandemics is increasing rapidly with the growing proximity of humans and wildlife (IPBES, 2020). Thus, the decline of biodiversity directly threatens our society, jeopardizing our food and water security, deteriorating our health and impacting our socioeconomic well-being.

1.2.2. How to protect biodiversity?

Biological conservation has evolved since the last century and thus, the way we protect nature has as well. Mace (2014) summarized this trend in four steps, showing the evolution from land sparing where nature and humans are separated, to land sharing where they interact sustainably: 1) “Nature for itself” based on protected areas and wilderness; 2) “Nature despite people”, considering human as threats to species and habitats, as well as strategies to reduce these threats; 3) “Nature for people” with the emergence of the concept of ecosystem services and that nature is vital for the good functioning of our society; 4) “People and nature” where the emphasis has moved from the previous utilitarian vision of nature to a cohabitation between the two worlds with sustainable and resilient interactions. This new paradigm encompasses the common health of human beings and natural systems at the same time and analyses social, economic and ecological systems as a whole. This novel framing illustrates our dependence upon ecosystems and emphasizes that people are part of nature, not apart from it (Mace, 2016). Despite human well-being sometimes resulting in deleterious outcomes for nature (i.e., creation of new agriculture areas for food production), we need to consider human interactions when developing biodiversity protection and conservation plans because we are at the very base of its collapse.

Many solutions contribute to help protecting nature at different levels. At the species level, the IUCN red list assesses the vulnerability of species to extinction by following a protocol measuring the evolution of species’ populations over the years. Despite not directly protecting species, the red list allows us to prioritize conservation efforts on the most threatened taxa but also to follow their overall extinction risk over the years. Species could also have international, national and regional protection/conservation statuses conferring various regulations regarding their trade or harvest such as the Convention on International Trade of Endangered Species (CITES). Protecting wild areas is efficient because it encompasses all levels of biodiversity and especially ecosystems functions, habitats, overlooked rare species and “invisible” biodiversity. Although the effectiveness of this method is proven (Lehikoinen *et al*., 2019; Rada *et al*., 2019; Rosso *et al*., 2018), anthropic pressures are still problematic (Geldmann *et al*., 2019). Natural reserves have high ecological interest and offer natural areas to rest, eat and reproduce far from human’s disturbances to wild species (Cantù-Salazar & Gaston, 2010). Protected areas should allow species movement and hence be connected (Brussard, 1991; McNeely, 1994; Saura *et al*., 2018). Indeed, ensuring species movement through a connected landscape, such as the Natura 2000 network in Europe, helps increase the genetic diversity in a metapopulation, which increases the chances of species’ survival by improving their resilience against climate change and other perturbations (Pauls *et al*., 2013).

1.2.2.1. Green infrastructure

Adapted from From: Honeck, E., Sanguet*, A., Schlaepfer, M. A., Wyler, N., & Lehmann, A. (2020). Methods for identifying green infrastructure. SN Applied Sciences, 2(11), 1-25.*

**: first authors.*

“The previously described context has led to a new concept named “Green Infrastructure” (GI) or “Ecological Infrastructure” to help preserve a functional ecosystem network through a sustainable land-use planning. GI describes an interconnected network of natural and semi-natural areas designed and managed to deliver a wide range of ecological, social and economic benefits (Benedict & McMahon, 2006; Da Silva & Wheeler, 2017; European Environment Agency, 2014; Fig. 4). GI are increasingly being considered as a nature-based solution (Cohen-Shacham *et al*., 2016) or natural and cost-effective alternative to anthropic infrastructure to help mitigate environmental impacts, adapt to climate change and build resilient societies. Considering environmental resources as infrastructure allows us to recognize their role in our livelihoods, and also to point out that ecosystem services also require maintenance to sustain their capacity to provide clean water and air, aesthetic benefits, physical and mental health, wildlife conservation and other community values.

One of the main assets of GI is its focus on landscape multifunctionality, i.e., promoting spatial areas that can serve more than one purpose, such as biodiversity conservation, climate change mitigation, the creation of recreational green spaces and supplying employment opportunities (European Environment Agency, 2014). While grey infrastructure is often designed for a single function (e.g., habitation, transport or economy), GI addresses multiple demands and contributes to finding solutions for a range of environmental, social and economic pressures (Naumann *et al*., 2011). To implement a conservation action, planners must know where the most urgent needs are and where actions will deliver optimal results. For this, it is necessary to identify areas where the landscape ensures ecological resilience and habitat quality, helps people and species adapt to climate change and enhances people’s physical and mental health. Visualizing priority conservation areas supports decision-makers to optimally allocate limited resources for ecosystems preservation. Having such priority areas mapped out in advance also saves time by avoiding conflicts when a key resource or environmental concern is brought up after a development project has been initiated (Firehock, 2015).

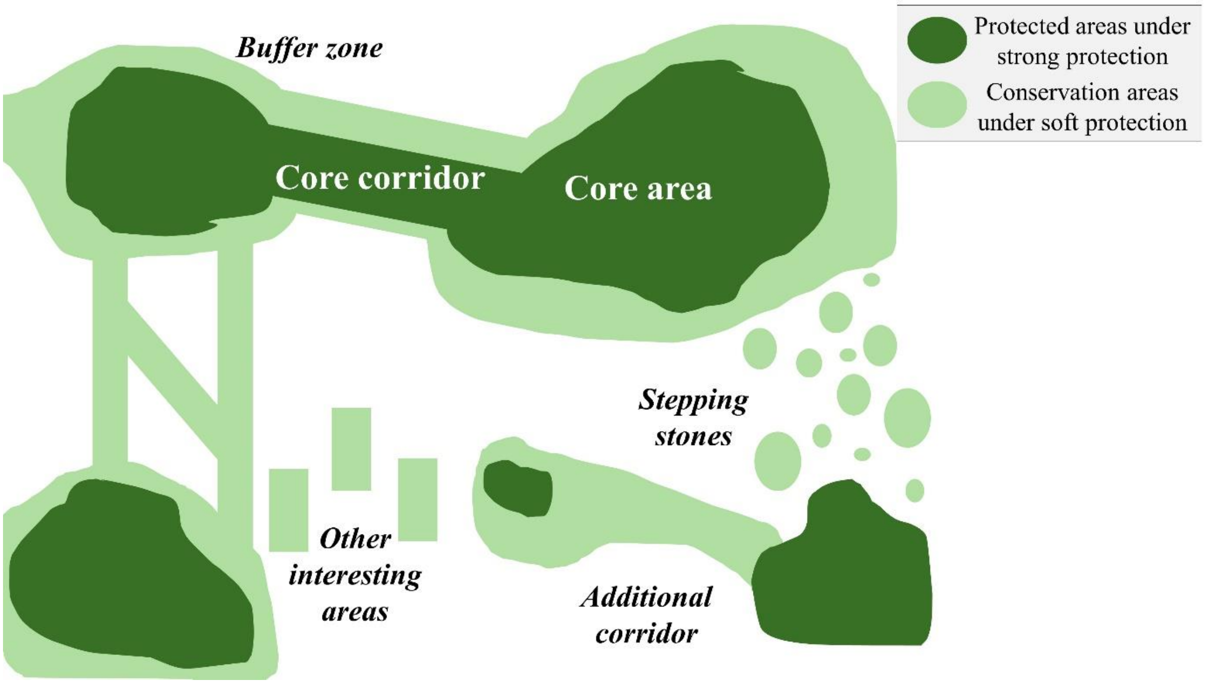


Figure 4. Example of a theoretical Green Infrastructure composed of core areas and corridors under strong protection as well as additional areas of high ecological interest used for connecting the core areas or as a buffer zone around them. Figure inspired from Diamond head consulting (2014).

General definitions of the concept

GI is regarded as a strategic tool to achieve sustainable development and to assess synergies and trade-offs between conservation goals and other conflicting land use interests (Lanzas *et al*., 2019). GI has been integrated into national, regional and continental environmental agendas (DETA *et al*., 2018; European Commission, 2013; FOEN, 2017), and has been applied in diverse policy-making settings, including biodiversity conservation (Garmendia *et al*., 2016; Hostetler *et al*., 2011; Salomaa *et al*., 2017), urban water management (Ellis, 2013; Keeley *et al*., 2013; Liu *et al*., 2014), disaster risk mitigation (Kim & Kim, 2017; Onuma & Tsuge, 2018), climate change adaptation (Demuzere *et al*., 2014; Lin *et al*., 2016; Matthews *et al*., 2015) and human health (Bowen & Lynch, 2017; Coutts & Hahn, 2015; Tzoulas *et al*., 2007). Some have used the GI concept as a strictly urban greening method or architectural element that can also be considered as nature-based solutions (Ignatieva & Ahrné, 2013; Irga *et al*., 2017; Jayasooriya *et al*., 2017; Maes & Jacobs, 2017). Others limit the GI to a network of natural and semi-natural core areas for preserving biodiversity and the supply of ES, with links between these areas to ensure ecological connectivity (Di Minin *et al*., 2017; Lafortezza *et al*., 2013; Liquete *et al*., 2015; Snäll *et al*., 2016).

GI that focus only on biodiversity indicators may not fully capture societal values that may resonate with a larger fraction of the population. In addition, implementing conservation actions based solely on habitats or abiotic surrogates may lack coverage of rare or functionally important species, since similar habitats can be biologically different (Virtanen *et al*., 2018). As ES locations may differ from where they are supplied to where they are consumed, their integration in GI requires special care on the type of connectivity involved in their treatment (Kukkala & Moilanen, 2017). Therefore, priority areas for ES supply and biodiversity distribution should be analysed separately, as they are not appropriate surrogates for each other.

The "three pillars approach" used in Geneva

In 2017, Switzerland approved the biodiversity strategy aiming at reinforcing the protection of Swiss' nature and especially developing and incorporating a Green Infrastructure at the national and cantonal scale (DETA, 2018; OFEV, 2017b, 2021). According to the strategy, GI is made of protected areas as well as connecting areas in order to improve the long-term conservation of biodiversity and ecosystem functions (OFEV, 2021). GI should represent 17% of the territory under strict protection with an additional 13% to buffer or connect protected areas, raising the total surface to 30% (DETA, 2018; OFEV, 2017b, 2021).

Snäll *et al.* (2016) and the European Environment Agency (2014) among others have argued that a functional GI network will require the integration of three main aspects, which we will call 'pillars' (Honeck* *et al*., 2020a): (1) the diversity of species and habitats (commonly referred to as "biodiversity pillar" or "composition pillar"), (2) ES supplies and (3) the structural and functional connectivity of the landscape. Functional connectivity measures the relative ease of mobility between landscape patches for selected species (Taylor *et al*., 1993; With *et al*., 1997), whereas structural connectivity (also named "connectedness") refers to the structural links or topological distance between landscape features (Tischendorf & Fahrig, 2000) but also to landscape's fragmentation.

This "three-pillars" approach enables addressing different levels of diversity (genes, species and ecosystems), as well as related structure, functions and services (Fig. 5). Studying species distribution, natural habitats and ES supply participate in integrating ecosystem and species diversity into GI design. Identifying ES supply can also reveals interactions between people and nature, and demonstrates the relevance of nature preservation to maintain benefits to human well-being among others. This approach, emphasizing the multifunctional aspect of GI, allows different weights to be attributed to selected features, which in turn ensures that the final GI map represents each component according to the study or conservation objectives agreed with stakeholders (e.g. prioritizing overall landscape diversity or prioritizing habitats for threatened species). "

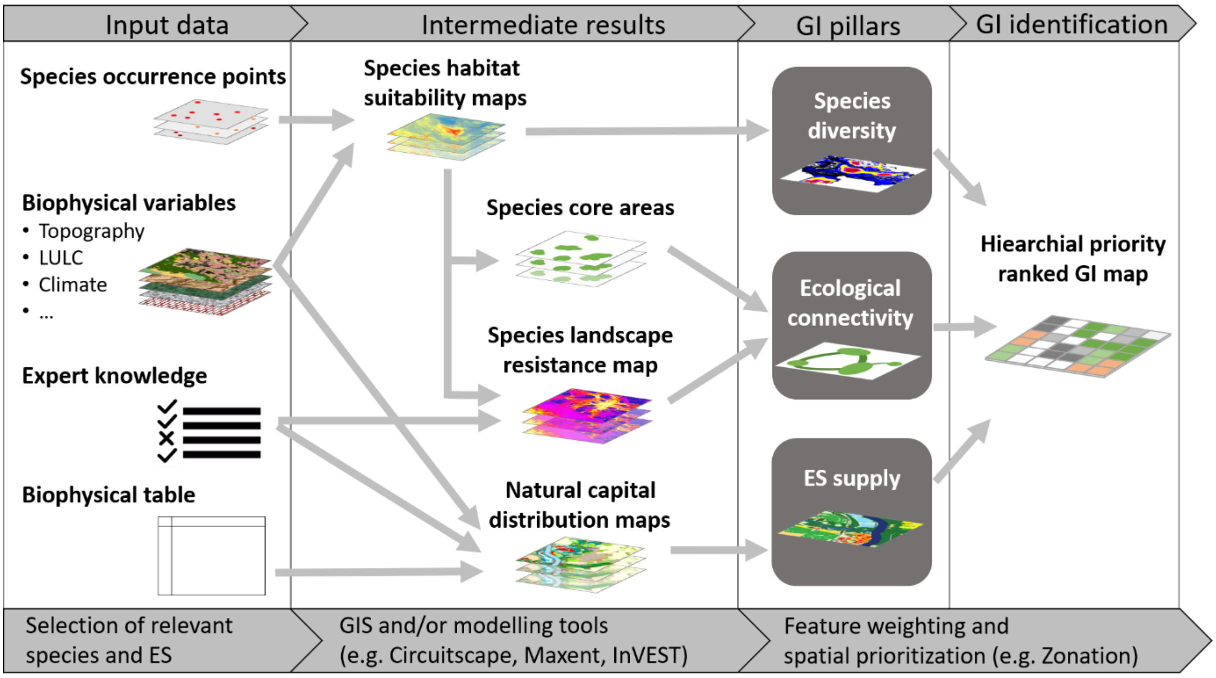


Figure 5. Example of a framework for identifying a GI network, from Honeck et al., (2020a).*

1.3. Assessing the distribution of biodiversity

The main focus of this work is to study the distribution of plant species and by extension the plant diversity in the territory named “Grand Genève”, as part of the assessment of the biodiversity/composition pillar of the Green Infrastructure. Understanding species distributions and communities in a changing environment helps in mitigating the negative impacts of human activities on ecosystems, and allows conservationists to anticipate environmental changes, improving the efficacy of their decisions (García-Diaz *et al*, 2019; Ceballos *et al*, 2017; Pimm *et al*, 2014). In this context, the use of predictive models, such as Species Distribution Models (SDMs), complemented with experts’ knowledge has been proven to be helpful in conservation (Addison *et al*, 2013; Guisan *et al*, 2013; Honeck *et al*, 2020b; Lehmann *et al*. 2002a; Mateo *et al*, 2013; Pullin *et al*, 2004).

SDMs are very useful to predict habitat suitability in a landscape and fill the gaps between the observations of species and their realized potential distributions (Cook *et al*, 2010; Guisan & Zimmermann, 2000; Hirzel & Le Lay, 2008; Lehmann *et al*. 2002b). The key principles of this method are to model the realized ecological niche of a species based on the environmental conditions of its known presences and absences, and project it on a landscape where these environmental conditions are fully described (Elith & Leathwick, 2009; Soberon & Nakamura 2009). The resulting habitat suitability map can be interpreted, with care, as a probability of presence if the model is based on presence and absence data. However, the effective occurrence of a species does not only depend on the suitability of the landscape, but also on: 1) its ability to colonize it and maintain a viable population, 2) the natural history of the area, 3) biotic interactions with other species and/or humans, 4) random unpredictable events, which demonstrates the limits of using the resulting map as a probability of presence instead of a habitat suitability distribution (Guisan *et al*., 2017).

1.3.1. Overview of SDM theory and methods

Understanding the relationship between species and their environment is one of the fundamental topics in ecology. More than one century ago, climate was already recognized as one of the main drivers to explain species distributions (De Candolle, 1855). However, it was during the 1990s that predictive geographical modelling gained importance in order to assess the consequences of, for example, environmental or land-use changes on species distributions as detailed in Guisan & Zimmermann (2000). These statistical methods to correlate environmental predictors and species distribution helped in the development of a more rigorous scientific ecology.

SDM are defined as empirical models relating field observations to environmentally relevant predictors (or explanatory variables), based on statistically or theoretically derived response surfaces (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). Field observations correspond to various forms of individuals’ observations such as presence only, presence/absence or abundance, extracted from several possible field sampling methods. Environmental predictors represent all factors influencing the ecological niche of the species, such as climate, topography, biotic interactions or the distribution of resources or habitats, and their relevance could vary according to the scale of the study area (Guisan & Thuiller, 2005). SDM analyses are highly dependent on 1) the quantity and quality of data used as input (Moudrý & Šímová, 2012) ; 2) the set of explanatory variables selected (Sillero & Barbosa, 2021); and 3) the choice of modelling methods (Araújo & New, 2007). SDM makes several assumptions regarding the ecology of the study area and of the species, the occurrences and the set of explanatory variables (Guisan *et al*., 2017). Indeed, the models capture the temporal snapshot of the equilibrium between the species and its environment, which implies that this method is not well suited for invasive species or those that are (re)colonizing a habitat (Guisan *et al*., 2017). Predictions of species distribution with changing climate are only valid under the strong hypothesis that this equilibrium remains the same under future conditions (Guisan & Thuiller, 2005).

Developing SDMs usually follows five different steps as described in Zurell *et al.*, (2020). First, the conceptualization of the experiment which addresses the objectives, the taxa considered, the study area and the scale. Second, the availability of input data and specifically the type of observations (presences only, presence/absences, background data, etc.), the environmental predictors and the data partitioning. Third, the computational settings for model's fit encompassing explanatory variables selection, model's settings and type of selection, spatial autocorrelation and bias corrections. Fourth, the model's assessment and its associated performances and plausibility, and fifth, the predictions and associated uncertainty which are the main outputs (Fig. 6).

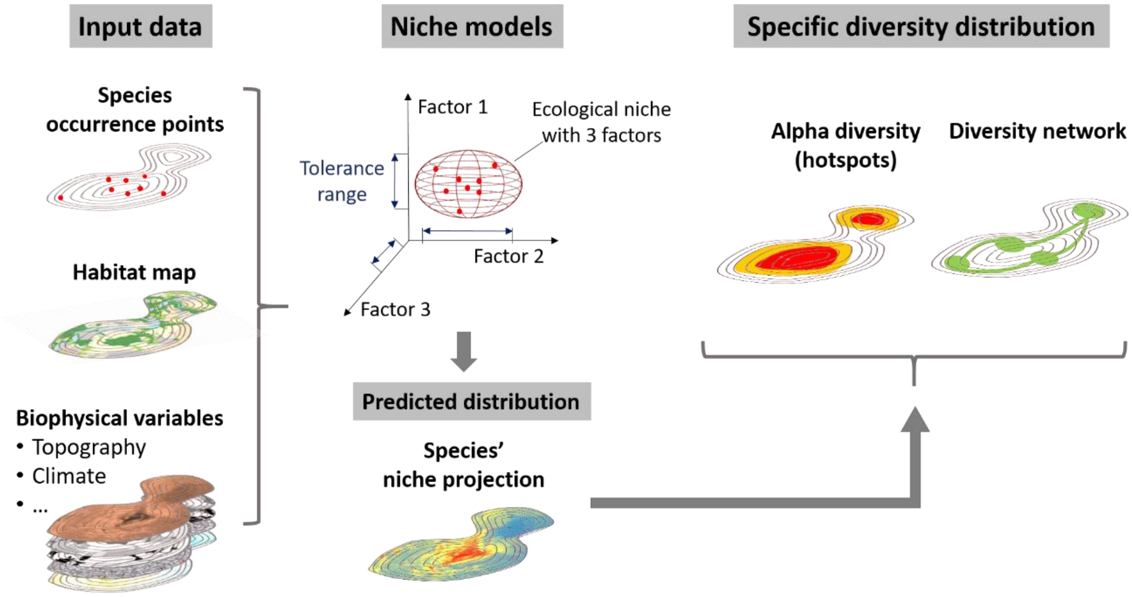


Figure 6. Simplified framework to use SDM and their outputs to derive currencies of biodiversity distribution. From Honeck et al., 2020a*

1.3.1.1. *Methodological approaches*

A large number of methods exist to model species distribution and the R software packages (R Core Team, 2020) have proven to be an efficient environment for statistical modelling and the prediction of species distribution. Several regression approaches exist and are used extensively in SDM because of their strong statistical foundation and their ability to model ecological relationships such as: Generalized Linear Models (GLMs) fitting parametric terms such as linear, quadratic or cubic responses of predictors; Generalized Additive Models (GAMs) which are extending GLMs by fitting non-parametric response shapes based on non-linear, smooth functions, allowing more complex ecological responses; or Multivariate Adaptive Regression Splines (MARS) which are further extending GAMs by allowing multiple responses and fitting interactions between predictors more easily. Machine learning methods have participated in creating new modelling techniques based on maximum entropy, such as MaxEnt, that we will develop in the next paragraph, Boosted Regression Trees (BRT) and Random Forest (RF) which are addressing the problem of small datasets by using shrinkage techniques to fit a series of small models and integrate them at the end without violating the available degrees of freedom. Envelope-style and distance-based methods are characterizing new sites with similarities to known areas of presences only using presence records (Austin, 2002; Elith* *et al.*, 2006; Elith & Leathwick, 2009; Guisan & Zimmermann, 2000; Guisan *et al.*, 2017). Finally, the ensemble forecasting is combining all the above methods to explore the uncertainty associated to the choice of the modelling approach and input variables (Araújo & New, 2007). We will not develop here models to predict community composition such as Generalized Dissimilarity Models (GDM) or Joint Species Distribution Models (JSDMs).

A focus is placed on MaxEnt because it is the selected algorithm for this work. MaxEnt is a modelling method based on machine learning and maximum entropy developed in the early 2000s in order to integrate large data sets and the presence-only data available from museum and herbarium collections into SDMs. The idea of MaxEnt is to estimate the distribution of a species by finding the distribution of the maximum entropy (closest to uniform) where the expected values of each predictor are constrained to match its empirical average given by the occurrences (Elith *et al*., 2011; Merow *et al*., 2013; Phillips *et al*., 2004, 2006). Often considered as a "black box", authors have recently released its code allowing a better understanding of its mechanisms (Mazzoni, 2016; Phillips *et al*., 2017). Nowadays, MaxEnt is widely used in SDM because it is not computationally intensive, allows many settings, and has a user-interface that expands its uses outside the academic community (Merow *et al*., 2013; Phillips & Dudík, 2008; Urbina-Cardona *et al*., 2019). It has been shown to have good performances (Fig. 7), especially with presence-background data (Rhoden *et al*., 2017; West *et al*., 2016), few occurrences or limited data (Baldwin, 2009; Costa *et al*., 2010; West *et al*., 2016; Wisz *et al*., 2008), with coarse predictor resolution (Guisan *et al*., 2007), at local scale (Fois *et al*., 2018), even showing similar performances and/or prediction maps than ensemble forecasting in some situations (Kaky *et al*, 2020). However, the algorithm sometimes finds patterns that do not exist in simulated species (Hoffman *et al*., 2010) or tend to be more sensitive to the sampling data if there is no bias correction or regularization settings (Radosavljevic & Anderson, 2014), which suggest that input data and model settings should be carefully selected to increase model's performances.

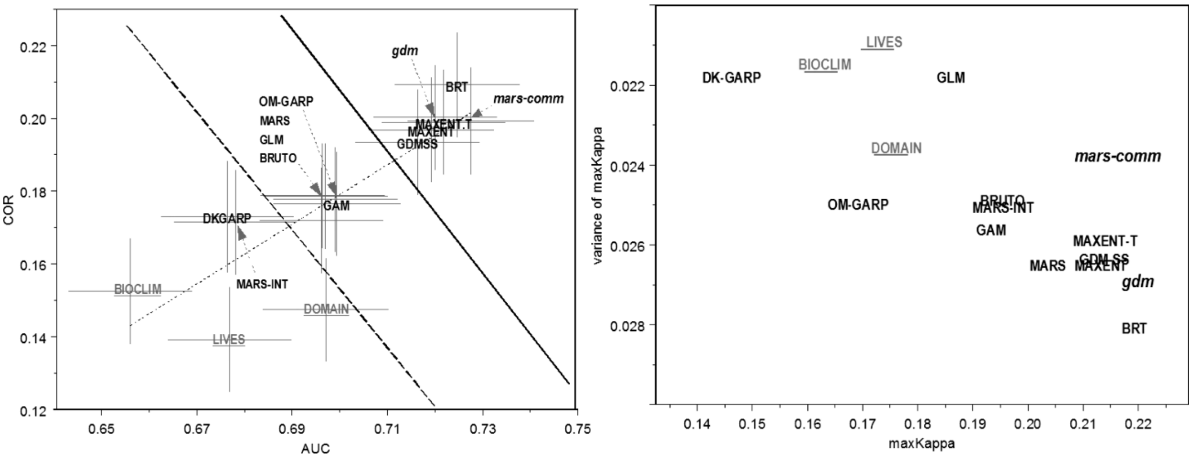


Figure 7. Two figures showing the performances of several SDM methods from Elith et al., (2006), representing presence only data (in grey), presence-background data (in black capitals) and community methods (black lower case italics). The left graph show the mean AUC vs mean correlation (COR), two measures of the performances of a modelling method, and the associated standard errors bars. The right graph show another measure of model's performances and its variance across the 226 species modelled. We can see here that MaxEnt and MaxEnt-T (using threshold features) are showing high performances for the AUC, COR and KAPPA, which is desirable when running SDMs.*

1.3.1.2. Predictors

SDMs results depend on the input data and more precisely on the quality and quantity of occurrences and predictors (Guisan *et al*., 2017; Moudrý & Šímová, 2012; Sillero & Barbosa, 2021). Predictors, or explanatory variables, must be chosen with care according to species' ecology, landscape characteristics, modelling importance and contribution as well as the scale of the study area (Araújo & Guisan, 2006; Guisan & Thuiller, 2005; Hirzel & Le Lay, 2008; Petitpierre *et al*. 2017). Furthermore, they should be as uncorrelated as possible in order to avoid collinearity (Dormann *et al*., 2013). While a set of climatic data is effective to understand the overall distribution of species at a large scale (climatic niche), they might not be as efficient to explain local distributions because the climate is unlikely to vary much over short distances (Fournier *et al*, 2017; McGill, 2010; Pearson & Dawson, 2003). They are, however, the most used predictors, especially when using MaxEnt (Bradie & Leung, 2016). At smaller scales, LULC, soil quality, or topography might represent better explanatory variables (Austin & Van Niel, 2011; Oliveira *et al*., 2021). The resolution of predictors should match the precision of occurrences and be relevant to the study area and species' ecology (Sillero & Barbosa, 2021). Considering climatic and habitat predictors also helps in evaluating the influence of climate and LULC future changes on local species distribution, ultimately improving our capacity to conserve rare habitats and species as well as local biodiversity hotspots.

Fine-scale and detailed classification of LULC is often lacking at local/regional scales resulting difficulties in modelling species distributions. Remote Sensed Information or Remote Sensing Images (RSI) are now widely available and could represent an interesting alternative to LULC information for SDM predictors. These images are already used to measure biodiversity changes in Essential Biodiversity Variables (Kissling *et al*., 2018; Skidmore *et al*., 2015; Vihervaara *et al*., 2017) as proposed by the Group on Earth Observations Biodiversity Observation Network (GEO BON) in 2013. RSI predictors have already been included in SDM at various scales (Amaral *et al*., 2007; Cord & Rödder, 2011; Randin *et al*., 2020; Wilson *et al*., 2013), for plants (Pérez Chaves *et al*., 2018; Cord *et al*., 2014a, 2014b), animals (Cord & Rödder, 2011), rare or invasive species (Amaral *et al*., 2007; Diao & Wang, 2014) but also for direct detection of individuals from space (He *et al*., 2015). While the use of RSI predictors is still quite new, they are able to improve SDMs predictions, especially when environmental information is missing (He *et al*., 2015; Leitão & Santos, 2019), even if they could induce some interpretational biases when used alone (Bradley *et al*., 2012).

1.3.1.3. Occurrences and spatial bias

Two dominant types of occurrences are usually used in SDMs: Presence-absence and "Presence only" usually referring to presence-background data (Guillera-Arroita *et al*., 2015). Presence-absence data for plants usually originate from vegetation plots distributed according to random or stratified sampling schemes that provide information on whether a species was detected or not at the sampling site. This type of occurrence allows for producing a probability of presence for species according to environmental predictors variation. Presence-background data are based on observations of individuals representing a non-exhaustive record of true presences without information on the absence of the species. In SDMs they are used to compare the characteristics of the environment at occurrence sites with those throughout the randomly sampled study area, named background data. Presence data are now widely available and MaxEnt has been shown to produce high-quality models with them (Fig. 7), especially when using a large number of background data (sometimes inadequately referred to as "pseudo-absences"), in order to fully capture the natural variability of predictors in the study area (Barbet-Massin *et al*., 2012; Elith *et al*., 2006, 2011; Phillips & Dudík, 2008).

One major problem with presence-background data is that the abundance of observations is rarely representative of the real abundance of the species but rather of the accessibility of the site (Elith *et al.*, 2011). This sampling bias is rarely considered nor corrected and has been shown to have major impacts on predictions especially when using MaxEnt (Syfert *et al.*, 2013; Yackulic *et al.*, 2013). Several methods have been developed in order to correct this sampling bias and they have been reviewed and tested with MaxEnt by Fourcade *et al*. (2014). One method consists of resampling the occurrences in order to keep a regular distribution in the geographic space by removing the closest observations. However, this method could be problematic if the occurrences are already rare. MaxEnt allows the use of a bias file representing the sampling effort that could be created using the Kernel density of all presences. Another method is to restrict the background data to the sampled area or by using a sampling probability file as a probability of randomly creating background data which induces the creation of more background data in highly sampled areas. These sampling bias correction methods have been used in this work and are further developed in the corresponding chapters of the results. Although MaxEnt is less sensitive to sample size than other methods, a large quantity of observations produces the highest performances (Wisz *et al.*, 2008). Good occurrences quality, a sufficient number of observations and corrected sampling bias contribute to increase the performances of the model (Barbet-Massin *et al.*, 2012; Elith *et al.*, 2006; Phillips *et al.*, 2009; Zaniewski *et al.*, 2002).

1.3.1.4. Evaluating performances

To evaluate the performances of a model, the occurrences are often randomly partitioned in two subsets, one used for fitting the model and the other to test its predictions using accuracy metrics (Araújo *et al.*, 2005). Several metrics allow the evaluation of the model's capacity to discriminate real presences from absences or background data, based on a confusion matrix. Three main metrics are commonly used and have been applied in this work: the Area Under the Curve of a receiver operating characteristics (AUC, Hanley & McNeil, 1982), Cohen's Kappa (Cohen, 1960) and the True Skill Statistic (TSS, Allouche *et al.*, 2006; Peirce, 1884). However, these metrics alone do not always reflect the true performance/quality of the predictions, especially when applied with "presence-only" models (Lobo *et al.*, 2008; Leroy *et al.*, 2018). Indeed, these metrics should not be used to describe an intrinsic quality of the model, especially if real absences or spatially independent presence-data are missing because these performance metrics are designed to work with real absences (Bahn & McGill, 2012; Jiménez-Valverde, 2012). The dependence of AUC and Kappa to the target taxa's prevalence is highly debated (Allouche *et al.*, 2006; Manel *et al.*, 2001; McPherson *et al.*, 2004) as is their reliability as a comparative measure of accuracy between predictions (Lobo *et al.*, 2008). Recently, TSS score has also been shown to be dependent on prevalence in some situations (Leroy *et al.*, 2018). The species' prevalence represents the proportion of the study area that is actually occupied by the species but mostly refers to the sample prevalence which corresponds to the proportion of sampled sites where the species is present, which is unknown most of the time, especially when using background data. Species' prevalence is thus driven by the extent of the study area and the number of presences and absences (or background data) used (Leroy *et al.*, 2018). Hence, when modelling species distribution within the same spatial extent, set of occurrences and background data, it is possible to use these metrics to compare model's performances because the prevalence remains the same across models.

1.3.2. Predicting species distributions under climate change

Climate change is believed to be one of the most important threats to biodiversity in the coming decades (Bellard *et al.*, 2012). The degree of future change is a fundamental variable to anticipate its impacts on biodiversity, knowing that it is one of the main drivers explaining and restricting species distribution (McGill, 2010; Pearson & Dawson, 2003). Thus, several scenarios were developed by the IPCC representing the evolution of greenhouse gas concentration in the atmosphere until the end of the century. These scenarios are named Representative Concentration Pathways (RCPs) and they were developed by the Coupled Model Intercomparison Project (CMIP) for the fifth assessment report of the IPCC published in 2013. As previously mentioned, new models named Shared Socioeconomic Pathways (SSPs) were developed since then for the sixth assessment report (CMIP6) but were not used in this work because the data were not available in due time. CMIP6 and CMIP5 models have similar predictions, although CMIP6 have finer resolution, improved dynamical climatic processes, less biases over various climatic regions and predict higher average temperatures than the previous models (Chen *et al.*, 2020; Dong *et al.*, 2020; Ortega *et al.*, 2021; Xin *et al.*, 2020). Four RCPs scenarios were developed for the CMIP5: RCP2.6 is a highly optimistic scenario where the peak of greenhouse gas emissions is around 2020 inducing an increase of the concentration in the atmosphere until 2050 followed by a constant decrease, keeping temperatures below +2°C compared to pre-industrial average in 2100; RCP4.5 and RCP6 are intermediate scenarios where efforts are made to reduce greenhouse gas emissions until they start decreasing or stabilize around 2050 while their concentration remains relatively similar or higher than today at the end of the century inducing a warming of around +2°C by 2050 and +3°C by 2100; Finally, RCP8.5 is a business-as-usual scenario where the greenhouse gas emissions and concentration continue to rise until 2100, leading to a global warming of approximately +2°C in 2050 and +4.5°C by 2100 (IPCC, 2013; van Vuuren *et al.*, 2010).

Predicting species distribution under climate change has been done widely over the last two decades and various methods have been proposed (Araújo *et al.*, 2005; Bellard *et al.*, 2012; Elith *et al.*, 2010; Hamann & Aitken, 2013; Hijmans & Graham, 2006; Pearson & Dawson, 2003; Porfirio *et al.*, 2014; Thuiller *et al.*, 2005). However, the use of SDM for future predictions has some limitations and several criticisms have been raised. First, climatic variables are not the only predictors impacting species distribution and even though they might represent the main driver explaining species' large-scale distribution, habitats and topography also play a major role and should be considered (Austin & Van Niel, 2010; Sanguet *et al.*, *under review*). Second, one assumption of SDM is that the considered taxa is in equilibrium with its environment, meaning that it is not in a process of colonization or expansion of its natural range, allowing the model to correctly calculate its realized ecological niche (Guisan *et al.*, 2017). In the case of a changing climate, it is expected that species will migrate in order to follow their optimum climatic niche which is difficult to integrate because the migration rate depends on the species, effective change of climate, local interactions and random events (Sinclair *et al.*, 2010; Woodin *et al.*, 2013). Third, new assumptions should be made regarding species dispersion ability, the absence of evolutionary adaptation processes, resilience and acclimatization between current and future considered time (Austin & Van Niel, 2010; Thuiller *et al.*, 2008). Fourth, new combinations of climatic conditions might appear in the future inducing models to run outside of the scope of their input data because these conditions do not currently exist and cannot be fitted in the model. This might lead to over- or under-estimation of species distributions (Fitzpatrick & Hargrove, 2009; Sinclair *et al.*, 2010). Fifth, the incomplete sampling of niche space for model's fitting biases the predictions because the model does not have access to the full range of predictors' values to calculate the realized ecological niche (Thuillet *et al.*, 2004).

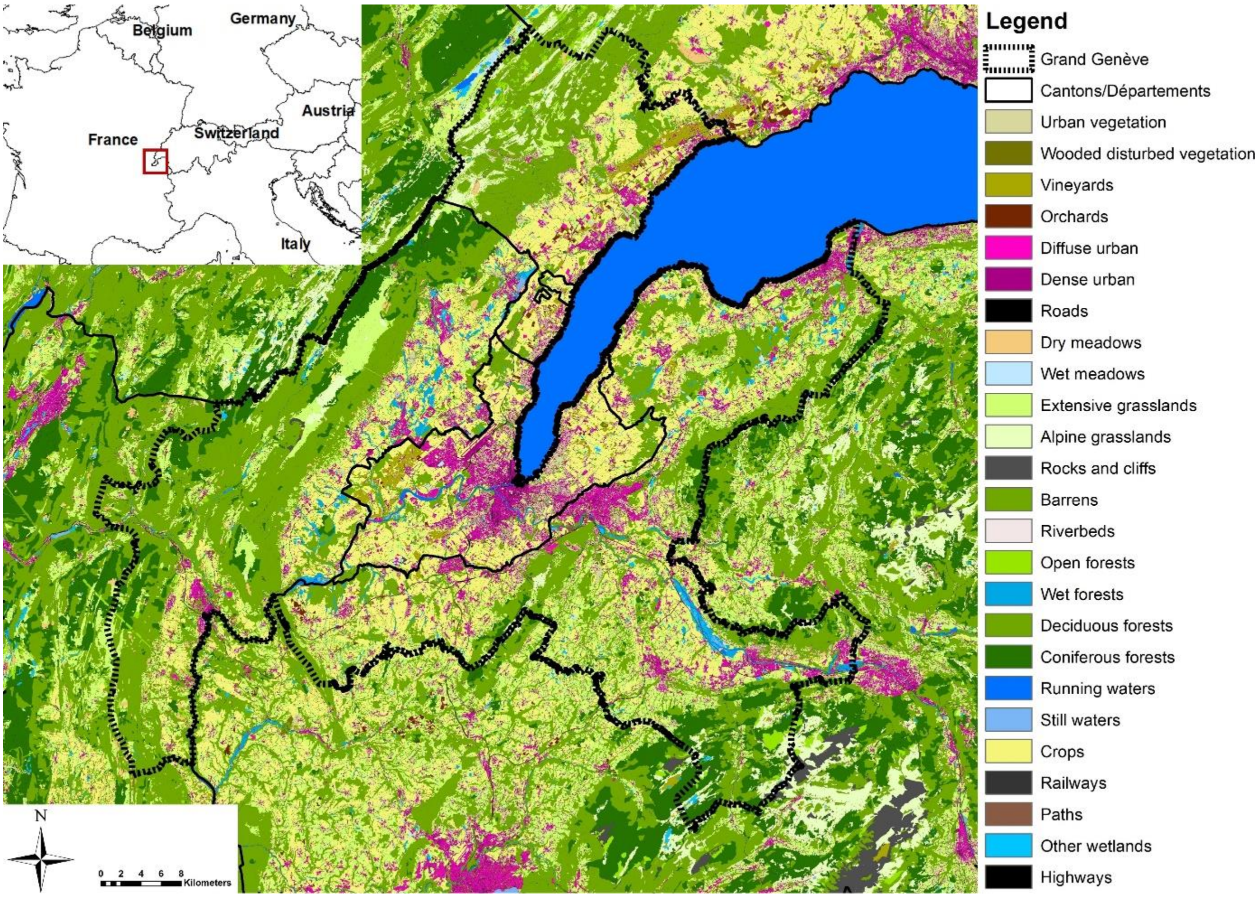


Figure 8. Land-Use-Land-Cover information and location of the study area in the dotted line. From Sanguet et al., under review.

1.4. Local context and research questions

1.4.1. Context and study area

This work is integrated into a larger project aiming at identifying the regional Green Infrastructure by mobilizing local conservation authorities, the University and High Schools of Geneva as well as the Conservatory and Botanical Garden. Thus, the experiments and the associated results are highly dependent on the characteristics of the study area and aligned with the aim of producing useful outputs for the local conservation planning. All the results of this work have been made within the same study area which is presented in Fig. 8.

The study area is a Swiss-French cross-border territory of approximately 2’000 km² integrating two Swiss cantons (Geneva and Vaud) and three French departments (Ain, Haute-Savoie, and Jura) grouped into two regions (Auvergne-Rhône-Alpes and Franche-Comté). It is located in the influence area of the city of Geneva (Switzerland) at the southern end of Lac Léman. The altitudinal range is about 2’000 meters between the lowland plateau – located between the upper right and lower left corner of the study area in Fig. 8 – and the top of mountain ranges located on both sides of the study area (Jura on the North-West and Alps on the South-East). It is mostly dominated by various types of managed and semi-natural forests integrating deciduous and coniferous trees (40%), man-made infrastructures and urban vegetation (17.5%), crops (17%), and finally meadows and pastures (12%). The flat plateau is highly urbanized and the cities around Geneva are increasing fast in size while the steep mountainous areas are mostly covered by (semi-)natural or extensively managed vegetation (Fig. 8).

1.4.2. Local threats and protection systems

The biodiversity in the study area faces specific threats that differ slightly from the global threats illustrated earlier. Indeed, the very dynamic region is home to around one million inhabitants and the population is growing rapidly (14’000 supplementary inhabitants between 2006 and 2014 according to the website of the territory https://www.grand-geneve.org). The urbanization has also grown rapidly to follow the affluence of people as illustrated in Fig. 9. The destruction of (semi-)natural and agricultural lands for urban areas and the resulting fragmentation of the remaining green spaces in the plateau represent one of the most visible threats to biodiversity. As an example, it has been shown that in the canton of Geneva alone, 22% of the surface represent urban impermeable infrastructure and this number has risen 0.6% in only four years, representing an additional 37 hectares (Mombrial *et al*., 2020). Changes in LULC, together with the fragmentation of natural areas represent important pressures for the lowland species. Invasive exotic species also are an additional threat to local plant diversity, especially in rare but highly diverse habitats such as wetlands.

As the study area is located inland, temperatures are expected to rise higher and faster than the global average because the heat is not partially absorbed by the ocean (IPCC, 2021). This phenomenon is already observed with a measured warming of around +2.1°C in Switzerland while global temperatures show an increase of around 1.0°C compared to pre-industrial levels (IPCC, 2018; MétéoSuisse, 2022; NOAA, 2022). Climate change thus represents a major threat, especially for species living in the mountainous parts of the study area. Indeed, it has already been shown that warming temperatures have effects on plants phenology and distribution, especially at middle to high elevations, in Switzerland (Vittoz *et al*., 2013), as well as in different parts of the Alps (Pauli *et al*., 2012; Vitasse *et al*., 2021). The distribution ranges of mountain plants are expected to drastically shrink over the coming decades in the Alps (Dullinger *et al*., 2012; Engler *et al*., 2011) and the observed increase of specific richness due to the altitudinal shift of mid-elevation species is also related to global warming (Pauli *et al*., 2012; Steinbauer *et al*., 2018). Together with changes in precipitation regimes, warming temperatures are thus expected to represent a major driver of change in future species distributions in the study area. This demonstrates the relevance of assessing the magnitude of this induced change.

In Switzerland, the protection of species partially depends on the international responsibility of the country in hosting a large part of their distribution named “priority species”. According to the Office Fédérale de l’Environnement, this concerns 1272 species of plants at the national level and 228 in Geneva (OFEV, 2017a). Protected and priority species’ habitats are also under protection or are part of action plans to ensure the persistence of those species (OFEV, 2017b). In a recent assessment, it was estimated that 37.2% of the flora of Geneva is endangered and this number rises to 49.5% if the near threatened species are added (Mombrial *et al*., 2020). In the metropolitan area of France, 534 plant species are under protection nationally and two lists of 250 species in the Rhône-Alpes region and 236 in the Franche-Comté region (which are part of the study area) complete the national one. It is strictly forbidden to harvest, destroy, use or sell wild specimens of these plants according to the Journal Officiel de la République Française (JORF, 1982, 1990, 1992). Some species could also help determine specific habitats (ZNIEFF), being part of action plans at the very local scale or being considered as of particular interest (named “espèces patrimoniales”).

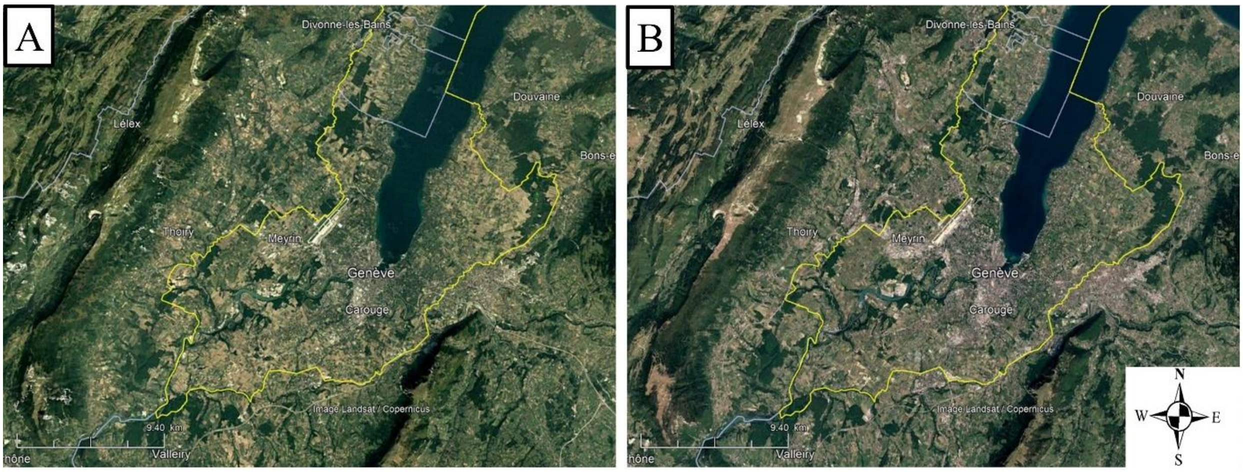


Figure 9. Aerial views of Geneva and its direct surrounding in 1984 (A) and 2020 (B) gathered from Google Earth (accessed in May 2022). Urban areas growth is highly visible especially on the Eastern and Western borders of Geneva.

1.4.3. Structure, objectives and research questions

The thesis' results are organized in four sections.

The first section (chapter 2) focuses on the Green Infrastructure concept, and especially existing methods to identify and implement it. Indeed, this concept has been widely used for various purposes from greening methods of the urban environment to the establishment of protected areas as presented in this introduction. Diverse scientific fields and concepts are integrated, or not, in the process and the methods to assess them also diverge from one study to another. The objective of this first chapter is to review the literature in order to clarify the concept of "Green Infrastructure", describe and evaluate existing methods based on the three pillars approach, and finally provide a guide toward possible tools and best practices to assess GI.

The second section (chapter 3) deals with the modelling process of species distribution in order to supply qualitative outputs for the biodiversity/composition pillar of the GI. SDM could be run with various types of predictors such as biotic (habitats distribution derived from LULC map), climatic (temperatures, precipitations), topographic predictors (slope, exposition) or remote sensing-based images. However, while it is acknowledged that the inclusion of biotic and topographic predictors globally increase model's performance, little is known on how detailed habitat predictors should be in order to maximize models' performance and prediction quality (a few broad classes vs many detailed classes). LULC information is often missing so the ability of Remote Sensing Images (RSI) to replace habitat predictors in SDMs has also been tested. Finally, models' performances for various ecological groups of plant species were compared and discussed. This section answers the following questions:

- *Which combination of predictors improves models' performances?*
- *Are few large habitat classes better than many detailed ones in SDM?*
- *How effective are RSI predictors and do they produce similar performances than models calibrated with habitat predictors?*
- *Do ecological groups respond similarly to the different predictor sets used in the modelling process?*

The third section (chapter 4) explores the consequences of climate and LULC changes on plant distributions in the study area, and examines species vulnerability to global changes according to their native and red list statuses. We have seen earlier that climate and LULC are among the most important drivers of species distribution and their future changes could have great impacts on plant communities. Thus, species distributions were modelled in 2050 for various future scenarios of climate and LULC changes to better understand the magnitude and impacts such changes could induce. However, there is no general agreement regarding the method to integrate a continental scale climatic model into a regional bio-topographic (biotopo) one and it has rarely been done at such small scale and fine resolution. Thus, two different methods to combine the predictions of climatic and biotopo models were tested and discussed. By measuring several currencies of distributional changes between current and future species range for climatic, biotopo as well as the two combining approaches predictions, a vulnerability index has been proposed to focus efforts on the most vulnerable species. This section answers the following questions:

- *How does the modelling method impact the predictions?*
- *How will climate and land-use changes impact the distributions of plant species?*
- *Which is the most vulnerable group of species?*

The fourth and last section of the results (chapter 5) aims at using previous results to evaluate the relevance of current Conservation Areas (CA) for future conditions, to propose a network of areas of high ecological interest for plant diversity conservation in order to complement current CA, and to participate in the GI elaboration of the territory. The relevance of CA for plant diversity conservation was evaluated by measuring their ability to integrate species' distribution for current and future conditions, and a focus is made on the native status of these species. A biodiversity network covering 30% of the territory was then created using the most interesting areas from the distribution of specific richness (hotspots) and from a prioritization ranking map (priority areas). The biodiversity network's ability to conserve species was then assessed and compared to current CA. The global trends that have been found were then discussed and some highly diverse areas were identified as potential candidates for expanding current CA in the conservation planning of local authorities. This last section is answering the following questions:

- *To which extent are the conservation areas able to conserve current and future plant diversity?*
- *Do suitability hotspots and priority areas are spatially congruent?*
- *Which areas could be used to expand current conservation areas?*

This work aims at bridging the gap between academic research and the work of conservationists by using statistical modelling methods to suggest concrete local biodiversity conservation actions. Identifying the trends of plants' spatial shifts helps in our understanding of the degree of which global changes will impact local plant diversity. Studying the evolution of species distribution in a trans-frontier, local to regional scale study area at fine resolutions represents many challenges but ultimately participates in making better decisions to mitigate the impacts of global changes and to develop a relevant green infrastructure on the territory. The overall aim of this work is to *assess the distribution of plant diversity for the identification of a green infrastructure in Grand Genève considering the context of global changes.*

Pinguicula alpina L. emerging from dormancy. This carnivorous plant species is considered as an indicative species for specific habitats and is not protected in France nor listed among endangered species. It is however protected in the canton of Vaud in Switzerland.

RESULTS

« Essentially, all models are wrong, but some are useful. »

« Globalement, tous les modèles sont faux, mais certains sont utiles »

- George EP. Box & Norman Draper, Empirical Model-Building and Response Surfaces, p.424, 1987

Chapter 2

Methods for identifying Green Infrastructure

From: Honeck*, E., Sanguet*, A., Schlaepfer, M. A., Wyler, N., & Lehmann, A. (2020). Methods for identifying green infrastructure. SN Applied Sciences, 2(11), 1-25.

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In this paper, I participated in the conceptualization and development of the methodology together with all the co-authors, and carried out the experiments and the writing of the original draft together with Erica Honeck, the other first author of this paper.

2.1. Context

Nature forms interdependent networks in a landscape, which is key to the survival of species and the maintenance of genetic diversity. Nature provides crucial socio-economic benefits to people, but they are typically undervalued in political decisions. This has led to the concept of Green Infrastructure (GI), which defines an interlinked network of (semi-)natural areas with high ecological values for wildlife and people, to be conserved and managed in priority to preserve biodiversity and ecosystem services. This relatively new concept has been used in different contexts, but with widely diverging interpretations. There is no consensus, either on its components or on the method to identify and map GI (Matsler et al., 2021; Wang & Banzhaf, 2018). Consequently, the concept of GI has been formulated and interpreted in divergent ways, and various concepts and names have emerged to refer to the same idea (e.g., greenprints, natural asset maps, ecological networks, green, blue, brown, black corridors) (Firehock, 2015). Inconsistent definitions can lead to misunderstandings among stakeholders and hinder efforts to mainstream GI into sustainable development actions and policy agendas. Operational definitions of GI vary both in the type of habitat they include, but also the biological value-sets that are incorporated. A typology of GI could help provide an overview of this variation. We argue in this paper that the identification and implementation of a GI should follow a separated assessment of three pillars: the distribution of biodiversity (composition), ecosystem services supply, and the connectivity of the landscape.

This paper reviews the different GI identification approaches used in case-studies that have the same GI definition as mentioned above. Following the foundations and recommendations of GI identification by Snäll et al. (2016), we analysed if and how the case-studies included the three pillars and how the areas were selected to be integrated in the GI network. We then evaluated the methods used to assess the three pillars and the identification of GI itself. We summarized these approaches in levels according to their representativeness and reliability in order to help future researchers identify the appropriate method for their own work. We also discussed some hypotheses explaining the observed tendencies in the method's choice, as well as future challenges for GI identification and mapping.

Methods for identifying Green Infrastructure

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Keywords: Green Infrastructure; spatial conservation prioritization; biodiversity; ecosystem services; connectivity

Abstract

Context

Nature forms interdependent networks in a landscape, which is key to the survival of species and the maintenance of genetic diversity. Nature provides crucial socio-economic benefits to people, but they are typically undervalued in political decisions. This has led to the concept of Green Infrastructure (GI), which defines an interlinked network of (semi-)natural areas with high ecological values for wildlife and people, to be conserved and managed in priority to preserve biodiversity and ecosystem services.

Objectives

This relatively new concept has been used in different contexts, but with widely diverging interpretations. There is no apparent consensus in the scientific literature on the methodology to map and implement a GI network. This paper aims to serve as an informed primer, to help researchers that are new to GI mapping understand the key principles and terminology, and provide them with an overview of different approaches to guide them towards the most appropriate tool choices for the needs of their own case-study.

Methods

Through a literature review of articles on creating GI networks, we summarized and evaluated commonly used methods to identify and map GI. We provided key insights for the assessment of diversity, ecosystem services and landscape connectivity, the three 'pillars' on which GI identification is based according to its definition.

Results and Conclusions

Based on this literature review, we propose 5 theoretical levels towards a more complex, reliable and integrative approach to identify GI networks. We then discuss the applications and limits of such method and point out future challenges for GI identification and implementation.

2.2. Introduction

2.2.1. Context

Climate change and biodiversity loss are two of the most urgent challenges of our time (IPBES, 2018a, 2019; IPCC, 2014; UN Environment, 2019). Biodiversity at all levels is declining worldwide at an unprecedented rate, due mainly to land and sea use changes, direct exploitation of organisms, climate change, pollution and invasive alien species, and are expected to continue declining if no concrete actions are taken (IPBES, 2019; Newbold et al., 2015; Visconti et al., 2016). Ecosystems are losing their resilience to maintain their functions, which will ultimately jeopardize our food and water security, deteriorate our health and threaten our social-economic well-being (Dawson et al., 2011; McGill et al., 2015; Scheffers et al., 2016).

It has been estimated that 68% of the world's growing population will live in urban areas by 2050 (United Nations, 2019), which will inevitably increase the pressure to develop the "grey" infrastructure for housing, mobility and economic use. Along with other human activities, urbanization continues to have serious consequences for biodiversity and the provision of ecosystem benefits to people. Growing demand for new residential areas is a major policy driver in urban land use planning and management, and road constructions also represent a global threat to biodiversity (Meijer et al., 2018). Despite numerous efforts devoted to nature conservation and the expansion of protected areas, we are failing to meet the Aichi Targets for 2020 (IPBES, 2019; Tittensor et al., 2014) We now face the urgent need for a credible agenda and well-defined action plan to safeguard the survival of species and restore the ecosystems on which we depend (Mace et al., 2018).

2.2.2. The concept of Green Infrastructure

As land degradation is one of the major threats to natural habitats and biodiversity (Arthington et al., 2016; Baur and Erhardt, 1995; IPBES, 2018b, 2019), the importance of our natural capital in decision-making must be better emphasized to improve the sustainability of landscape management (Blaikie and Brookfield, 2015). This recognition has led to the concept of 'Green Infrastructure' (GI) (Benedict and McMahon, 2006) to help preserve a functional ecosystem network through land use planning. GI describes an interconnected network of natural and semi-natural areas designed and managed to deliver a wide range of ecological, social and economic benefits (Benedict and McMahon, 2006; European Environment Agency, 2014). It is regarded as a strategic tool to achieve sustainable development and to assess synergies and trade-offs between conservation goals and other conflicting land use interests (Lanzas et al., 2019). GI has been integrated into national, regional and continental environmental agenda (DETA et al., 2018; European Commission, 2013; FOEN, 2017), and has been suggested as a spatial planning tool in diverse policy-making settings, including biodiversity conservation (Garmendia et al., 2016; Hostetler et al., 2011; Salomaa et al., 2017), urban water management (Ellis, 2013; Keeley et al., 2013; Liu et al., 2014), disaster risk mitigation (Kim and Kim, 2017; Onuma and Tsuge, 2018), climate change adaptation (Demuzere et al., 2014; Lin et al., 2016; Matthews et al., 2015) and human health (Bowen and Lynch, 2017; Coutts and Hahn, 2015; Tzoulas et al., 2007).

One of the main assets of GI is its focus on landscape multifunctionality, i.e. promoting spatial areas that can serve more than one purpose, such as biodiversity conservation, climate change mitigation, the creation of recreational green spaces and supplying employment opportunities (European Environment Agency, 2014). While grey infrastructure is often designed for a single function (e.g. habitation, transport, or economy), GI addresses multiple demands and contributes to finding solutions for a range of environmental, social and economic pressures (Naumann et al., 2011). Da Silva and Wheeler (2017) have traced the history of the concept of ecosystems as an infrastructure, and synthesized the concept of GI as a network of natural, semi-natural areas that are designed and managed at different spatial scales for the preservation of biodiversity and a wide range of ecosystem services, to ensure resilient ecosystems and societies.

To implement a conservation action, planners must know where the most urgent needs are and where actions will deliver optimal results. For this, it is necessary to identify areas where the landscape ensures ecological resilience and habitat quality, helps people and species adapt to climate change and enhances people's physical and mental health. Visualizing priority conservation areas will support decision-makers to optimally allocate limited resources for ecosystems preservation.

However, there is no consensus, neither on its components nor on the method to identify and map GI (Wang and Banzhaf, 2018). Consequently, the concept of GI has been formulated and interpreted in divergent ways, and various concepts and names have emerged to refer to the same idea (e.g. greenprints, natural asset maps, ecological networks, green, blue, brown, black corridors) (Firehock, 2015). Inconsistent definitions can lead to misunderstandings among stakeholders and hinder efforts to mainstream GI into sustainable development actions and policy agendas. Operational definitions of GI vary both in the type of habitat they include, but also the biological value-sets that are incorporated. A typology of GI could help provide an overview of this variation.

Some have used the GI concept as a strictly urban greening method or architectural element that can also be considered as nature-based solutions (Ignatieva and Ahrné, 2013; Irga et al., 2017; Jayasooriya et al., 2017; Maes and Jacobs, 2017). Others limit the GI to a network of natural and semi-natural core areas for preserving biodiversity and the supply of ecosystem services (ES), with links between these areas to ensure ecological connectivity (Di Minin et al., 2017; Lafortezza et al., 2013; Liquete et al., 2015; Snäll et al., 2016).

GI that focus only on biodiversity indicators fail to capture societal values that may resonate with a larger fraction of the population. In fact, while the supply of ES implies a minimal level of biodiversity, spatial synergies among different ES or between ES and biodiversity may be weak (Cimon-Morin et al., 2013). In some specific eco-regions, areas with high species diversity provide more ES than areas with low levels of diversity (Maestre et al., 2012), but this is not always the case (Manhães et al., 2016). In addition, implementing conservation actions based only on habitats or abiotic surrogates may lack coverage of rare or functionally important species, since similar habitats can be biologically different (Virtanen et al., 2018). As ES locations may differ from where they are supplied to where they are consumed, their integration in GI requires special care on the type of connectivity involved in their treatment (Kukkala and Moilanen, 2017). Therefore, priority areas for ES supply and biodiversity distribution should be analyzed separately, as they are not appropriate surrogates for each other.

In this paper, we explore how a multidimensional GI, which integrates both numerous biodiversity and ES indicators, could be implemented. Snäll et al. (2016) and the European Environment Agency (2014) among others have argued that a functional GI network will require the integration of three main aspects, which we will call 'pillars': (i) the diversity of species and habitats (commonly referred to as "biodiversity"), (ii) ecosystem services (also referred to as nature's contributions to people) (Díaz et al., 2018), and (iii) the structural and functional connectivity of the landscape. Biodiversity is the variability of living organisms at various scales from genes, to species and landscapes (CBD, 1992). ES are nature's benefits and contributions to our society and our well-being (Costanza et al., 1997; MEA, 2005). Functional connectivity measures the relative ease of mobility between landscape patches for selected species (Taylor et al., 1993; With et al., 1997), whereas structural connectivity (also named "connectedness") refers to the structural links or topological distance between landscape features (Tischendorf and Fahrig, 2000). This paper aims to serve as a primer, to help researchers that are new to GI mapping understand the key principles and terminology. We provide a structured catalogue (typology) of existing GI methods, and a guide towards possible tool choices for the needs of their own case-study.

2.2.3. Objectives

This paper reviews the different GI identification approaches used in case-studies that have the same GI definition as mentioned above. Following the foundations and recommendations of GI identification by Snäll et al. (2016), we analyzed if and how the case-studies included the three pillars (diversity, ES, and connectivity), and how the areas were selected to be integrated in the GI network. We then evaluated the methods used to assess the three pillars and the identification of GI itself. We summarized these approaches in levels according to their representativeness and reliability in order to help future researchers identify the appropriate method for their own work. We also discussed some hypotheses explaining the observed tendencies in the method's choice, as well as future challenges for GI identification and mapping.

2.3. Methods

2.3.1. Articles selection

We focused our articles on search results from Web of Science using the following topic keywords: "ecosystem service*" AND "biodiversity" AND ("corridor*" or "connect*") AND "green infrastructure*". We then filtered out articles defining GI as strictly urban greening methods or architectural elements and used those that interpret GI as a strategically planned network of interlinked natural and semi-natural areas to preserve biodiversity and ES, to compare different GI identification approaches. We then looked at how many case-studies explicitly performed a separate assessment of each of the three pillars for their GI design: 1) biological diversity (habitats, species occurrences, species distributions), 2) ES (relations between vegetation types and services, modelling of ES), and connectivity (functional connectivity with species dispersion and resistance maps, landscape structure). The full dataset of references is available in the additional resources (Appendix 1).

2.3.2. Evaluation methods

We focused our analysis of different GI identification approaches on our review of the literature (Appendix 1). The methodological review consisted in analyzing for each pillar the type of data used as input, the software and methods used, the quality and quantity of items calculated, modelled or mapped, the choice of surrogates, the conceptual approach, the representativity and reliability of the results in the context of nature conservation. Following the foundations and recommendations of GI identification by Snäll et al. (2016) and our review of the literature (Appendix 1 - articles with similar GI definition), we then classified GI identification approaches into 5 levels, according to the complexity of their methods. The lower level methods would represent a GI identification considering one or two pillars, a few surrogates and simplified analysis, and higher-level methods would consider all pillars, many surrogates, and a complex methodology to identify GI. We discussed these complexity levels and their relevance in the discussion.

Having a common baseline to identify and map GI is necessary, since there are as many methods as articles in the literature. The aim of this work is not to evaluate the quality of GI identification method for each article, but to point out general, theoretical, conceptual and methodological directions to assess each pillar to reach a more reliable, functional and efficient GI network.

2.4. Results

2.4.1. Bibliographic search

The topic keywords search in Web of Science resulted in 67 articles (Appendix 1). Those defining GI as strictly urban greening methods or architectural elements were filtered out, leaving 32 articles that interpret GI as a strategically planned network of interlinked natural and semi-natural areas to preserve biodiversity and ES. We excluded reviews and conceptual papers, even if they considered the importance of the three pillars, to only keep case-studies for the evaluation of GI mapping methods. Among them, only 7 case-studies explicitly took all three pillars into account - biological diversity, ES, and connectivity - for their GI design (Table 1).

Table 1: approaches used in the 7 case-studies identifying GI with all three pillars. The table lists the scale of the study, the resolution of the resulting maps, the approach used to compile the pillars into a final GI map, the type of data and methods used for the assessment of each pillar, as well as the surrogates used.

Article		(Hermoso et al., 2020)	(Capotorti et al., 2019b)	(Lanzas et al., 2019)	(Capotorti et al., 2019a)	(Hu et al., 2018)	(Cannas et al., 2018)	(Liquete et al., 2015)
Information on the study	**scale**	continental/ national	local	regional	local (city)	regional	regional	continental
	resolution	10km²	2km²	1km²	1.5 km²	30m²	25m²	1km²
	method for final GI network identification	prioritization	prioritization	prioritization	overlap analysis	prioritization with overlay	prioritization	maximum value of pixels for the pillars
Species and habitat diversity pillar	**type of data**	species occurrences, vegetation map	occurrences (trees, shrubs), species distribution maps, natura2000 protected sites, LULC map	Species distribution maps, LULC map	vegetation map	habitat map	habitat map	habitats (for large mammals)
	surrogates	767 vertebrate species, 229 habitats	species richness and conservation concerns of vascular plants, mammals, birds, Amphibians & reptiles	birds of interest, habitats of interest	vegetation types	habitat types	habitat types	large mammals

	software/ methods	compilation of existing data	compilation of existing data	compilation of existing data	vegetation species recognized for their performance in provision of air purification service	InVEST’s “habitat quality” tool	conservation value based on a regional report, natural value including ecological integrity with InVEST's "habitat quality" tool	compilation of existing data
ES pillar	**type of data**	raster maps	LULC habitats map	CORINE LULC and Remote Sensing maps	vegetation map	habitat map	LULC, habitat types, threats raster map, sources of degradation	maps of indicators
	ES types considered	5 ES supplies of cultural, supporting and regulating services	supply of cultural, supporting and regulating services	10 ES supplies of regulating, cultural and provisioning services	air purification service (supply and demand)	"biodiversity service equivalent" including recreation and agriculture	cultural services (recreation, anthropic heritage)	8 ES supplies of regulating, supporting services
	software/ methods	none, used the maps directly as inputs for Marxan	ES supplies of each vegetation type (biophysical table method)	none, used the maps directly as inputs for Marxan	overlap between recognized critical ecosystems, population density and the particulate matter mean annual concentrations	China ecosystem services evaluation indicator based on surveys	conservation value and natural value including levels of ecosystem functions and capacity to provide ES (InVEST’s “habitat quality” tool)	proxy measures
Structure and connectivity pillar	**type of data**	species, ES supplies and habitat maps	LULC	results from biodiversity and ES assessments	vegetation map	habitat map	habitat suitability map based on literature, resistance map based on the inverse of habitat suitability	habitats quality
	structural /functional	structural	structural and functional	structural	structural and functional	structural	functional->corridors (and structural)	functional

	software/ methods	Marxan Zones	structural connectivity with FRAGSTAT's Euclidean Nearest-Neighbor Distance index, and functional connectivity with plant dispersal and plant-animal interactions	Marxan zones	vegetation species composition and planting patterns, biogeographic representativity, dispersal potential. Use of Mean Nearest Neighbor Distance and Proximity Index with FRAGSTAT	Conefor Sensinode	expert opinion, resistance map, least-cost path with ArcGIS Linkage Mapper Cost-Weighted distance-based	habitats quality ranking

Once the three pillars are calculated, they must be compiled to perform a spatial selection of most ecologically valuable areas in order to build a GI network. Although many use conventional overlay analyses by combining GIS data, Snäll et al. (2016) argue that priority areas could be optimized with a spatial conservation prioritization (SCP) method. Despite SCP tools being appropriate for GI network mapping, case-studies applying them to solve the challenges of spatial planning remain scarce. In fact, among the 7 selected case-studies that identified GI based on all three pillars, only 4 used a prioritization method to identify their GI, including 2 using the SCP tool Marxan.

There is a research gap in the literature of studies using SCP methods for GI identification: even when including conceptual GI papers, only 9 papers used or mentioned "spatial prioritization" (Figure 1).

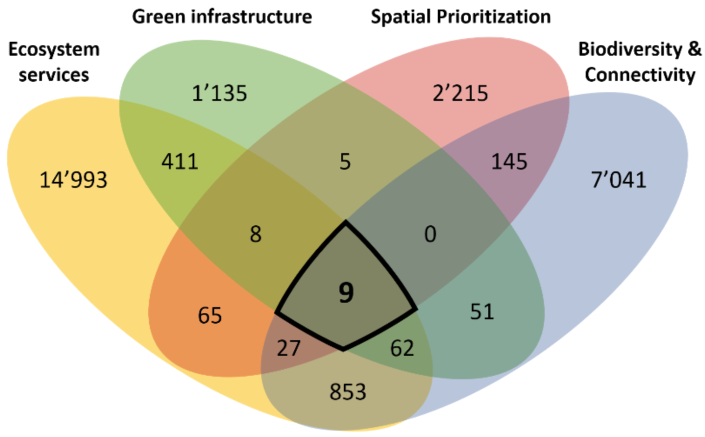

Figure 1: Research gaps in GI studies using SCP. Numbers represent the quantity of results obtained in Web of Science using the corresponding combination of keywords. See Appendix 2 for the exact query.

Box 1: Spatial Conservation Prioritization and its benefits

Methods commonly used for mapping GI include overlay analyses with Geographic Information Systems (GIS), morphological spatial pattern analysis, minimum path model, and landscape-functional units (Niedźwiecka-Filipiak et al., 2019). Yet, these are not well suited for maximizing synergies and minimizing trade-offs between ES and biodiversity, which is the aim of efficient conservation planning (Chan et al., 2006).

SCP is widely used in systematic conservation planning by conservation biologists who are also confronted with finding optimal areas to allocate protected areas or restoration actions (Kukkala and Moilanen, 2013; Moilanen et al., 2009a). SCP software uses computational methods to optimize the selection of priority areas in a landscape for a given target. Weights can be attributed to some features to influence the outcome in order to account for factors such as species rarity, ecological connectivity and opportunity costs. The most widely used prioritization software include Marxan (Ball et al., 2009) and Zonation (Moilanen et al., 2009a).

2.4.2. Approaches to GI mapping

2.4.2.1. Pillars assessment methods and dimensions of a holistic GI

The complexity and precision of the evaluation of each GI pillar will depend on the objectives of each case-study, the needs of the map's end-users, as well as the allocated time and resources. The precision of each pillar will be determined by the source and quality of data (up to date and adequate resolution), the approach, and a sufficient number of surrogates representing the pillar (for instance, supply and demand of various ES, separate consideration of red list species, use of species distribution models together with complementary indices including specific richness/hotspots, naturality, etc.). This section presents different assessment approaches for each pillar to help find the optimal balance between the required information and the resources necessary to acquire it.

Species and habitat diversity

Using perimeters of existing protected areas or (semi-) natural areas in a broad sense (such as forests) is sometimes used to map biodiversity, but this remains a rough estimation of how diversity is distributed in the study area. Considering a broad range of biodiversity surrogates would enable to integrate multiple aspects of biodiversity. Using species distribution models of multiple groups of fauna and flora species, precise habitat maps, and diversity indices such as specific richness, Shannon index, and Simpson index (Shannon and Weaver, 1949 ; Simpson, 1949 ; Forman, 1995) would increase the representativity of the pillar.

Species distribution modeling is a powerful method to model species' realized ecological niches in a landscape and to extrapolate corresponding geographic distributions (Guisan et al., 2017; Pearson and Dawson, 2003; Scherrer et al., 2018; Snäll et al., 2016; Zhang et al., 2018). This method has several advantages, since the distribution of all species cannot be monitored exhaustively in space and time. Species distribution maps can be aggregated in order to map species richness (alpha diversity) and identify "hotspots", i.e. areas where many species live relative to the study area (Lehmann et al., 2002; Scherrer et al., 2018). However, considering only alpha diversity might lead to rare, specialist, endangered or isolated species being overlooked, and could miss most of the global diversity in computer simulations (Lyashevska and Farnsworth, 2012). A specific modelling and assessment of such species could be beneficial. Although relatively uncommon in conservation planning (McKnight et al., 2007), beta diversity, the change of diversity between areas, could also be calculated and mapped (Socolar et al., 2016).

ES supply and demand

ES are sometimes included solely as potential co-benefits of identified high-ecological areas, without separate assessment of specific services. Yet, this may result in overlooking areas providing important ecosystem functions, as the distribution of ES and biodiversity are not appropriate surrogates for each other (Manhães et al., 2016). To have a better representation of ES provided by a territory, multiple services of both regulating and supporting ES should be assessed, as well as their spatial flow from where the service is supplied to where it is consumed (Kukkala and Moilanen, 2017). The choice of services included in the GI design will be influenced by the type of landscape (coastal, mountainous, urban, etc.), and the most relevant services to communicate to the targeted users or audience. Cultural and provisioning ES should, however, be integrated with caution as they may be in opposition with biodiversity and connectivity conservation (Snäll et al., 2016). Conserving biodiversity and connectivity may benefit cultural and provisioning services indirectly and/or in the long-term but including them for the GI design may lead to too many trade-offs or contradictory messages.

ES mapping approaches can roughly be categorized into five types (Martínez-Harms and Balvanera, 2012): 1) the “lookup tables” method links land-cover classes with values derived from the literature to estimate ES supply (natural capital) or ES demand; 2) the “expert knowledge” method relies on specialists to rank land cover classes based on their potential to provide services; 3) the “causal relationships” method incorporates statistics and existing knowledge from the literature to create spatial proxies of ES; 4) the “extrapolation of primary data” method associates weighted field data with land cover and other cartographical data; 5) the “regression models” method combines biophysical information from field data and the literature into a quantitative ecological system model.

Modelling is widely applied for ES assessment. In addition to the methods described above, process-based models are typically used to evaluate key environmental systems such as air, water (Soil and Water Assessment Tool – SWAT; swat.tamu.edu) or soil (Revised Universal Soil Loss Equation – RUSLE). Many models have specifically been developed to analyze ES. For instance, IMAGE, EcoPath and ARIES (Villa et al., 2014) can project future changes in ES; InVEST and TESSA are two static models which describe the state of ES at points in time (IPBES, 2016); and NAIS and Ecosystem Valuation Toolkit are designed for monetary valuation of ES (Bagstad et al., 2013). Grêt-Regamey et al. (2015) have proposed a three tiered-approach for assessing ES in function of policy needs.

Structural and functional landscape connectivity

Spatial structure refers to the topological distance between landscape features (Tischendorf and Fahrig, 2000) or the spatial arrangement of landscape elements, and determines the mosaic of contiguous land cover types (Benedict and McMahon, 2006). Functional connectivity refers to the relative ease of mobility between landscape patches for a specific species (Taylor et al., 1993; With et al., 1997). For instance, spatially unconnected landscape elements (e.g. low connectedness) may represent strong constraints for species with low vagility (D’Eon et al., 2002), but may not necessarily reduce connectivity for flying species (Bélisle, 2005). Corridors structurally connecting two patches may also be too narrow to have any functional connectivity values for some species. Considering only one or the other in a broad sense risks overlooking important corridors, and the pillar would lack representativity of ecological processes and functions.

Analyzing landscape connectivity for multiple species groups (mammals, insects, birds, etc.) helps identify corridors that are more frequently used, to ensure connections between natural patches of habitats, and allow gene exchanges among populations. Tracking animals can be difficult and costly but remains the best method to collect data on the actual use of the landscape. Modeling species connectivity is a suitable alternative (or complement) to animal radio tracking. Information regarding reproduction, habitat preference and dispersion ability is collected to identify suitable habitats for each species. Results from species distribution models can also be used to help identify habitat preferences. A resistance map can be created based on identified core areas, a land use – land cover (LULC) map and expert knowledge. This resistance map attributes a score to each LULC class representing the difficulty of the selected species to travel across it.

Commonly used metrics for modeling functional connectivity include Euclidean distance (centrality analysis), least-cost path length and cost (an extension of graph theory), and circuit theory’s resistance (McRae et al., 2008). Popular corridor modelling tools include Linkage Mapper Connectivity Analysis Software (www.circuitscape.org/linkagemapper) (Belote et al., 2016), GuidosToolbox (forest.jrc.ec.europa.eu/download/software/guidos/), Corridor Design (http://corridordesign.org), Circuitscape (Braaker et al., 2014), Conefor (Saura and Torné, 2009) and Graphab (Foltête et al., 2012). FRAGSTAT (McGarigal et al., 2012) is also a widely used spatial pattern analysis program to calculate various landscape pattern indices.

2.4.2.2. Overall GI identification approaches

Based on the literature review and the precision of each pillar’s assessment, we identified 5 broad levels of GI identification. Case-studies corresponding to levels 1 and 2 without separate analysis of the pillars or with only one or two pillars are often more biocentric-focused, whereas case-studies including all three pillars are more polycentric.

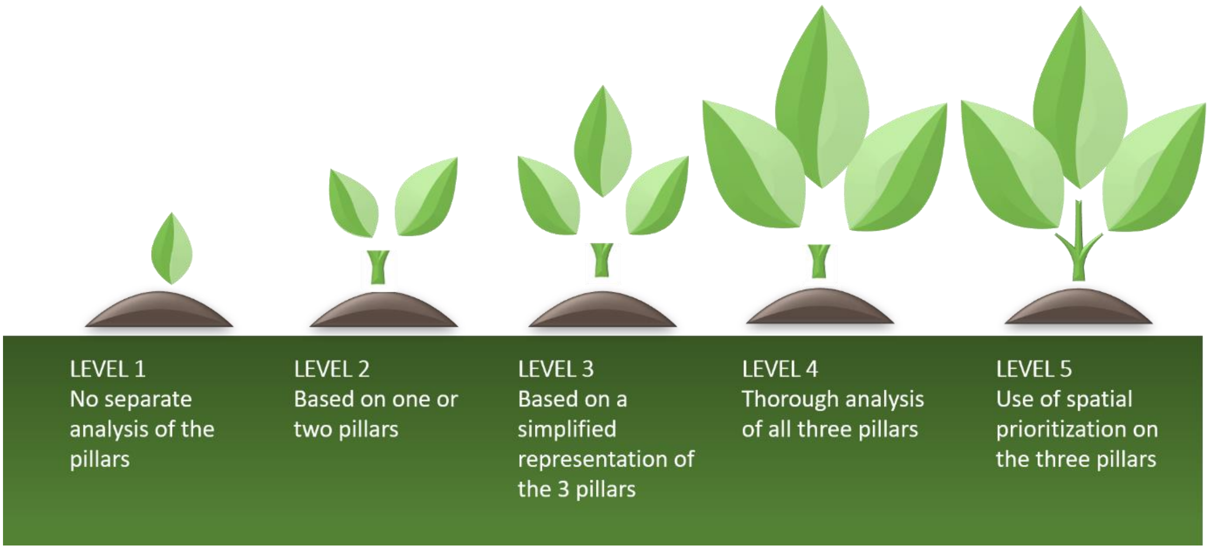

Figure 2: representation of levels in GI identification approaches

Level 1. No separate analysis of the pillars. The GI is identified with existing protected areas and natural spaces, or based on a matrix of qualitative values for each land cover type estimated with expert opinions and the literature. This approach may be quick and simple to compute, but lacks representativity and reliability to distinguish key areas to protect biodiversity, ES, and connectivity.

Level 2: Based on one or two pillars. GI is identified using one or two of the three pillars while mentioning the co-benefit for the remaining one(s), such as habitat distribution and species corridors, or species distributions and ES. Some high-quality areas could be missed if the three pillars are not assessed equally and separately, and the resulting GI network may not effectively preserve resilient natural processes.

Level 3: Based on a simplified representation of the 3 pillars. GI is identified through the separate assessment of all three pillars, but without using a broad range of surrogates. For example, using existing reserves to identify biodiversity-rich areas, or a limited number of ES. This type of GI risks missing important corridors, buffer zones around core areas, or interesting (semi-)natural areas for ES supply or biological diversity (rare species distribution or habitats), especially for large scale studies (see discussion).

Level 4: Thorough analysis of all three pillars. GI is identified on the separate assessment of all three pillars, using a broad range of surrogates. Consideration of many representative natural habitats and species groups (birds, mammals, insects, flowering plants, pteridophytes, coniferous, etc.), several ES, and the evaluation of structural and functional landscape connectivity. The results from the pillars are sufficiently representative of Nature's multi-aspects, but no prioritization method is used to select area to include in the final GI network.

Level 5: In addition to the conditions of level 4, use of spatial prioritization on the three pillars instead of an overlap analysis, in order to rank each pixel of the map according to their multifunctional quality (see Box 1). The resulting map would theoretically represent the most valuable areas to optimize the conservation of natural entities, processes and functions. Below is an illustration of a framework that would correspond to this type of GI identification (Figure 3).

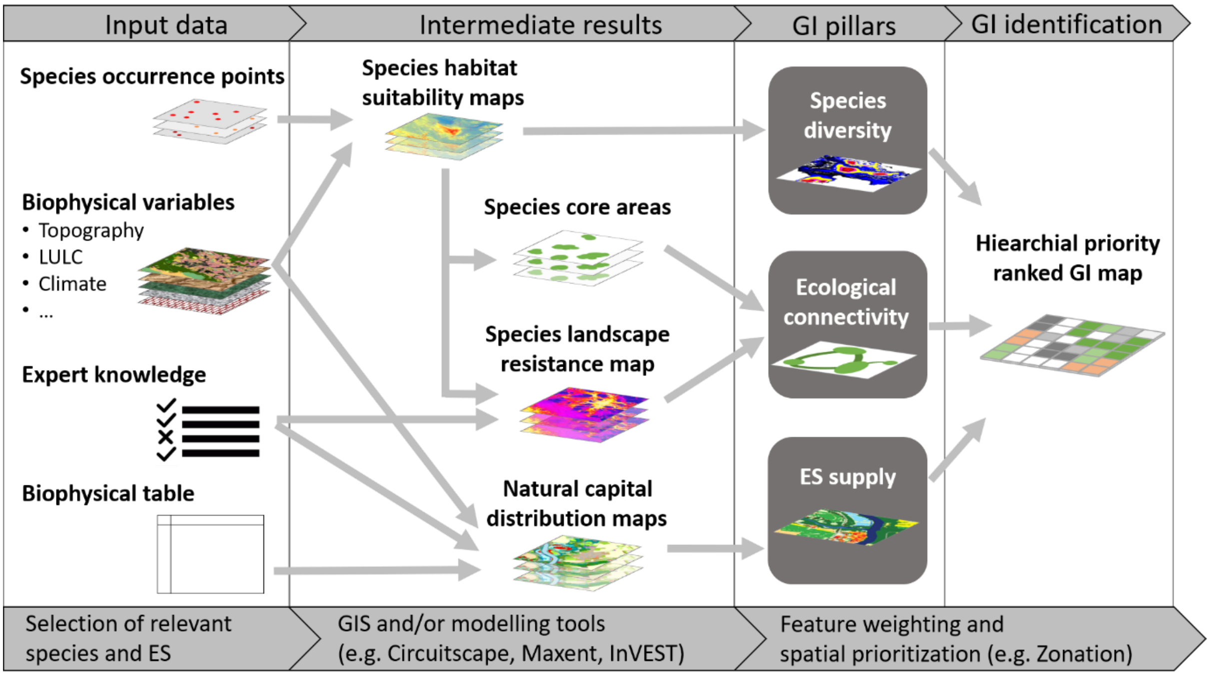

Figure 3: Example of a framework for a case-study requiring precise and detailed GI map, corresponding to a level 5 GI identification approach described above.

2.5. Discussion and Conclusion

The different definitions of GI in the scientific literature have led to highly variable assessment methods and results. GI are sometimes interpreted as interlinkages between core areas for species (Hermoso et al., 2020; Lanzas et al., 2019), and in other cases it is applied to identify areas of interest for specific groups of organisms such as pollinators (Roeland et al., 2019). The GI concept is adaptable and can be used from local scales and urban contexts (Capotorti et al., 2019a, 2019b) to a regional/continental scales and in mosaic landscapes (Hermoso et al., 2020; Kopperoinen et al., 2014; Liquete et al., 2015). Yet, such analyses and purpose widely differ from one another, making it difficult to compare their methods and the identified networks.

To identify GI networks, most studies have relied on a few selected ecosystem functions or services, sometimes including habitats in a broad sense, without considering a wider range of ES and species (Wang and Banzhaf, 2018). Used in this way, GI is suited to address specific environmental concerns such as storm water management or coastal erosion control. GI based solely on habitat and species richness would also fail to account for ecosystem functions, and ecological processes that generate and maintain biodiversity, such as meta-populations dynamics and large effective population sizes. If the concept of GI seeks to support a conservation plan for enhancing the sustainability of a landscape, it is important to search for synergies and trade-offs when setting priority areas for conservation.

Several hypotheses may help explain the scarcity of articles relying on a separated assessment of the three pillars, a wide range of surrogates and spatial prioritization. 1) The restricted availability and accessibility of qualitative data (species occurrences, LULC map etc.) is often a major obstacle to fulfill the numerous inputs required to run a complete analysis (levels 3 to 5) of the proposed methodologies. In fact, compiling data from flora and fauna monitoring or atlas and creating a precise LULC map with several natural habitat categories are the first and fundamental steps in GI identification (Figure 3). 2) Cooperation among many scientific fields is necessary to cover the wide knowledge and skills set required to use the complex methods and software, such as Geographic Information Systems (GIS), species distribution and ES models, as well as field data acquisition (for cultural ES, species occurrences, etc.). Thus, the identification and implementation of GI networks is a transdisciplinary approach that would greatly benefit from creating and maintaining a solid collaboration between stakeholders, landscape planners, technicians and scientists from various fields. 3) Pre-processing data and running models are time consuming and require a specific skillset that may not be readily available in a team. 4) The use of spatial prioritization methods has a steeper learning curve than overlay methods, and may not be as widespread outside conservation biologists.

The levels proposed in this paper represent steps toward methodological complexity and an integrative approach. The more complex the method, the more inputs and data must be integrated, the more processing time and skills are required to run the analyses, and the more multidisciplinary collaboration is necessary for the implementation of the resulting GI network. There is a tradeoff between complexity, representativeness, quantity and quality of inputs and surrogates on one hand, and the accessibility, feasibility and comprehensibility of the methods and results on the other hand. The choice, complexity, and precision of GI identification methods will ultimately depend on the needs of the end-users, as well as the allocated time and financial resources. In fact, a policy-maker may have tight deadlines and only need to have an approximate idea of the distribution of natural capital in a territory, whereas a conservation practitioner may wish to retrace which species and ecosystem functions are behind certain priority conservation areas identified in the GI map.

Overly complex models that are too difficult to explain to decision-makers may not be desirable or suitable for a ‘real-world' application (Ruckelshaus et al., 2015). Yet nature is complex, and includes genetic, species, habitat diversity as well as interactions between organisms, ecosystem functions, individual mobility and functional traits. An overly simplified model will not capture enough facets of the natural world. For example, Kujala et al. (2018) showed that considering many different species increases the stability of modelled conservation areas in spatial prioritization models. But even when many species are considered, the addition of a few randomized rare species in the models could still greatly alter the final result. It is therefore recommended to add as much pertinent information and data as available in the GI identification process, if they fit the global aim of the study (García-Díaz et al., 2019).

Future challenges of GI identification and mapping include: 1) Approving on a common baseline and definition of GI to move from a theoretical framework to an applicable and testable approach. GI as urban nature-based solutions and architectural elements and GI following the definition presented in this paper should be differentiated in particular to avoid potential confusions. 2) A closer collaboration among scientific fields and between research and policy, in order to share skills and knowledge among researchers, conservation practitioners, landscape planners, decision-makers, and other stakeholders. Since biodiversity loss is a global problem and a threat to the resilience of our societies, nature's conservation cannot be efficient without an integrative and transdisciplinary approach. 3) A better accessibility to software and data to integrate as many aspects of diversity, ES and connectivity in GI identification and mapping for landscape planners as possible. Improving data sharing between countries and institutions would also be beneficial to expand this effort.

We believe this work would clarify conceptual aspects of GI identification and serve as a primer for researchers and practitioners that are new to GI mapping, and provide them with an overview of different approaches to guide them towards the most appropriate tool choices for the needs of their own case-study.

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2.7. Appendix 1

Appendix 1-Table 1: *67 articles found using the following keywords in Web Of Science the 24.03.2020 : "TOPIC: ("ecosystem service*") AND TOPIC: ("biodiversity") AND TOPIC: ("corridor*" or "connect*") AND TOPIC: ("green infrastructure*") Timespan: All years"*

The articles are sorted by their GI definition then by year of publication. We analyzed whether the authors considered each pillar in a broad sense, even if they do not specifically assess the pillar in the study. We verified if the authors were interpreting GI as an architectural element or a nature-based solution tool for urban greening, or if they were using the same GI definition than the one presented in this paper. We also categorized each type of article (review, case study or conceptual paper).

Article	year	title	Pillars consideration			Similar GI definition	Article type		
			ES	Diversity	Connectivity		Review	case study	conceptual
Hermoso et al., 2020	2020	Designing a network of green infrastructure for the EU	yes	yes	yes	yes	no	yes	(yes)
Wanghe et al., 2019	2019	Assessment of Urban Green Space Based on Bio-Energy Landscape Connectivity: A Case Study on Tongzhou District in Beijing, China	yes	yes	yes	yes	no	yes	no
Cunha et al., 2019	2019	Methodology for mapping the national ecological network to mainland Portugal: A planning tool towards a green infrastructure	yes	yes	no	yes	no	yes	no
Capotorti et al., 2019	2019	Local Scale Prioritisation of Green Infrastructure for Enhancing Biodiversity in Peri-Urban Agroecosystems: A Multi-Step Process Applied in the Metropolitan City of Rome (Italy)	yes	yes	yes	yes	no	yes	no
Gocheva et al., 2019	2019	Ecosystem restoration in Europe: Can analogies to Traditional Chinese Medicine facilitate the cross-policy harmonization on managing socioecological systems?	yes	no	no	yes	no	no	yes
Lanzas et al., 2019	2019	Designing a network of green infrastructure to enhance the conservation value of protected areas and maintain ecosystem services	yes	yes	yes	yes	no	yes	no

Carlier et al., 2019	2019	Landscape typology and ecological connectivity assessment to inform Greenway design	no	no	yes	yes	no	yes	no
Svensson et al., 2019	2019	Landscape trajectory of natural boreal forest loss as an impediment to green infrastructure	yes	yes	yes	yes	no	yes	no
Capotorti et al., 2019	2019	Biodiversity and ecosystem services in urban green infrastructure planning: A case study from the metropolitan area of Rome (Italy)	yes	yes	no	yes	no	yes	no
Hu et al., 2018	2018	Integrated methods for determining restoration priorities of coal mining subsidence areas based on green infrastructure: -A case study in the Xuzhou urban area, of China	yes	yes	yes	yes	no	yes	no
Vasiljevic et al., 2018	2018	The concept of green infrastructure and urban landscape planning: a challenge for urban forestry planning in Belgrade, Serbia	yes	yes	yes	yes	no	yes	no
de la Fuente et al., 2018	2018	Natura 2000 sites, public forests and riparian corridors: The connectivity backbone of forest green infrastructure	no	yes	yes	yes	no	yes	no
Cannas et al., 2018	2018	Green Infrastructure and Ecological Corridors: A Regional Study Concerning Sardinia	yes	yes	yes	yes	no	yes	no
Albert et al., 2017	2017	Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change	no	yes	yes	yes	no	yes	no
Elbakidze et al., 2017	2017	A bottom-up approach to map land covers as potential green infrastructure hubs for human well-being in rural settings: A case study from Sweden	yes	no	no	yes	no	yes	no
Bellamy et al., 2017	2017	A spatial framework for targeting urban planning for pollinators and people with local stakeholders: A route to healthy, blossoming communities?	yes	yes	yes	yes	no	yes	no

Pelorosso et al., 2017	2017	PANDORA 3.0 plugin: A new biodiversity ecosystem service assessment tool for urban green infrastructure connectivity planning	yes	yes	yes	yes	no	yes	yes
Salomaa et al., 2017	2017	Can green infrastructure help to conserve biodiversity?	yes	yes	yes	yes	no	yes	no
Angelstam et al., 2017	2017	Gap analysis as a basis for strategic spatial planning of green infrastructure: a case study in the Ukrainian Carpathians	yes	yes	yes	yes	no	yes	no
Capotorti et al., 2016	2016	Combining the Conservation of Biodiversity with the Provision of Ecosystem Services in Urban Green Infrastructure Planning: Critical Features Arising from a Case Study in the Metropolitan Area of Rome	yes	yes	no	yes	no	yes	no
Kukkala et al., 2017	2017	Ecosystem services and connectivity in spatial conservation prioritization	yes	yes	no	yes	no	no	yes
Garmendia et al., 2016	2016	Biodiversity and Green Infrastructure in Europe: Boundary object or ecological trap?	yes	yes	yes	yes	no	no	yes
Green et al., 2016	2016	Insurance Value of Green Infrastructure in and Around Cities	yes	yes	no	yes	yes	no	yes
Lynch et al., 2016	2016	Is It Good to Be Green? Assessing the Ecological Results of County Green Infrastructure Planning	yes	no	yes	yes	yes	no	no
Snäll et al., 2016	2016	Green Infrastructure Design Based on Spatial Conservation Prioritization and Modeling of Biodiversity Features and Ecosystem Services	yes	yes	yes	yes	no	(yes)	yes
Liquete et al., 2015	2015	Mapping green infrastructure based on ecosystem services and ecological networks: A Pan-European case study	yes	yes	yes	yes	no	yes	no
Fichera et al., 2015	2015	Application, validation and comparison in different geographical contexts of an integrated model for the design of ecological networks	no	yes	yes	yes	no	yes	no

Dupras et al., 2015	2015	Towards the Establishment of a Green Infrastructure in the Region of Montreal (Quebec, Canada)	yes	yes	yes	yes	no	yes	yes
Kopperoinen et al., 2014	2014	Using expert knowledge in combining green infrastructure and ecosystem services in land use planning: an insight into a new place-based methodology	yes	yes	no	yes	no	yes	no
Phillips et al., 2020	2020	Ecosystem service provision by road verges	yes	no	no	no	yes	no	no
Roeland et al., 2019	2019	Towards an integrative approach to evaluate the environmental ecosystem services provided by urban forest	yes	yes	yes	no	yes	no	no
Wang et al., 2019	2019	Spatial patterns of urban green infrastructure for equity: A novel exploration	no	no	yes	no	no	yes	no
Knapp et al., 2019	2019	Biodiversity Impact of Green Roofs and Constructed Wetlands as Progressive Eco-Technologies in Urban Areas	yes	yes	yes	no	yes	no	no
Park et al., 2019	2019	Urban food systems that involve trees in Northern America and Europe: A scoping review	yes	no	no	no	yes	no	no
Donaldson et al., 2019	2019	Using green infrastructure to add value and assist place-making in public realm developments	yes	no	no	no	no	yes	no
Diduck et al., 2020	2020	Pathways of learning about biodiversity and sustainability in private urban gardens	no	no	no	no	no	yes	no
Pirnat et al., 2019	2019	A tale of two cities-From separation to common green connectivity for maintaining of biodiversity and well-being	yes	yes	no	no	no	yes	no
Lahde et al., 2019	2019	Can We Really Have It All? Designing Multifunctionality with Sustainable Urban Drainage System Elements	yes	yes	no	no	no	yes	no

Suchocka et al., 2019	2019	Transit versus Nature. Depreciation of Environmental Values of the Road Alleys. Case Study: Gamerki-Jonkowo, Poland	yes	yes	no	no	no	yes	no
Ferreira et al., 2019	2019	Impact of the Urbanisation Process in the Availability of Ecosystem Services in a Tropical Ecotone Area	yes	no	no	no	no	yes	no
Auerswald et al., 2019	2019	HESS Opinions: Socio-economic and ecological trade-offs of flood management - benefits of a transdisciplinary approach	yes	no	no	no	no	yes	no
Zang et al., 2019	2019	Enhancing landscape connectivity through multifunctional green infrastructure corridor modeling and design	no	no	yes	no	no	yes	no
Lin et al., 2019	2019	Establishing Priorities for Urban Green Infrastructure Research in Australia	no	no	no	no	no	no	yes
Shi et al., 2018	2018	Research on the Optimization of Regional Green Infrastructure Network	no	no	yes	no	no	yes	no
Dhyani et al., 2018	2018	Ecosystem based Disaster Risk Reduction approaches (EbDRR) as a prerequisite for inclusive urban transformation of Nagpur City, India	yes	no	no	no	no	yes	no
Rolf et al., 2018	2018	Farmland - an Elephant in the Room of Urban Green Infrastructure? Lessons learned from connectivity analysis in three German cities	no	no	yes	no	no	yes	no
Singh et al., 2018	2018	Simulating stream response to floodplain connectivity and revegetation from reach to watershed scales: Implications for stream management	yes	no	no	no	no	yes	no
Artmann et al., 2018	2018	The Role of Urban Agriculture as a Nature-Based Solution: A Review for Developing a Systemic Assessment Framework	no	no	no	no	yes	no	no

Qu et al., 2018	2018	Identifying conservation priorities and management strategies based on ecosystem services to improve urban sustainability in Harbin, China	yes	no	no	no	no	yes	no
Zefferman et al., 2018	2018	Knoxville's urban wilderness: Moving toward sustainable multifunctional management	yes	yes	no	no	no	yes	no
Schifman et al., 2017	2017	Situating Green Infrastructure in Context: A Framework for Adaptive Socio-Hydrology in Cities	yes	no	no	no	no	yes	no
Angelstam et al., 2017	2017	Green infrastructure development at European Union's eastern border: Effects of road infrastructure and forest habitat loss	no	yes	yes	no	no	yes	no
Brill et al., 2017	2017	Methodological and empirical considerations when assessing freshwater ecosystem service provision in a developing city context: Making the best of what we have	yes	no	no	no	no	yes	no
Nilon et al., 2017	2017	Planning for the Future of Urban Biodiversity: A Global Review of City-Scale Initiatives	yes	yes	yes	no	yes	no	no
Sikorska et al., 2017	2017	High Biodiversity of Green Infrastructure Does Not Contribute to Recreational Ecosystem Services	yes	yes	no	no	no	yes	no
Artmann et al., 2017	2017	Using the Concepts of Green Infrastructure and Ecosystem Services to Specify Leitbilder for Compact and Green Cities-The Example of the Landscape Plan of Dresden (Germany)	yes	no	no	no	no	yes	no
Ochoa et al., 2017	2017	Vegetation conservation to reduce hidrometeorological risks on a border metropoli	yes	no	no	no	no	yes	no
Bujs et al., 2016	2016	Active citizenship for urban green infrastructure: fostering the diversity and	yes	no	no	no	no	no	yes

		dynamics of citizen contributions through mosaic governance							
Säumel et al., 2016	2016	Toward livable and healthy urban streets: Roadside vegetation provides ecosystem services where people live and move	yes	no	no	no	no	yes	no
Fattorini et al., 2016	2016	Role of urban green spaces for saproxylic beetle conservation: a case study of tenebrionids in Rome, Italy	no	yes	no	no	no	yes	no
Wang et al., 2016	2016	Urban Watershed Framework Plan for Conway, Arkansas: A Reconciliation Landscape	yes	no	no	no	no	yes	no
Opdam et al., 2015	2015	Framing ecosystem services: Affecting behaviour of actors in collaborative landscape planning?	yes	no	no	no	no	yes	yes
Orsini et al., 2014	2014	Exploring the production capacity of rooftop gardens (RTGs) in urban agriculture: the potential impact on food and nutrition security, biodiversity and other ecosystem services in the city of Bologna	yes	no	no	no	no	yes	no
Schwartz et al., 2014	2014	Outstanding challenges for urban conservation research and action	no	yes	no	no	yes	no	no
Kuttner et al., 2014	2014	Do landscape patterns reflect ecosystem service provision? - A comparison between protected and unprotected areas throughout the Lake Neusiedl region	yes	no	yes	no	no	yes	no
Andrade et al., 2013	2013	Assembling the pieces: a framework for the integration of multi-functional ecological main structure in the emerging urban region of Bogota, Colombia	no	no	no	no	no	yes	no

Mörtberg et al., 2012	2012	Urban ecosystems and sustainable urban development-analysing and assessing interacting systems in the Stockholm region	yes	no	no	no	no	yes	yes

Appendix 1.2 : Number of results in Web of Science using a combination of keywords (1st of May 2020)

14’993 **TOPIC:**("ecosystem service*") *NOT* **TOPIC:**("green infrastructure*") *NOT* **TOPIC:**(spatial AND prioritiz*) *NOT* **TOPIC:**(connect* OR corridor*) *NOT* **TOPIC:**(biodiversity)

411 **TOPIC:**("ecosystem service*") *AND* **TOPIC:**("green infrastructure*") *NOT* **TOPIC:**(spatial AND prioritiz*) *NOT* **TOPIC:**(connect* OR corridor*) *NOT* **TOPIC:**(biodiversity)

145 **TOPIC:**(biodiversity) *NOT* **TOPIC:**("ecosystem service*") *AND* **TOPIC:**(spatial AND prioritiz*) *AND* **TOPIC:**(connect* OR corridor*) *NOT* **TOPIC:**("green infrastructure*")

1135 **TOPIC:** ("green infrastructure*") *NOT* **TOPIC:**("ecosystem service*") *NOT* **TOPIC:**(spatial AND prioritiz*) *NOT* **TOPIC:**(connect* OR corridor*) *NOT* **TOPIC:**(biodiversity)

51 **TOPIC:** ("green infrastructure*") *NOT* **TOPIC:**("ecosystem service*") *NOT* **TOPIC:**(spatial AND prioritiz*) *AND* **TOPIC:**(connect* OR corridor*) *AND* **TOPIC:**(biodiversity)

65 **TOPIC:**("ecosystem service*") *NOT* **TOPIC:**("green infrastructure*") *AND* **TOPIC:**(spatial AND prioritiz*) *NOT* **TOPIC:**(connect* OR corridor*) *NOT* **TOPIC:**(biodiversity)

7041 **TOPIC:** (connect* OR corridor*) *NOT* **TOPIC:**("ecosystem service*") *NOT* **TOPIC:**(spatial AND prioritiz*) *AND* **TOPIC:**(biodiversity) *NOT* **TOPIC:** ("green infrastructure*")

2215 **TOPIC:** (spatial AND prioritiz*) *NOT* **TOPIC:** ("ecosystem service*") *NOT* **TOPIC:** (connect* OR corridor*) *NOT* **TOPIC:** (biodiversity) _NOT_**TOPIC:** ("green infrastructure*")

5 **TOPIC:** (spatial AND prioritiz*) *NOT* **TOPIC:** ("ecosystem service*") *NOT* **TOPIC:** (connect* OR corridor*) *NOT* **TOPIC:** (biodiversity) _AND_**TOPIC:** ("green infrastructure*")

8 **TOPIC:**("ecosystem service*") *AND* **TOPIC:**(“green infrastructure*”) *AND* **TOPIC:**(spatial AND prioritiz*) *NOT* **TOPIC:**(connect* OR corridor*) *NOT* **TOPIC:**(biodiversity

0 **TOPIC:** (“green infrastructure*”) *NOT* **TOPIC:** ("ecosystem service*") *AND* **TOPIC:** (spatial AND prioritiz*) *AND* **TOPIC:** (connect* OR corridor*) *AND* **TOPIC:** (biodiversity)

9 **TOPIC:**("ecosystem service*") *AND* **TOPIC:**(“green infrastructure*”) *AND* **TOPIC:**(spatial AND prioritiz*) *AND* **TOPIC:**(connect* OR corridor*) *AND* **TOPIC:**(biodiversity)

27 **TOPIC:**("ecosystem service*") *NOT* **TOPIC:**(green infrastructure*) *AND* **TOPIC:**(spatial AND prioritiz*) *AND* **TOPIC:**(connect* OR corridor*) *AND* **TOPIC:**(biodiversity)

62 **TOPIC:**("ecosystem service*") *AND* **TOPIC:**(green infrastructure*) *NOT* **TOPIC:**(spatial AND prioritiz*) *AND* **TOPIC:**(connect* OR corridor*) *AND* **TOPIC:**(biodiversity)

27 **TOPIC:**("ecosystem service*") *NOT* **TOPIC:**(green infrastructure*) *NOT* **TOPIC:**(spatial AND prioritiz*) *AND* **TOPIC:**(connect* OR corridor*) *AND* **TOPIC:**(biodiversity

Chapter 3

Beyond topo-climatic predictors: does habitats distribution and remote sensing information improve predictions of species distribution models?

From: Sanguet *et al.*, under review in Global Ecology and Conservation

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In this paper, I participated in the conceptualization and in the development of the methodology together with all the co-authors, and carried out the experiments, the analyses, and the writing of the original draft.

3.1. Context

After a comprehensive review of GI identification and assessment methods, a focus is made on one of the three pillars: the distribution of biodiversity and more especially the distribution and composition of species. Species Distribution Models (SDMs) have been widely used in theoretical studies of species niches as well as in conservation applications, and they represent a powerful tool to produce continuous maps of habitat suitability and fill the gaps within truncated observation data. In order to run performant models and thus, to have reliable predictions, an effective set of predictors must be selected among topographic, edaphic, climatic and habitat explanatory variables (Mod *et al*., 2016). Habitat predictors are composed of the extraction of various classes derived from the local Land-Use-Land-Cover (LULC) map. This chapter allows to find the set of predictors inducing the highest average performances among different ecological groups composing the species' dataset of the thesis. The predictors identified here will be used in the following chapters of the thesis and represent comprehensive set of variables describing the territory and the ecology of the species.

Using a subset of the database composed of 72 plant species belonging to six different ecological groups, SDM were run using several sets of various predictors' type and their associated performances and spatial predictions were compared in order to find the most relevant combination of predictors in the study area. Several sets integrating various number and complexity of derived habitat classes' predictors were also created and compared in order to find how many and how complex habitat predictors should be to maximize model's performances. The ability of Remote Sensing Images (RSI) to replace habitat predictors was also tested because this data if often missing. Results have shown that performances were varying depending on the ecological group of species and the set of predictors used in the models. RSI predictors were less performant for all models suggesting they are not a relevant replacement for habitat predictors.

Beyond topo-climatic predictors: does habitats distribution and remote sensing information improve predictions of species distribution models?

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Abstract

Species Distribution Models (SDM) represent a powerful tool to predict species’ habitat suitability on a landscape and fill the gap between truncated observation data and all possible locations. SDMs have been widely used in theoretical studies of species niches as well as in conservation applications. Here, we evaluated the impacts of predictors’ type on models’ performances and spatial predictions using 72 plant species belonging to six ecological groups at a regional scale in the area of Geneva (Switzerland). Twelve models were created using various combinations of high-resolution (25m) explanatory variables including topography, pedology, climate, habitats and remote sensing data. Models integrating a combination of habitats and topopedo-climatic predictors had significantly higher performances, while remote sensing predictors showed low performances. Our results suggest that the number and the level of details of habitat predictors (broad or very precise) do not fundamentally affect prediction maps. However, selecting too few, overly simplified or exceedingly complex habitat predictors tend to lower models’ performances. The use of eight habitat categories complemented with eight topopedo-climatic predictors produced models with the highest performances. Ecological groups of species responded differently to models and while alpine and ruderal species have greater average performances due to a high affinity with topopedo-climatic predictors, wetlands’ species were less performant on average. These results underline the necessity of developing or having access to habitats distribution data especially in a conservation context.

Keywords: plant distribution; explanatory variables; model performances; land-use-land-cover; MaxEnt.

3.2. Introduction

Accelerating biodiversity loss is mainly due to changes in land uses, overexploitation of organisms and resources, climate change, various forms of pollution and exotic invasive species (IPBES 2019; Newbold et al, 2015; Pacifici et al, 2015). Globally, none of the 20 Aichi targets for 2020 were fully met (Global Biodiversity Outlook 5, 2020; Xu et al., 2021), one species out of seven is threatened with extinction and climate change is expected to increase extinction rate in the near future (IPCC, 2018; IPBES, 2019; Thomas et al., 2004). Facing this alarming state and trend in biodiversity, effective conservation practices and species monitoring are crucial (Cook et al, 2010). Understanding species distributions and communities in a changing environment helps to mitigate the negative impacts of human activities on ecosystems, and allows conservationists to improve the efficiency of their decisions and anticipate environmental changes (García-Diaz et al, 2019; Ceballos et al, 2017; Pimm et al, 2014). In this context, the use of predictive models complemented with experts' knowledge has been proven to be helpful in conservation (Addison et al, 2013; Guisan et al, 2013; Honeck et al, 2020a; Mateo et al, 2013; Pullin et al, 2004).

SDM are very useful to predict habitat suitability on a landscape and fill the gaps between documented observations of species and their potential distributions (Cook et al, 2010; Elith & Leathwick, 2009; Guisan & Zimmermann, 2000; Hirzel & Le Lay, 2008; Lehmann et al. 2002b; Soberon & Nakamura 2009). They are now widely used in conservation and could be adapted in various contexts (García-Diaz et al, 2019; Guisan et al, 2013, 2017; Lehmann et al. 2002a). As part of the identification of a "Green Infrastructure" in the "Grand Genève" territory (France, Switzerland), this study aims at improving SDM predictions for conservation purposes. Indeed, Green Infrastructure is a network of (semi-)natural habitats managed to deliver ecological, social and economic benefits (Benedict and McMahon, 2006; European Environment Agency, 2014; Honeck et al, 2020a, 2020b). Thus, having access to reliable species distribution predictions would greatly benefit nature's conservation efforts.

Model's performances and prediction quality are highly influenced by the sampling and statistical methods as well as the quality of input data (Elith et al. 2006; Elith & Graham, 2009). The best input data are those based on vegetation plots distributed according to random or stratified sampling schemes, allowing to define presences and absences of species in each plot. Unfortunately, these data sets are relatively rare and most available data come from "presence-only" information without specific sampling design. However, empiric comparisons have demonstrated that good performance and relative predictions can be obtained from presence-only data by creating pseudo-absences or background data (Barbet-Massin, 2012; Elith et al. 2006; Phillips et al. 2009; Zaniewski et al. 2002).

Predictors, or explanatory variables, must be chosen with care according to species' ecology, landscape characteristics, modelling importance as well as the scale of the study area (Araújo & Guisan, 2006; Guisan & Thuiller, 2005; Hirzel & Le Lay, 2008; Petitpierre et al. 2017). Furthermore, they should be as uncorrelated as possible in order to avoid collinearity. While a set of climatic data is effective to understand the overall distribution of species at a large scale (climatic niche), they might not be as efficient to explain local distributions because the climate is unlikely to vary much on small distances (Fournier et al, 2017; McGill, 2010; Pearson & Dawson, 2003). In this situation, land-use-land-cover (LULC), natural habitats distribution, soil quality, or topography might represent better explanatory variables (Austin & Van Niel, 2011). Considering climatic and habitat predictors also help evaluating the influence of climate and LULC future changes on local species distribution, ultimately improving our capacity to conserve rare habitats and species as well as local biodiversity hotspots. However, it remains unclear how detailed habitat predictors should be to maximize models' performances and prediction quality (a few broad classes VS many detailed classes).

Fine-scale and detailed classification of LULC is often lacking at local/regional scale inducing difficulties to model species distributions. Remote Sensing Images (RSI) are now widely available and could represent an interesting alternative to LULC information for SDM predictors. These images are already used to measure biodiversity changes in Essential Biodiversity Variables (Kissling et al., 2018; Skidmore et al., 2015; Vihervaara et al., 2017) as proposed by the Group on Earth Observations Biodiversity Observation Network (GEO BON) in 2013. RSI predictors have already been included in SDM at various scales (Amaral et al., 2007; Cord & Rödder, 2011; Randin et al., 2020; Wilson et al., 2013), for plants (Pérez Chaves et al., 2018; Cord et al., 2014a, 2014b), animals (Cord & Rödder, 2011), rare or invasive species (Amaral et al., 2007; Diao & Wang, 2014) but also for direct detection of individuals from space (He et al., 2015). While the use of RSI predictors is still quite new, they are able to improve SDM predictions, especially when environmental information is missing (He et al., 2015; Leitão & Santos, 2019), even if it could induce some interpretational biases (Bradley et al., 2012). Although RSI predictors have already been used to compare models' performances with other predictors types (Cisneros-Araujo *et al*., 2021; Zimmermann *et al*., 2007), the relative performances of models integrating RSI predictors have rarely (if not never) been explicitly compared to models integrating well identified habitats, especially at a regional scale and using fine resolution rasters.

In this article, we tested how the choice of predictors impacts SDM performances using combinations of topographic, pedologic and climatic predictors (named hereafter topopedo-climatic), habitats (described as LULC classes), and RSI predictors at a regional scale with a 25-meter resolution. Using the MaxEnt algorithm in R (Phillips et al., 2004, 2006), we compared models' performances and studied their associated projections in order to answer the following questions: which combination of predictors increases model's performances? Are few large habitat classes better than many detailed classes in SDM? How efficient are RSI predictors and do they produce similar performances than models calibrated with habitat predictors?

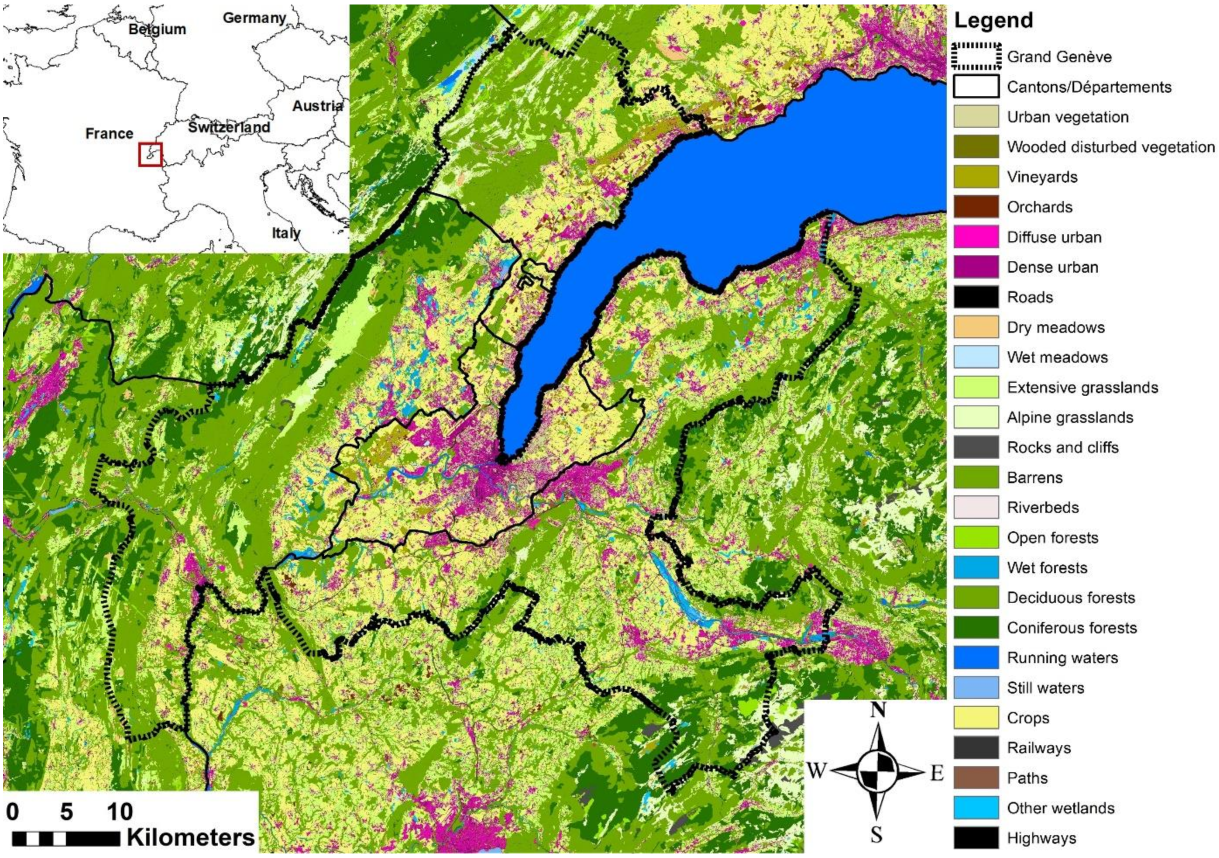


Fig. 1. Land-Use-Land-Cover (LULC) information on the study area.

3.3. Data and methods

3.3.1. Study area

The study area named “Grand Genève”, represented in black bold dashes in Fig. 1, is a Swiss-French cross-border territory of approximately 2 000 km² in the middle of Europe integrating two Swiss cantons (Geneva and Vaud) and three French departments (Ain, Haute-Savoie, Jura). The square extent including the full Grand Genève territory where models were run is dominated by forests (40%), crops (17%), meadows and pastures (12%), man-made infrastructures together with anthropic vegetation (17.5%) (Fig.1). The altitudinal range is about 2 000 meters between the plateau and the top of mountain ranges located on both sides of Geneva city (Jura on the West and Alps on the East).

3.3.2. Species Data

We compiled georeferenced presence-only occurrences of wild plant species from Swiss and French botanical conservatories and monitoring programs. They represent indigenous as well as exotic species from Pteridophytes, Gymnosperms, and Angiosperms groups. Only occurrences observed after the year 2000 were kept, as well as the ones with a precision equal or finer than 25 meters, corresponding to the predictors’ map resolution. We selected twelve plant species belonging to each of six ecological groups described in the local book “Flora Indicativa” (Landolt et al., 2010), namely: ruderal, alpine, wetlands, dry/poor meadows, nitrogen-rich meadows, and forests. Species were selected for their large number of occurrences (>200) to avoid computational biases. The 72 plant species and their associated ecological group are presented in supplementary materials (table A1). The species selected are mostly perennial, annual or biannual herbaceous species, but also cover other life forms such as shrubs, trees, and lianas.

3.3.3. Predictors

Twelve sets of models were created with various combinations of topopedo-climatic, habitats, and RSI predictors, using the same extent and resolution (25 meters, Fig. 1). The topopedo-climatic set of variables was selected in regards to its capacity to affect plant species distribution in the mountainous study area and the predictors' low spatial correlation (see Fig. A3 in supplementary materials). It includes topographic, pedologic and climatic predictors composed of mean annual temperatures, annual precipitation, northness index (orientation), slope, mean summer and winter solar radiation, upland index (describing the altitudinal dominance of each pixel on a 2km buffer area, derived from TPI method from Weisse, 2001) and finally the type of soil (cambisols or podzols, see Table A2 in supplementary materials for details). The two climatic variables were initially downloaded from Worldclim (Fick & Hijmans, 2017, version 2.1) and were downscaled using a linear regression with altitude. Although the R squared from the regressions were high (0.991 for temperatures and 0.934 for precipitations), the downscaled maps were corrected, integrating local variabilities from the regression models. Topographic variables were calculated using ArcMap (version 10.2.1) tools, and pedologic variables were downloaded from the global gridded soil information modelled with machine learning by Hengl et al. (2017).

Habitat variables consist of LULC categories compiled from French and Swiss maps (Fig.1). They were separated into three levels of details, each set covering the whole study area: basic habitats (BH) with four broad categories, advanced habitats (AH) with eight categories derived from the previous set, and specific habitats (SH) with eight categories specifically selected for each ecological group (six SH sets in total) according to their ecological requirements and local expert knowledge (see Tables A3 and A4 in supplementary materials for details). All habitat variables were transformed from categorical to continuous values using focal statistics at 100 meters. Their values represent habitat proportion in the direct surrounding of the pixel and ranges from 0 if the habitat is completely absent to 1 if the pixel is surrounded by the same class. It has a value comprised between 0 and 1 when surrounded by a mix of its own and other categories, depending on their relative density. This means that 1) small isolated habitat patches have lower values than bigger homogenous patches and 2) the margins of two habitats overlap and thus influence each other (ecotone effect). This partially participates in taking into account habitats' quality and structure in models.

RSI variables consist of Normalized Differentiation Vegetation and Water Indices (NDVI (1) and NDWI (2)) data extracted from the Swiss Data Cube (https://www.swissdatacube.org). NDWI is sensitive to the water content of vegetation (Gao, 1996) as well as open water features (McFeeters, 1996) and can represent a significant contribution to SDM (Manyangadze et al., 2016), while NDVI has been used to classify vegetation types (Gamon et al., 1995; Geerken et al., 2005) but also as a predictor for SDM (Amaral et al., 2007; Bonthoux et al., 2018; Wen et al., 2015). We assume that the combination of these two indices is able to replace basic habitat categories by discriminating wetlands, forest types, meadows and urban areas. They are calculated as followed:

$$(1)\quad NDVI = \frac{p_{NIR} - p_{RED}}{p_{NIR} + p_{RED}}$$

$$(2)\quad NDWI = \frac{p_{NIR} - p_{SWIR}}{p_{NIR} + p_{SWIR}}$$

Where P_{NIR}, P_{RED}, and P_{SWIR} are the reflectance for near infrared (0.77 – 0.90 µm), visible red (0.63 – 0.69 µm) and shortwave infrared (1.55 – 1.75 µm) respectively (see Table A5 in supplementary materials). These indices are calculated from multi-temporal and multi-spectral remote sensing images from the Landsat series (Landsat-5, Landsat-7 and Landsat-8) at 30 meters resolutions for the time period 2000-2018. Due to artefacts in some images such as clouds cover and technical issues, years 2002 and 2003 were not considered for NDVI calculation, and years 2009, 2016 and 2017 for NDWI. Remote sensing data were then downscaled to 25 meters resolution and aggregated into 8 variables (4 for each index) namely: mean maximum value, mean minimum value, mean value and mean seasonality value (variation between annually maximum and minimum values) on the time period (see Table A6 in supplementary materials). Finally, we created two subsets of four variables, the former from topopedo-climatic predictors and the later from remote sensing images, selecting the most significant variables according to models' contribution and importance. These new sets were named "best topopedo-climatic" (BTC) and "best remote sensing images" (BRSI).

3.3.4. SDM and evaluation

12 models were created using various combinations of predictors presented above. They were aggregated into five groups: 1) topopedo-climatic predictors only (model TC), 2) topopedo-climatic and habitat predictors with different numbers of predictors and varying levels of details for habitat categories (models TC_BH, BTC_BH, TC_AH, BTC_AH, TC_SH, BTC_SH), 3) specific habitats set of predictors only, selected according to the ecological requirements of species (model SH), 4) topopedo-climatic and remote sensing predictors with varying number of variables (models TC_RSI, BTC_RSI, BTC_BRSI), and 5) remote sensing predictors only (model RSI). Details of each model are described in Table 1.

Models were run and evaluated using Dismo (Hijmans et al., 2017), ENMeval (Muscarella et al., 2014) and sdm (Naimi & Araújo, 2016) packages on R (R core team, 2019) and MaxEnt algorithm (Phillips et al., 2004, 2006, version 3.4.1). MaxEnt is widely used in SDM (Guillera-Arroita et al., 2015) and is known to perform well, especially with presence-only data (Elith et al., 2006; Hijmans & Graham, 2006). We selected MaxEnt because it is easy to use for planners in a conservation context, especially when using its user interface, and because it is not computationally intensive. We used default settings except for the beta multiplier which was increased from 1.00 to 2.00 to avoid overfitting (Costa et al., 2010; Radosavljevic & Anderson, 2014) for all species. The same algorithm and settings were used for all species in order to assess the impacts of predictors' types on models' performances, avoiding possible biases linked to the modelling design. More information on MaxEnt uses, settings and functioning can be found in the following articles (Elith et al., 2011; Hallgren et al., 2019; Merow et al., 2013; Phillips et al., 2006; Phillips & Dudik, 2008; Phillips, 2017; Radosavljevic & Anderson, 2014).

For these experiments, we used presence-only data and created 10 000 randomized background data for each species. To evaluate model's performances, sampling data were split into calibration (75%) and evaluation (25%) 10 times for each species. The area under the curve of a receiver operating characteristics (AUC; Zweig and Campbell 1993) and the maximized true skill statistic (TSS, also known as the corrected Kappa, Allouche et al., 2006) were calculated for each of the 10 evaluated models and the average value was extracted. AUC has been criticized when used to compare models with different prevalence or spatial extent (Lobo et al., 2008), but here, only the set of predictors varies between models, the spatial extent and prevalence remaining the same. Then, a model was calibrated with all occurrences in order to create a projection map with all information available and the calibration slope was also measured (slope of observed proportion of occupied sites versus predicted probabilities). Mean and standard deviation of variable contributions were measured for all models, excepting the ones using specific habitat variables, and the spatial correlation between all predictors were calculated. In total, 864 projection maps (12 for each of the 72 species) were created and average models' performances were compared using Wilcoxon's paired data mean tests. Predicted map's spatial heterogeneity was assessed by measuring the variance of an aggregation of habitat suitability values in a 250m resolution moving window for all species across all models. Higher mean variance would significate a higher heterogeneity in predicted maps. Finally, a correlation matrix was calculated to visualize similarities in predicted habitat suitability maps. To avoid bias in the results, only models with the same number of variables were initially statistically compared, but since the number of variables used in models did not play a role as important as their intrinsic type (topopedo-climatic, habitats or RSI), all models were used for statistical performances' comparisons. The general methodological framework is described in Fig. 2.

Table 1. Models' code and associated predictors information.

MODEL'S CODE	PREDICTORS' SET USED	NUMBER OF PREDICTORS	MODEL'S GROUP
TC	Topopedo-climatic only	8	Topo-climatic
TC_BH	Topopedo-climatic and basic habitats	12	Topopedo-climatic and habitats
BTC_BH	Best topopedo-climatic and basic habitats	8	
TC_AH	Topopedo-climatic and advanced habitats	16	
BTC_AH	Best topopedo-climatic and advanced habitats	12	
TC_SH	Topopedo-climatic and specific habitats	16	
BTC_SH	Best topopedo-climatic and specific habitats	12	
SH	Specific habitats only	8	Habitats
TC_RSI	Topopedo-climatic and remote sensing images	16	Topo-climatic and remote sensing images
BTC_RSI	Best topopedo-climatic and remote sensing images	12	
BTC_BRSI	Best topopedo-climatic and best remotes sensing images	8	
RSI	Remote sensing images only	8	Remote sensing images

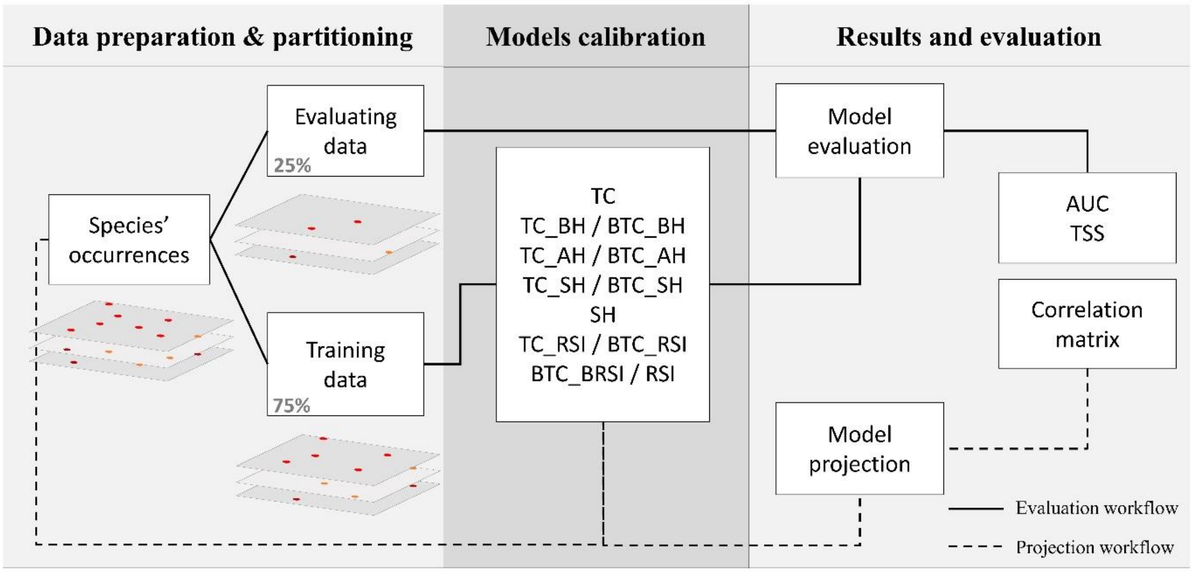


Fig. 2. General methodological framework. Three quarter of occurrences are used to calibrate models and one quarter to evaluate performances. The entire set of occurrences is used for projections.

3.4. Results

3.4.1. Models' performances

Average AUC, TSS and calibration slope scores show similar patterns. However, p-values extracted from Wilcoxon's paired data mean tests tend to be higher (less significant) when considering calibration slope or TSS compared to AUC. The group of models using topopedo-climatic combined with habitat predictors (*TC_*H) always statistically outperforms the other groups of models. Indeed, within models using eight predictors, model BTC_BH has the highest AUC and TSS scores compared to TC, SH, BTC_BRSI and RSI models (p-value <0.001, Fig. 3). The model with 12 predictors having RSI variables shows significantly lower performances compared to the others having habitats variables instead (Fig. 3). The same pattern is observed for models with 16 predictors. P-values from models' comparisons are available in supplementary materials (Table A10). Results from the calibration slope show similar results (see Fig. A4 in supplementary materials). Habitat predictors have high contributions to models, especially in the basic set, but also in the advanced one, specifically closed forests, wetlands and transportation (see tables A12 in supplementary materials). These results together underline the benefits brought by the integration of habitat predictors in SDM.

Comparable performances are observed among models with topopedo-climatic and habitat predictors despite the fact that they have different number of predictors and habitats categories. Indeed, the prediction maps of this group of models have a Pearson's correlation rate always above 0.90 (ranging between 0.923 and 0.972, see Table A11 in supplementary materials) and no significant differences in calibration slope were found for models using the same number of variables (Fig. A4 in supplementary materials). This means that using a basic or a sophisticated set of habitats – associated with topopedo-climatic predictors – does not fundamentally change the global spatial pattern of the predictions, although performances depict some differences for AUC and TSS scores. Indeed, models using four habitat predictors have significantly lower performances than models using the eight advanced habitats set although they have the same topopedo-climatic predictors. However, models using eight specific habitats have similar performances than models using four broad habitats and thus, lower performances than models TC_AH and BTC_AH (see table A9 in supplementary materials). This result is a bit surprising knowing that the SH sets of habitats were specifically selected based on ecological relevance and experts' knowledge on the species' ecological group while AH set include the same habitat predictors for all species (discussed in section 4.1). This also suggests that the number of habitat predictors hardly affects models' performances. Nevertheless, the model producing highest average performances is TC_AH, closely followed by BTC_AH and TC_SH (depending on the index considered), indicating that the use of eight habitat categories instead of four seems to globally increase models' performances.

Topopedo-climatic predictors have a major impact on performances and models' quality. Models using the full topopedo-climatic set of predictors (TC_*** models) always depict higher performances than their sibling models with a truncated set of four topopedo-climatic predictors (BTC_*** models) but the same other variables (see Table A9 and Fig. A2 & A4 in supplementary materials for details). When used alone (model TC), topopedo-climatic predictors tend to show better average performances than when habitat or RSI predictors are used alone, although this is not always statistically supported. Finally, most predictors from the topopedo-climatic set show high average contributions to models and the two climatic ones have the highest average contribution in all models where they are used (see tables A12 in supplementary materials). These results emphasis the relevance of using topographic, pedologic and especially climatic predictors in SDM, especially in mountainous landscapes.

3.4.2. Remote sensing predictors

Models with RSI and topopedo-climatic predictors show lower performances than models with topopedo-climatic and habitat predictors. This is especially true when comparing performances of model RSI with the other models using eight predictors where it has the lowest average performances of all (Fig. 3 and A4 in supplementary materials). However, it shows relatively good performances for some species (i.e. *Campanula rhomboidalis* L.: AUC = 0.877, TSS = 0.663 and calibration slope = 0.681) but fails to outperform the other models, except for model SH in some situations. In other words, when model RSI produces great performances, the species always produce higher performances for most to all models. This also suggests that some species better respond to SDM than others in this experiment. Thus, RSI predictors alone fail at producing performant models.

Even used in association with topopedo-climatic predictors, models with RSI predictors tend to have low performances when compared to other models with the same number of variables. This is particularly true for model TC_RSI when compared to TC_AH and TC_SH, BTC_RSI when compared to TC_BH, BTC_AH, BTC_SH and RSI when compared to TC, BTC_BH and SH (Fig. 3 and Fig. A4 in supplementary materials). TC_RSI seems to produce the highest performances of all RSI-based models which might be due to the inclusion of the full topopedo-climatic set of predictors. However, it is outperformed by TC_BH which possesses the same topopedo-climatic set but complemented with an additional four habitat predictors (forests, open habitats, urbanized areas and wetlands) while model TC_RSI has an additional eight RSI predictors. These observations show that raw RSI predictors are not able to replace a basic set of habitat predictors.

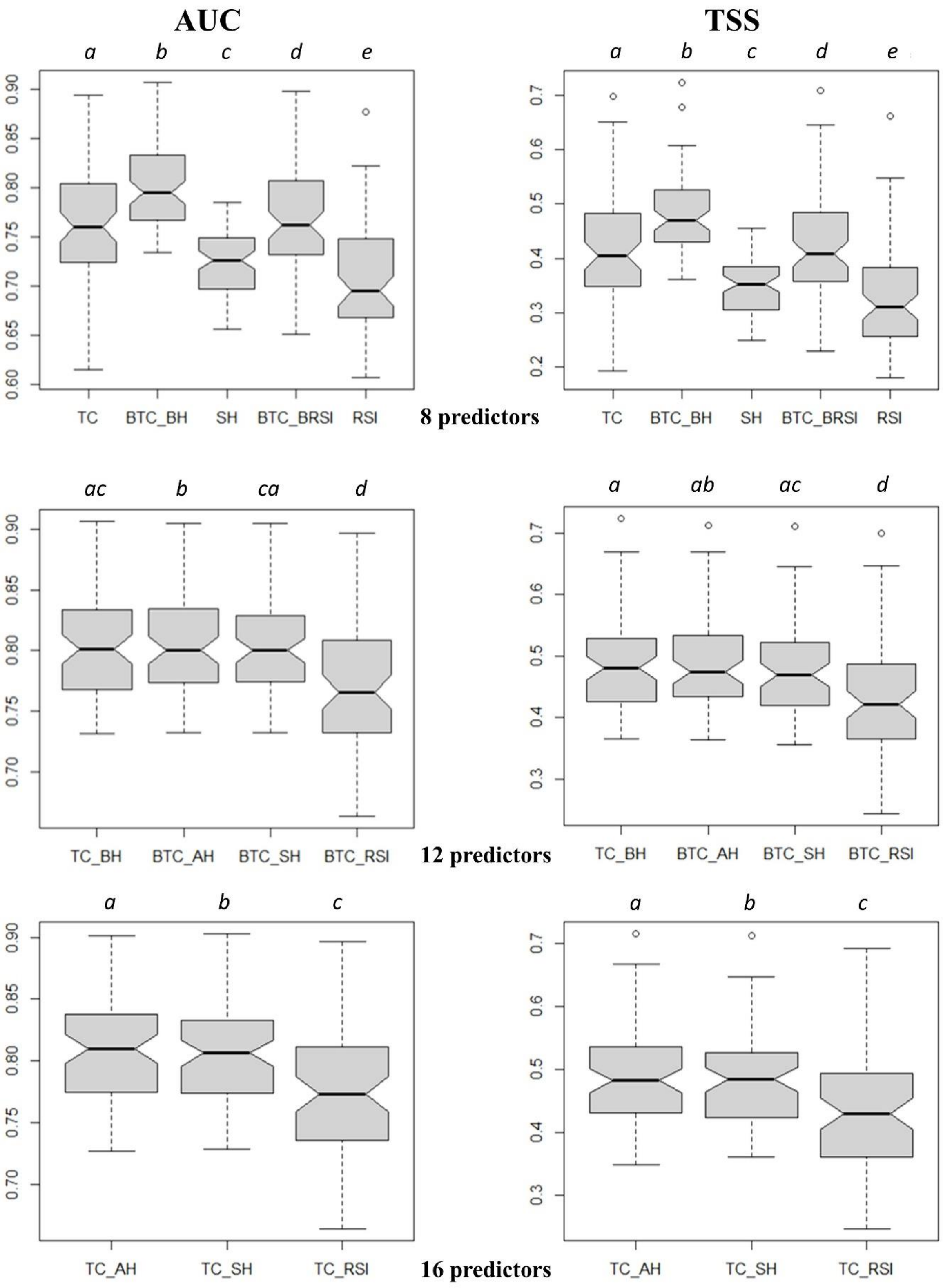
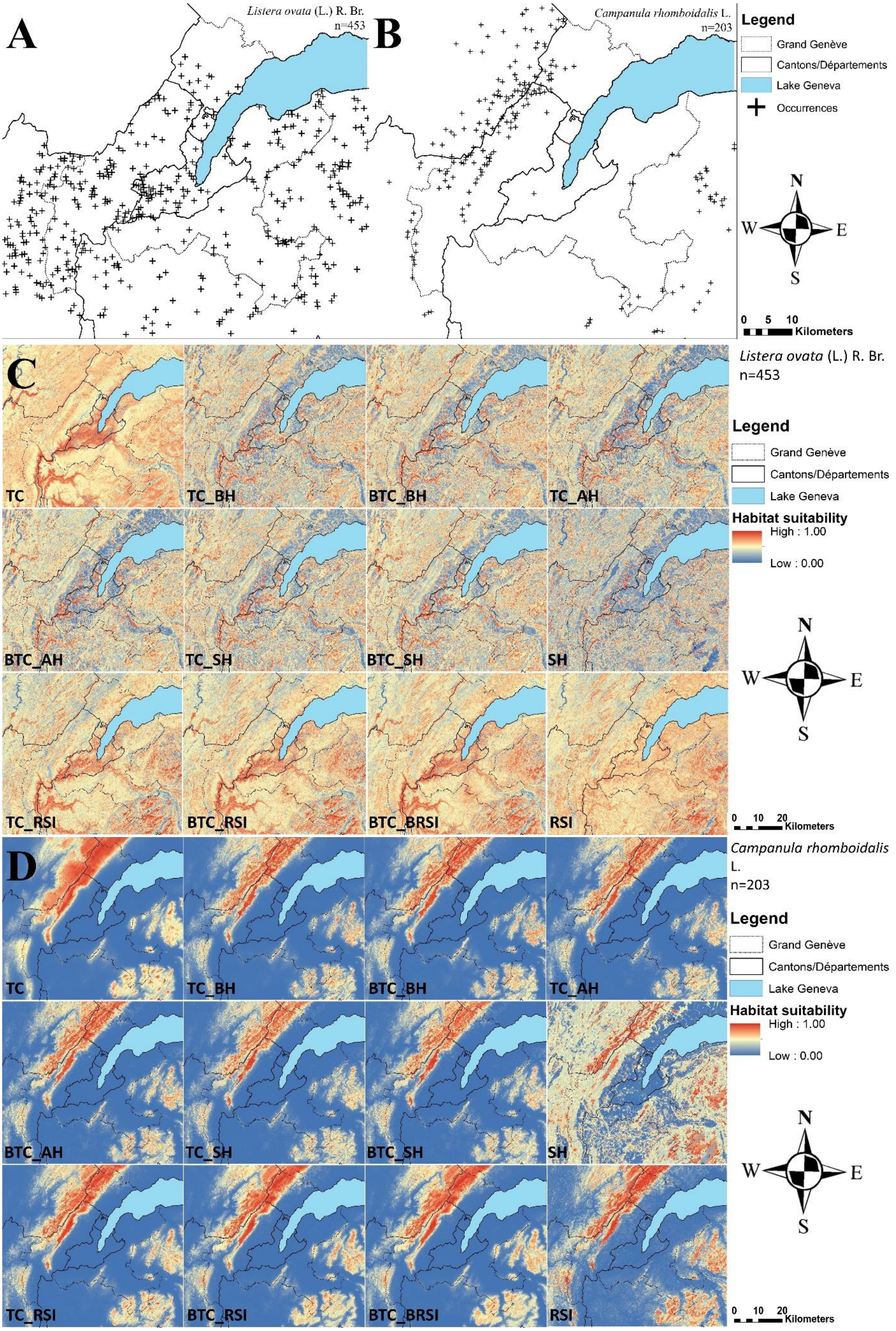


Fig. 3. Boxplots of AUC (left column) and TSS (right column) scores for all models. Models with the same number of predictors were aggregated in the same row and their performances were compared. Legends above the boxplots indicate if the models show differing performances (different letter) or not (similar letter) according to a paired data Wilcoxon mean tests with threshold set at p-value = 0.05. Boxplots of performances of all models together are available in supplementary materials.


A
Listera ovata (L.) R. Br.
n=453
B
Campanula rhomboidalis L.
n=203
Legend
Grand Genève
Cantons/Départements
Lake Geneva
Occurrences
N
W
E
S
0 5 10
Kilometers
C
Listera ovata (L.) R. Br.
n=453
TC
TC_BH
BTC_BH
TC_AH
BTC_AH
TC_SH
BTC_SH
SH
TC_RSI
BTC_RSI
BTC_BRSI
RSI
Legend
Grand Genève
Cantons/Départements
Lake Geneva
Habitat suitability
High : 1.00
Low : 0.00
N
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Campanula rhomboidalis L.
n=203
TC
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BTC_BH
TC_AH
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TC_SH
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Cantons/Départements
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Habitat suitability
High : 1.00
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Fig. 4. A) distribution of occurrences for *Listera ovata* (L.) R. Br. B) distribution of occurrences for *Campanula rhomboidalis* L. C) Prediction maps of *Listera ovata* (L.) R. Br. for the 12 models. D) Prediction maps of *Campanula rhomboidalis* L. for the 12 models.

3.4.3. The influence of species' ecology

AUC and TSS values were compared according to the ecological group of species (Fig. 5 and A1 in supplementary materials). Alpine and ruderal species show high performances compared to the other groups. Wetland species usually have the lowest performances except for model SH where they mostly outperform forest species. Wetland species show an interesting pattern in Fig. 5 as model TC shows very low performances compared to the other groups. SH models tend to have relatively high performances for this group sometimes even outperforming model TC. The same observations could be made for species growing in poor/dry meadows ("Pmeadows", Fig. 5). Ruderal and alpine species show very low performances for model SH relatively to the performances of models using a combination of topopedo-climatic and habitats predictors. For most ecological group, TC_AH is the model with the highest performances on average, but this is not always the case. Indeed, it is outperformed by TC_SH for nitrogen rich meadows' species and poor/dry meadows' species or TC_BH for alpine species. However, TC_AH is still having great performances even in those cases indicating once again the close proximities between all topopedo-climatic and habitats-based models (see Tables A7 and A8 supplementary materials).

As illustrated in the Fig. 4., predicted habitat suitability maps show different spatial heterogeneity according to the set of predictors used and to the ecological group of species. In general, topopedo-climatic and RSI models tend to produce smooth suitability variations while models integrating habitat predictors produced more disconnected patches of suitable areas. This is demonstrated by the higher spatial heterogeneity, measured as the variance of habitat suitability values in a 250-meters resolution moving window, for models integrating habitats sets compare to the other (see table A13 in supplementary materials). Ecological groups with the highest spatial heterogeneity are poor/dry meadows and wetlands species (illustrated by the species *Listera ovata* (L.) R. Br in the example of Fig. 4.), indicating a more fragmented, habitat-dependent distribution across the study area (see table A13 in supplementary materials). On the contrary, forest and alpine species (illustrated by *Campanula rhomboidalis* L. in the example of Fig. 4.), have low variance, indicating low spatial heterogeneity and thus, more continuous habitats (see table A13 in supplementary materials). These results demonstrate that the set of predictors should be adapted according to the ecology of species to increase models' performances. While habitat-dependent species such as wetlands or poor and dry meadows might benefit from specific habitat predictors to fit their fragmented distributions, species less dependent to precise habitats such as alpine or ruderal groups would rely less on specific habitat predictors and more on topopedo-climatic ones to fit their continuous distributions.

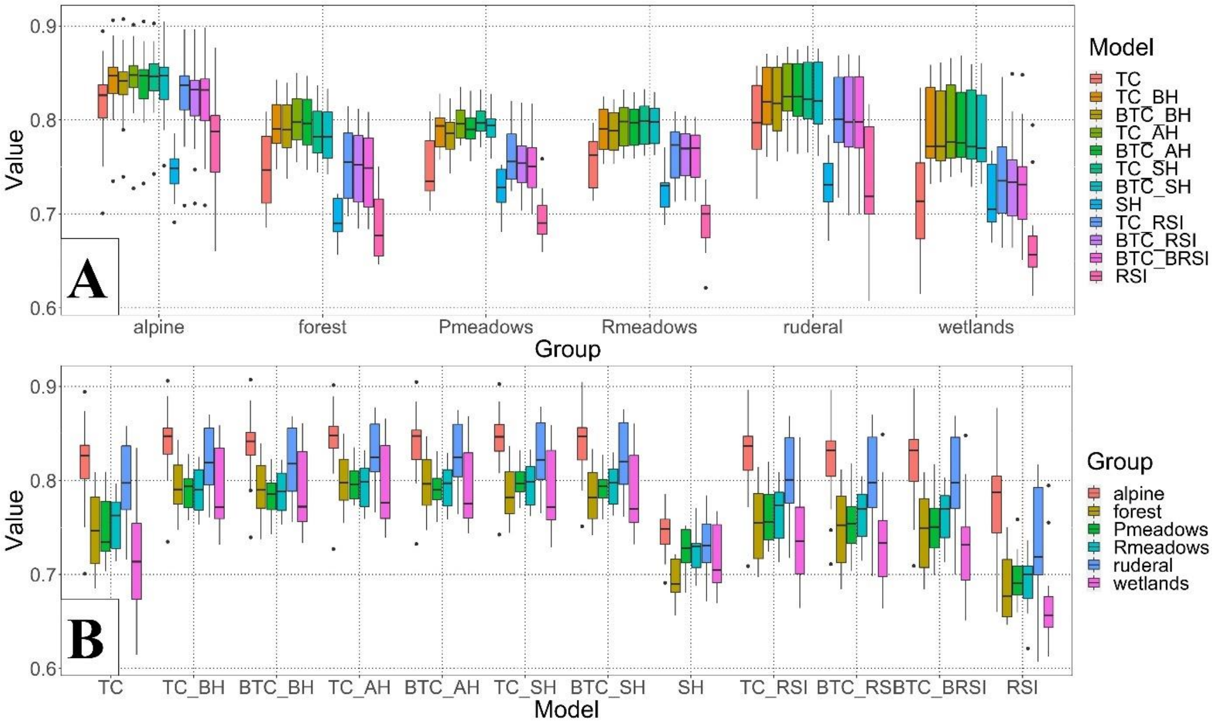

Fig. 5. Boxplots of AUC values of all models per ecological group (A) and of all groups per model (B). Boxplots of TSS values are available in supplementary materials.

3.5. Discussion

3.5.1. Predictors' selection and limits

The topography of the study area and especially its mountainous landscape driven by a steep elevational gradient (up to 2000 m.a.s.l.) strongly affects temperature and precipitation regimes. Variations in altitude and exposure create micro-climates that can sustain various habitats and plant communities in a relatively small area (Barthlott et al., 1996; Körner, 2004; Körner & Spehn, 2019; Oke & Thompson, 2015). These observations probably explain why topopedo-climatic predictors have had such importance in this experiment. In addition, they were carefully selected for their ecological meaning in the study area and were previously tested for their relevance, modelling importance and spatial correlation (see Fig. A3 and Tables A12 in supplementary material). Thus, this experiment confirms that the use of topopedo-climatic predictors improves SDM performances even at a fine-scale and especially in mountainous landscapes.

The advanced habitat set composed of eight habitat categories is a detailed classification of the landscape integrated into the broader four habitat categories and it could explain the high correlation between associated predicted maps (i.e. the category "forests" in the BH set is divided into two classes "open forests" and "closed forests" in AH set). This suggests that the level of details used for habitat predictors might not be as important as the overall quality of the original LULC map from which habitats are derived. This hypothesis is also supported by the comparable performances of models integrating eight or four habitat predictors. Thus, having a very accurate, high resolution LULC map, even with only a few classes, might represent a great asset in SDM, underlining the absolute need of creating such data, especially in biodiversity conservation and landscape planning contexts.

The fact that models with specific habitat predictors have on average slightly lower performances than models using the advanced habitat set may seem counter-intuitive, especially because they are not spatially correlated with the topopedo-climatic predictors (Fig. A3 in supplementary materials). The explanation of this result raises several hypotheses and identifies some limits to our approach. First, models' performances are evaluated using the widely used AUC and TSS scores (Allouch et al., 2006; Fielding & Bell, 1997; Peirce, 1884). However, although these indices alone do not always reflect the true intrinsic performance/quality of the predictions, especially when applied with presence-only models (Lobo et al., 2008; Leroy et al, 2018), they can still be used to compare predictions with similar extent and predictors. In consequences, the performances of models using advanced or specific sets of habitat predictors being relatively similar, it might be interesting for local experts to compare associated predicted maps as performances might not be the only valuable criteria in a conservation context. Indeed, the specific habitats set integrates very detailed habitat classes, and models using it could produce finer prediction maps which would represent a great interest for conservation, although their associated performances are slightly lower than other types of models. Second, this result could reflect the limits of our approach in two different ways: 1) we might have partially failed at precisely classifying small, rare habitats in our LULC map, although we are using high resolution raster maps. It could explain why models considering very specific habitats tend to show lower performances. Indeed, as presented in the methods section, the LULC map from which habitats were derived is a combination of several maps from different countries and regions with varying complexity and methods of classification. Even if the categories were carefully selected and classified, mistakes could still occur in the process or in the original maps; 2) the georeferenced occurrences might lack of precision for the models to correctly distinguish precise habitat preferences of species, even though we selected occurrences for their high precision (< 25 meters which equals to pixel's resolution). These two hypotheses are supported by the presence of occurrences of habitat-dependent species (such as wetland plants) outside their supposed habitat. It demonstrates the difficulty of mapping certain types of habitat such as wetlands when water availability comes from water sources, underground reservoirs or temporary humidity, leading to an incomplete mapping of humid habitats and raises questions about habitats mapping methods and their reliability for SDM. Third, the use of highly detailed classes of habitats may not be relevant for SDM, especially at such fine scales. Indeed, the presence or absence of individuals might be more driven by random events and biotic interactions – that are difficult to model (McGill, 2010; Pearson & Dawson, 2003) – rather than specific habitat characteristics. This means that there could be an optimum in models' performances between the use of overly simplified and overly complex habitats classes, and this optimum would depend on the precision, resolution and quality of inputs, as well as the overall characteristics of the study area (landscape, scale etc.). Thus, performances would be at a maximum when habitats are sufficiently broad for the models to statistically infer habitat preferences, and eventually decrease if habitat predictors are too detailed and complex where models fail at inferring species' habitat suitability accurately. Fourth, only species with many occurrences were selected in order to mitigate differences in degrees of freedom, but this might also affect the results. Indeed, they have to be common enough to have at least 200 georeferenced wild observations and they might be more generalist than highly habitat-dependent species. Rare, specialist species would have certainly responded differently to this type of models and further research on this subject would be beneficial.

3.5.2. Performances of ecological groups and insights for conservation

Species showing high performances are widespread stenotherm species without strict habitat preferences, usually living in alpine environment at high elevation or in the plateau at lower altitudes where expand the urban area of Geneva and its surrounding (ruderal group). Topopedo-climatic conditions – such as temperatures – are the stressful limiting factors of alpine species distributions and biotic interactions play a less important role for modelling this community of species (Mitchell et al., 2009). Ruderal species are very adaptable and grow preferentially in disturbed areas, without a clear habitat preference (Theurillat et al., 2011). Urban areas being mostly found in the flat lowlands of the study area - better suited for urban expansion and human disturbances - topopedo-climatic predictors seem to drive the distribution of ruderal species.

On the contrary, species' distribution highly driven by habitats (stenoece) are more challenging to model because their distributions also depend on random events and complex ecological interactions (i.e. orchids) that are nearly impossible to map and consider in models (Austin, 2007; Hirzel & Le Lay, 2008). The fragmented distributions of wetland species could be a result of fine-scale biotic interactions, the crucial role of habitats in driving and explaining their distributions, and the limits in mapping water availability as described in section 4.1 (Pottier et al., 2013; Soberón, 2007). These hypotheses could explain why wetland species show lower performances on average but the same hypothesis could be raised for other habitat-specific species globally.

Species from different ecological groups responded differently to models and knowing the ecology of the studied taxa helps selecting useful predictors, benefits models' quality and facilitates the understanding of predicted maps. Topopedo-climatic predictors would thus be highly beneficial to model widespread species, at continental scale or in mountainous landscape while precise and detailed habitat predictors would rather help model habitat-dependent species at smaller scale (Guisan & Thuiller, 2005). In this study the simple consideration of habitat predictors greatly increased models' performances although they are usually not considered in SDM (Mod et al., 2016). However, in a conservation purpose, the performances are not the only criteria to consider and the integration of experts' opinions on predicted maps is a relevant complement (Addison et al, 2013; Guisan et al, 2013; Honeck et al, 2020a; Mateo et al, 2013; Pullin et al, 2004). Indeed, if performances are closely related, the overall aspect of prediction maps could help selecting the proper set of predictors, according to local knowledge of the territory as explained in section 4.1.

In this experiment, raw RSI predictors were not relevant to help modelling the distribution of plant species and performed poorly to replace habitat predictors, although the max_ndvi predictors have shown interesting contribution to models (see tables A12 in supplementary materials). A few hypotheses could be raised to explain this observation. First of all, only two indices were used (NDVI and NDWI) and more research should be made using several other remote sensing-based images and indices as predictors. Second, they were used raw but might benefit from being transformed into a basic habitats map using GIS landscape classification tools, which might eventually improve their predictive efficiency. Third, they were compared to models integrating detailed, high resolution habitat predictors specifically developed for the study area. However, they might still be interesting as predictors for territories with no LULC maps and their ability to model various groups of species in different contexts should be further investigated. Nevertheless, efforts should be focused on the creation of LULC maps to extract at least a few broad habitat categories which would also help habitat conservation, landscape planning and biodiversity monitoring programs.

3.6. Conclusion

Our results have shown that the combination of topographic, pedologic, climatic and habitat variables produced models with the highest performances. The addition of more habitat predictors tended to increase models' performances but using highly detailed habitat classes did not increase performances. Indeed, the AUC, TSS and calibration slope of these models have shown similar values to models using four broad habitat categories. There is somehow a tradeoff between the use of overly simplified and exceedingly complex habitat classification as predictors but more research should be done on this aspect in different contexts, for example integrating rare species. Models using raw RSI predictors did not perform as well as the other models but they might improve their predictive efficiency if transformed into broad habitat classes prior to be used in SDM.

Species and ecological groups have shown varying performances according to predictors' combinations which demonstrates the absolute need to understand species' ecology before planning to model their distributions. Alpine and ruderal species were easier to model because topopedo-climatic factors seem to drive their distributions, while wetlands species, which depend on the presence of a specific habitat, tend to show lower performances and are more challenging to model. Understanding species ecological preferences also help anticipate and mitigate impacts of urban sprawl, habitats destruction and climate change on species' distribution and thus, help taking better decision to conserve and protect natural systems.

Topopedo-climatic predictors are easier to produce and access than LULC information but the addition of habitat predictors significantly increased models' performances for all species considered. Harmonized LULC information is becoming increasingly available and it will help build more reliable species distribution models leading to more sustainable land-use planning and better conservation practices. It provides new insights into SDM and more research should be done on the integration of rare habitat predictors (such as wetlands), or the detailed levels of habitat classification.

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Glossary

AUC: Area Under the Curve of a receiver operating characteristics

LULC: Land-Use-Land-Cover

NDVI: Normalized Differentiation Vegetation Indices

NDWI: Normalized Differentiation Water Indices

RSI: Remote Sensing Images

SDM: Species Distribution Models

TSS: maximized True Skill Statistic

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3.8. APPENDIX

Groups	Taxa	Groups	Taxa
Ruderal	***Cirsium arvense*** (L.) Scop ***Convolvulus arvensis*** L. ***Equisetum arvense*** L. ***Erigeron annuus*** (L.) Desf. ***Galeopsis tetrahit*** L. ***Galium aparine*** L. ***Geranium robertianum*** L. ***Plantago major*** L. ***Poa annua*** L. ***Potentilla reptans*** L. ***Ranunculus repens*** L. ***Veronica persica*** Poir.	**Dry/poor meadows**	***Briza media*** L. ***Bromus erectus*** Huds. ***Daucus carota*** L. ***Euphorbia cyparissias*** L. ***Galium verum*** L. ***Hippocrepis comosa*** L. ***Hypericum perforatum*** L. ***Origanum vulgare*** L. ***Plantago media*** L. ***Potentilla erecta*** (L.) Raeusch. ***Sanguisorba minor*** Scop. ***Silene vulgaris*** (Moench) Garcke
Alpine	***Astrantia major*** L. ***Brachypodium rupestre*** (Host) Roem. &Schult. ***Campanula rhomboidalis*** L. ***Carduus defloratus subsp defloratus*** L. ***Cerastium fontanum*** Baumg. ***Gentiana lutea*** L. ***Geranium sylvaticum*** L. ***Laserpitium latifolium*** L. ***Phyteuma orbiculare*** L. ***Picris hieracioides*** L. ***Ribes alpinum*** L. ***Rosa pendulina*** L.	**Nitrogen rich meadows**	***Achillea millefolium*** L. ***Ajuga reptans*** L. ***Arrhenatherum elatius*** (L.) J. Presl & C. Presl ***Dactylis glomerata*** L. ***Lotus corniculatus*** L. aggr ***Medicago lupulina*** L. ***Plantago lanceolata*** L. ***Poa trivialis*** L. ***Prunella vulgaris*** L. ***Taraxacum officinale*** aggr ***Trifolium pratense*** L. ***Trifolium repens*** L.
Wetlands	***Agrostis stolonifera*** L. ***Carex flacca*** Schreb. ***Deschampsia cespitosa*** (L.) P. Beauv. ***Eupatorium cannabinum*** L. ***Festuca arundinacea*** Schreb. ***Filipendula ulmaria*** (L.) Maxim. ***Gymnadenia conopsea*** (L.) R. Br. ***Linum catharticum*** L. ***Listera ovata*** (L.) R. Br. ***Platanthera bifolia*** (L.) Rich. ***Rhinanthus alectorolophus*** (Scop.) Pollich ***Solidago gigantea*** Aiton	**Forests**	***Acer pseudoplatanus*** L. ***Cornus sanguinea*** L. ***Corylus avellana*** L. ***Crataegus monogyna*** Jacq. aggr ***Fagus sylvatica*** L. ***Fragaria vesca*** L. ***Fraxinus excelsior*** L. ***Galium mollugo*** L. aggr ***Geum urbanum*** L. ***Hedera helix*** L. ***Lonicera xylosteum*** L. ***Picea abies*** (L.) H. Karst.

Table A1. Selected species per ecological group from Landolt et al., 2010.

Table A2. Topopedo-climatic predictors used in models, description and origin.

Name	Description	Origin
Temp	Mean annual temperature	Worldclim, R
Prec	Annual precipitations	Worldclim, R
N_index	Northness index	ArcMap 10.2.1
Slope	Continuous slope	ArcMap 10.2.1
Sol_rad	Mean seasonal solar radiation	ArcMap 10.2.1
Upland index	Index of landscape domination	ArcMap 10.2.1, modified from Weiss, 2001
Cambisol	Cambisol proportion in the surrounding soil	Hengl et al. 2017
Podzol	Podzol proportion in the surrounding soil	Hengl et al. 2017

Table A3. Habitat predictors and habitats categories included in Basic Habitats set (BH) and Advanced Habitats set (AH). They are all derived from a compilation of Swiss and French LULC maps.

Basic habitats set (BH)	Advanced habitats set (AH)	Categories included
Forests	**Closed forests**	Deciduous forests
		Coniferous forests
	Open forests	Open forests
		Barrens
Urban areas and habitats	**Urbanized areas**	Dense urban areas
		Diffused urban areas
	Transportation	Railways
		Paths
		Highways
		Roads
	Anthropic vegetation	Urban vegetation
		Wooded disturbed vegetation
Open habitats	**Natural meadows**	Dry meadows
		Alpine grasslands
		Extensive grasslands
	Agriculture	Crops
		Vineyards
		Orchards
Wetlands	**Wetlands**	Wet meadows
		Other wet habitats
		Riverbeds
		Wet forests

Table A4. Habitat categories included in Specific Habitats set of predictors (SH) for each ecological group.

Eco group	Specific variables	Eco group	Specific variables
Ruderal	Dense urban areas	**Dry/poor meadows**	Dry meadows
	Diffuse urban areas		Alpine grasslands
	Transportation		Extensive grasslands
	Urban vegetation		Crops
	Wooded disturbed vegetation		Vineyards and Orchards
	Forests		Wetlands
	Open habitats		Urban areas and habitats
	Wetlands		forests
Alpine	Dry meadows	**Nitrogen rich meadows**	Crops
	Alpine grasslands		Vineyards and Orchards
	Extensive grasslands		Natural meadows
	Crops		Transportation
	Urban areas and habitats		Anthropic vegetation
	Closed forests		Urbanized areas
	Open forests		Wetlands
	Wetlands		Forests
Wetlands	Wet meadows	**Forest**	Deciduous forests
	Other wet habitats		Coniferous forests
	Riverbeds		Open forests
	Wet forests		Barrens
	Open habitats		Wetlands
	Urban areas and habitats		Open habitats
	Closed forests		Anthropic vegetation
	Open forests		Transportation + urbanized areas

Table A5. Information on the datasets used to calculate NDVI and NDWI predictors.

Optical Satellite Platform		**Landsat-5**	**Landsat-7**	**Landsat-8**
Sensor		TM	ETM+	OLI/TIRS
Period (start-end)		2000 – 2011	2000 - 2018	2013 - 2018
Revisit time (day)		16	16	16
Spatial resolution (m)		30	30	30
Bands used		Red, Nir, Swir1, Pixel QA	Red, Nir, Swir1, Pixel QA	Red, Nir, Swir1, Pixel QA
Wavelenght (µm)	**Red**	0.63 – 0.69	0.63 – 0.69	0.64 – 0.67
	Nir	0.77 – 0.90	0.77 – 0.90	0.85 – 0.88
	Swir1	1.55 - 1.75	1.55 – 1.75	1.57 – 1.65

Table A6. RSI predictors names, description and origin. Due to artefacts in some images, years 2002 and 2003 were not considered for NDVI calculation, and years 2009, 2016 and 2017 for NDWI.

Name	Signification	Origin
Max NDVI	Mean of maximal NDVI 2000-2018	Swiss Data Cube
Min NDVI	Mean of minimal NDVI 2000-2018	Swiss Data Cube
NDVI seasonality	Mean of Max NDVI – Min NDVI 2000-2018	Swiss Data Cube
Mean NDVI	Mean NDVI 2000-2018	Swiss Data Cube
Max NDWI	Mean of maximal NDWI 2000-2018	Swiss Data Cube
Min NDWI	Mean of minimal NDWI 2000-2018	Swiss Data Cube
NDWI seasonality	Mean of Max NDWI – Min NDWI 2000-2018	Swiss Data Cube
Mean NDWI	Mean NDWI 2000-2018	Swiss Data Cube

Table A7. Mean AUC value of models per ecological group.

MEAN AUC	FORESTS	WETLANDS	ALPINE	RMEADOWS	PMEADOWS	RUDERAL
TC	0.747	0.720	0.815	0.754	0.746	0.798
TC_BH	0.794	0.793	0.840	0.789	0.790	0.821
BTC_BH	0.792	0.792	0.836	0.788	0.782	0.818
TC_AH	0.800	0.797	0.841	0.794	0.798	0.828
BTC_AH	0.798	0.795	0.837	0.793	0.791	0.826
TC_SH	0.787	0.791	0.841	0.795	0.799	0.826
BTC_SH	0.785	0.790	0.838	0.794	0.793	0.823
SH	0.694	0.719	0.743	0.725	0.726	0.732
TC_RSI	0.754	0.740	0.823	0.764	0.762	0.804
BTC_RSI	0.750	0.735	0.818	0.763	0.755	0.800
BTC_BRSI	0.747	0.730	0.817	0.762	0.752	0.800
RSI	0.688	0.672	0.771	0.691	0.697	0.731

Table A8. Mean TSS value of models per ecological group.

MEAN TSS	FORESTS	WETLANDS	ALPINE	RMEADOWS	PMEADOWS	RUDERAL
TC	0.393	0.354	0.529	0.389	0.384	0.470
TC_BH	0.461	0.464	0.562	0.456	0.459	0.506

BTC_BH	0.459	0.461	0.559	0.455	0.448	0.504
TC_AH	0.470	0.466	0.561	0.455	0.466	0.523
BTC_AH	0.469	0.464	0.558	0.455	0.456	0.520
TC_SH	0.451	0.462	0.560	0.460	0.464	0.518
BTC_SH	0.451	0.460	0.555	0.458	0.457	0.515
SH	0.307	0.342	0.387	0.349	0.349	0.368
TC_RSI	0.404	0.379	0.543	0.410	0.405	0.480
BTC_RSI	0.400	0.370	0.535	0.411	0.393	0.475
BTC_BRSI	0.395	0.362	0.534	0.408	0.387	0.474
RSI	0.294	0.274	0.453	0.292	0.302	0.368

Table A9. Mean AUC and TSS values and Standard Deviation (STDEV) for all models.

MODELS	**MEAN AUC**	**STDEV AUC**	**MEAN TSS**	**STDEV TSS**
TC	0.763	0.055	0.420	0.095
TC_BH	0.805	0.039	0.485	0.073
BTC_BH	0.801	0.040	0.481	0.075
TC_AH	0.81	0.038	0.490	0.074
BTC_AH	0.807	0.039	0.487	0.074
TC_SH	0.806	0.039	0.486	0.072
BTC_SH	0.804	0.039	0.483	0.073
SH	0.723	0.031	0.350	0.050
TC_RSI	0.775	0.051	0.437	0.091
BTC_RSI	0.77	0.053	0.431	0.093
BTC_BRSI	0.768	0.054	0.427	0.096
RSI	0.708	0.058	0.331	0.100

Table A10. P-values of Wilcoxon paired data mean tests between models. *** p-value < 0,0001; ** p-value < 0,001; * p-value < 0,05.

AUC	**TC_BH**	**BTC_BH**	**TC_AH**	**BTC_AH**	**TC_SH**	**BTC_SH**	**SH**	**TC_RSI**	**BTC_RSI**	**BTC_BRSI**	**RSI**
TC	1,69E-13***	1,69E-13***	1,69E-13***	1,69E-13***	1,69E-13***	1,69E-13***	1,89E-09***	1,23E-12***	5,70E-06***	4,98E-04**	2,80E-13***
TC_BH		1,98E-06***	2,41E-10***	8,84E-04**	2,19E-02*	5,10E-01	1,69E-13***	2,47E-13***	2,58E-13***	2,37E-13***	1,69E-13***
BTC_BH			2,04E-11***	3,46E-10***	2,47E-05***	5,15E-03*	1,69E-13***	3,04E-13***	2,18E-13***	2,09E-13***	1,69E-13***
TC_AH				4,48E-06***	1,14E-04**	7,27E-08***	1,69E-13***	1,69E-13***	1,77E-13***	1,77E-13***	1,69E-13***
BTC_AH					8,25E-01	1,31E-03*	1,69E-13***	1,69E-13***	1,69E-13***	1,69E-13***	1,69E-13***
TC_SH						3,58E-05***	1,69E-13***	1,69E-13***	1,69E-13***	1,69E-13***	1,69E-13***
BTC_SH							1,69E-13***	1,69E-13***	1,69E-13***	1,69E-13***	1,69E-13***
SH								4,45E-12***	3,76E-11***	2,08E-10***	4,40E-03*
TC_RSI									4,40E-03*	2,70E-07***	4,21E-11***
BTC_RSI										1,69E-13***	3,16E-09***
BTC_BRSI											1,69E-13***
TSS											
TC	1,69E-13***	1,69E-13***	1,69E-13***	1,77E-13***	1,77E-13***	2,00E-13***	3,34E-10***	3,65E-12***	6,87E-06***	9,58E-04**	2,27E-13***
TC_BH		3,41E-02*	1,25E-04**	8,85E-02	4,85E-01	3,30E-01	1,69E-13***	5,67E-13***	4,25E-13***	4,25E-13***	1,69E-13***
BTC_BH			4,48E-06***	1,76E-04**	9,60E-03*	1,83E-01	1,69E-13***	8,20E-13***	2,80E-13***	2,37E-13***	1,69E-13***
TC_AH				4,79E-02*	1,11E-02*	3,67E-05***	1,69E-13***	2,37E-13***	2,37E-13***	2,37E-13***	1,69E-13***
BTC_AH					5,96E-01	2,32E-02*	1,69E-13***	3,04E-13***	1,84E-13***	1,92E-13***	1,69E-13***
TC_SH						3,37E-02*	1,69E-13***	2,58E-13***	2,00E-13***	2,00E-13***	1,69E-13***
BTC_SH							1,69E-13***	4,81E-13***	2,18E-13***	2,18E-13***	1,69E-13***
SH								3,80E-12***	2,88E-11***	9,25E-11***	1,06E-02*
TC_RSI									1,06E-02*	3,32E-04**	2,87E-07***
BTC_RSI										1,69E-13***	4,47E-07***
BTC_BRSI											1,69E-13***

Table A11. Average Pearson’s correlation rate between all predicted maps.

	TC	TC_BH	BTC_BH	TC_AH	BTC_AH	TC_SH	BTC_SH	SH	TC_RSI	BTC_RSI	BTC_BRSI
TC_BH	0,835										
BTC_BH	0,799	0,971									
TC_AH	0,800	0,950	0,923								
BTC_AH	0,764	0,923	0,948	0,972							
TC_SH	0,819	0,964	0,936	0,957	0,930						
BTC_SH	0,784	0,936	0,962	0,931	0,955	0,972					
SH	0,347	0,634	0,649	0,656	0,670	0,689	0,705				
TC_RSI	0,939	0,829	0,798	0,796	0,765	0,813	0,782	0,393			
BTC_RSI	0,904	0,803	0,815	0,772	0,781	0,788	0,798	0,395	0,969		
BTC_BRSI	0,908	0,800	0,813	0,768	0,777	0,784	0,795	0,389	0,965	0,994	
RSI	0,636	0,592	0,591	0,570	0,567	0,580	0,578	0,439	0,760	0,779	0,771

Tables A12. Mean and standard deviation of predictors contribution based on the values of all species (n=72).

	Predictors	**Mean %**	**StDv**
TC	cambisol	10.08	10.39
	n_index	4.24	5.62
	podzol	6.11	9.08
	precipitation	27.88	15.86
	slope	19.57	14.04
	sol_rad	2.27	2.44
	temp	28.12	14.70
	upland_index	1.73	1.88

	Predictors	**Mean %**	**StDv**
TC_BH	cambisol	6.59	6.93
	forest	13.74	11.60
	wetland	13.26	13.01
	n_index	2.40	3.12
	open_habitats	5.61	6.51
	podzol	5.70	7.73
	precipitation	17.48	11.77
	slope	6.45	5.13
	sol_rad	1.14	1.33
	temp	16.49	10.91
	upland_index	1.09	1.01
	urban	10.04	6.79

	Predictors	**Mean %**	**StDv**
BTC_BH	cambisol	7.55	7.44
	forest	14.38	12.35
	wetlant	13.90	13.72
	open_habitats	5.57	6.35
	precipitation	22.63	18.22
	slope	7.45	5.82
	temp	17.79	11.18
	urban	10.74	7.26

	Predictors	**Mean %**	**StDv**
TC_AH	cambisol	5.89	6.35
	closed_forest	12.09	10.30
	open_forest	0.58	0.78
	wetland	12.51	12.40
	crops	5.12	4.27
	n_index	2.34	2.71
	podzol	5.13	7.63
	natural_meadows	4.55	5.02
	precipitation	15.68	11.23

	slope	5.58	4.89
	sol_rad	1.20	1.20
	temp	13.94	8.73
	transportation	11.59	7.73
	upland_index	1.01	0.87
	urbanized_area	2.01	2.38
	anthropic_vegetation	0.79	0.91

BTC_AH	**Predictors**	**Mean %**	**StDv**
	cambisol	6.70	6.81
	closed_forest	12.94	11.01
	open_forest	0.61	0.84
	wetland	13.45	13.39
	crops	5.39	4.71
	natural_meadows	4.66	5.06
	precipitation	19.66	17.40
	slope	6.56	5.49
	temp	14.59	9.21
	transportation	12.10	8.07
	urbanized_area	2.34	2.77
	Anthropic_vegetation	0.98	1.10

TC_RSI	**Predictors**	**Mean %**	**StDv**
	cambisol	7.53	8.20
	max_ndvi	8.12	7.07
	max_ndwi	6.42	8.92
	mean_ndvi	1.22	1.78
	mean_ndwi	0.70	1.13
	min_ndvii	9.08	8.44
	min_ndwi	1.24	1.27
	n_index	2.86	3.70
	podzol	5.53	8.56
	precipitation	20.99	12.95
	season_ndvi	0.74	1.29
	season_ndwi	1.01	1.58
	slope	11.27	9.74
	sol_rad	1.49	1.55
	temp	20.15	11.82
	upland_index	1.64	1.68

BTC_RSI	**Predictors**	**Mean %**	**StDv**
	cambisol	8.99	9.12
	max_ndvi	8.31	7.31
	max_ndwi	7.18	9.62
	mean_ndvi	1.51	2.25
	mean_ndwi	1.20	1.48
	min_ndvii	9.77	9.45

	min_ndwi	1.52	1.56
	precipitation	25.97	18.86
	season_ndvi	1.05	1.65
	season_ndwi	1.01	1.49
	slope	11.91	10.11
	temp	21.58	11.93

	Predictors	**Mean %**	**StDv**
BTC_BRSI	cambisol	8.86	9.21
	max_ndvi	9.55	8.03
	max_ndwi	7.47	9.86
	min_ndvii	10.99	9.70
	min_ndwi	1.96	2.22
	precipitation	26.70	19.67
	slope	12.55	10.71
	temp	21.91	12.53

	Predictors	**Mean %**	**StDv**
RSI	max_ndvi	22.69	13.52
	max_ndwi	32.26	26.61
	mean_ndvi	4.71	6.42
	mean_ndwi	5.94	8.28
	min_ndvii	23.97	20.02
	min_ndwi	4.83	4.97
	season_ndvi	2.51	3.36
	season_ndwi	3.08	4.03

Table A13. Mean and standard deviation of habitat suitability variance using an aggregation of prediction map’s pixels values in a moving windows of 250-meters resolution for all species and all models.

ECO GROUP	SPECIES	TC	TC_BH	BTC_BH	TC_AH	BTC_AH	TC_SH	BTC_SH	SH	TC_RSI	BTC_RSI	BTC_BRSI	RSI	MEAN	STDEV
ALPINE	*Astrantia_major*	0.0024	0.005	0.0041	0.0053	0.0046	0.0052	0.0044	0.0095	0.0039	0.0032	0.003	0.0065	0.0048	0.0019
	Brachypodium_rupestre	0.003	0.0127	0.0111	0.013	0.0117	0.0124	0.0112	0.0168	0.0047	0.0039	0.003	0.0068	0.0092	0.0047
	Campanula_rhomboidalis	0.0009	0.0028	0.0025	0.0031	0.0028	0.0032	0.0029	0.0117	0.0027	0.0024	0.0021	0.0065	0.0036	0.0029
	Carduus_defloratus	0.0027	0.004	0.0034	0.0044	0.0042	0.0044	0.0042	0.0117	0.0048	0.0047	0.0047	0.0091	0.0052	0.0026
	Cerastium_fontanum	0.0117	0.0106	0.0086	0.0119	0.0103	0.011	0.0095	0.0088	0.0113	0.009	0.009	0.0063	0.0098	0.0016
	Gentiana_lutea	0.0017	0.0052	0.0044	0.0062	0.0056	0.0058	0.0052	0.0135	0.0058	0.0049	0.0052	0.0095	0.0061	0.0029
	Geranium_sylvaticum	0.0026	0.0048	0.0044	0.0054	0.0047	0.0053	0.0049	0.0105	0.0033	0.0027	0.0027	0.0069	0.0049	0.0022
	Laserpitium_latifolium	0.0052	0.0072	0.0063	0.0075	0.0066	0.0076	0.0068	0.0139	0.008	0.0073	0.0075	0.0125	0.0080	0.0025
	Phyteuma_orbiculare	0.0022	0.0059	0.0052	0.0076	0.0071	0.0067	0.0062	0.0134	0.0073	0.007	0.0071	0.0113	0.0072	0.0028
	Picris_hieracioides	0.003	0.0059	0.0052	0.0081	0.0077	0.0067	0.0061	0.0142	0.0037	0.0031	0.0031	0.0074	0.0062	0.0031
	Ribes_alpinum	0.0016	0.0074	0.0069	0.0097	0.0096	0.0088	0.0085	0.0147	0.0036	0.0027	0.0023	0.0077	0.0070	0.0038
	Rosa_pendulina	0.0013	0.0039	0.0035	0.0044	0.0038	0.0044	0.004	0.0127	0.0023	0.002	0.0019	0.0082	0.0044	0.0032
														0.0064	**0.0034**
FOREST	*Acer_pseudoplatanus*	0.002	0.0076	0.007	0.0102	0.0099	0.0065	0.0062	0.0072	0.0031	0.0027	0.0026	0.0049	0.0058	0.0028
	Cornus_sanguinea	0.0023	0.0067	0.0062	0.0086	0.0083	0.006	0.0056	0.0097	0.003	0.0025	0.0024	0.0075	0.0057	0.0026
	Corylus_avellana	0.0021	0.0077	0.0074	0.0092	0.0088	0.0062	0.0059	0.0082	0.0024	0.0022	0.0022	0.0044	0.0055	0.0028
	Crataegus_monogyna	0.0017	0.0078	0.0073	0.0088	0.0077	0.0068	0.0061	0.0109	0.0027	0.002	0.002	0.0056	0.0058	0.0030
	Fagus_sylvatica	0.0019	0.0086	0.0087	0.0096	0.0097	0.0073	0.0075	0.01	0.0026	0.0027	0.0021	0.0051	0.0063	0.0032
	Fragaria_vesca	0.0024	0.0106	0.0102	0.0127	0.0124	0.0089	0.0085	0.0095	0.003	0.003	0.0024	0.004	0.0073	0.0040
	Fraxinus_excelsior	0.0018	0.0064	0.0061	0.0079	0.0078	0.0061	0.0059	0.0077	0.0023	0.002	0.002	0.004	0.0050	0.0024
	Galium_mollugo	0.0036	0.0085	0.0079	0.0108	0.0101	0.0075	0.0065	0.0052	0.0057	0.0055	0.0055	0.0053	0.0068	0.0022
	Geum_urbanum	0.0019	0.0058	0.0054	0.0077	0.0074	0.0047	0.0042	0.0065	0.0028	0.0024	0.0022	0.0057	0.0047	0.0020
	Hedera_helix	0.0019	0.0058	0.0057	0.008	0.0079	0.0054	0.0052	0.0105	0.0025	0.0024	0.0024	0.007	0.0054	0.0027
	Lonicera_xylosteum	0.0031	0.0107	0.0104	0.0112	0.0109	0.009	0.0086	0.0113	0.0041	0.0038	0.0026	0.0064	0.0077	0.0035
	Picea_abies	0.0015	0.0105	0.0101	0.0103	0.0099	0.0089	0.0086	0.0106	0.0031	0.0026	0.0026	0.0044	0.0069	0.0037
														0.0061	**0.0030**
	Briza_media	0.0037	0.0115	0.0106	0.0128	0.0119	0.0119	0.0111	0.0149	0.0073	0.0068	0.0067	0.0083	0.0098	0.0032

NITROGEN POOR AND DRY MEADOWS	*Bromus_erectus*	0.0085	0.0141	0.0112	0.0165	0.0142	0.0138	0.0116	0.0147	0.0094	0.0055	0.0054	0.0063	0.0109	0.0039
	Daucus_carota	0.0029	0.0056	0.0047	0.0075	0.0067	0.006	0.0052	0.0112	0.0038	0.0032	0.0031	0.0077	0.0056	0.0024
	Euphorbia_cyparissias	0.005	0.0101	0.0092	0.013	0.0122	0.0118	0.0112	0.0143	0.0085	0.0083	0.0081	0.0078	0.0100	0.0026
	Galium_verum	0.005	0.0085	0.0079	0.0107	0.0102	0.0094	0.0088	0.0137	0.0062	0.0055	0.0055	0.0097	0.0084	0.0026
	Hippocrepis_comosa	0.0043	0.0132	0.0123	0.0136	0.0125	0.0128	0.0121	0.0161	0.0089	0.0099	0.0094	0.0113	0.0114	0.0030
	Hypericum_perforatum	0.0061	0.0087	0.0064	0.0107	0.0085	0.0099	0.0079	0.0115	0.0059	0.004	0.0038	0.0065	0.0075	0.0025
	Origanum_vulgare	0.0051	0.0095	0.0093	0.0141	0.0144	0.0109	0.0111	0.0166	0.007	0.0064	0.0064	0.0062	0.0098	0.0038
	Plantago_media	0.0048	0.0098	0.0088	0.0129	0.0121	0.0113	0.0104	0.0151	0.0081	0.0079	0.0079	0.0112	0.0100	0.0027
	Potentilla_erecta	0.0062	0.0115	0.0112	0.0117	0.0115	0.0114	0.0113	0.012	0.0089	0.0087	0.008	0.0067	0.0099	0.0021
	Sanguisorba_minor	0.0076	0.0114	0.0092	0.0158	0.0143	0.0116	0.0098	0.0123	0.0074	0.0049	0.0048	0.0061	0.0096	0.0036
	Silene_vulgaris	0.0029	0.0077	0.0073	0.0117	0.0113	0.01	0.0101	0.0143	0.0064	0.0066	0.0066	0.0092	0.0087	0.0031
														0.0093	**0.0032**
NITROGEN RICH MEADOWS	*Achillea_millefolium*	0.0043	0.0079	0.007	0.0094	0.0089	0.0096	0.0088	0.015	0.0061	0.0055	0.0055	0.0099	0.0082	0.0028
	Ajuga_reptans	0.0031	0.0062	0.0055	0.0089	0.0083	0.0088	0.0082	0.012	0.0035	0.0023	0.0023	0.0036	0.0061	0.0032
	Arrhenatherum_elatius	0.0045	0.0078	0.0072	0.0099	0.0095	0.0098	0.0094	0.0162	0.0057	0.0046	0.0048	0.0083	0.0081	0.0033
	Dactylis_glomerata	0.004	0.0073	0.0065	0.01	0.0092	0.01	0.0094	0.0132	0.0052	0.0045	0.0042	0.0066	0.0075	0.0029
	Lotus_corniculatus	0.0023	0.0073	0.0067	0.009	0.0087	0.0095	0.009	0.0134	0.004	0.0037	0.0036	0.0068	0.0070	0.0032
	Medicago_lupulina	0.0039	0.0077	0.0067	0.0102	0.0095	0.0103	0.0096	0.0159	0.0055	0.0045	0.0046	0.0071	0.0079	0.0034
	Plantago_lanceolata	0.0043	0.0067	0.0063	0.0089	0.0085	0.0089	0.0085	0.0132	0.0049	0.0045	0.0046	0.0075	0.0072	0.0026
	Poa_trivialis	0.0045	0.0073	0.0068	0.0086	0.0083	0.0089	0.0085	0.013	0.0051	0.0046	0.0046	0.0066	0.0073	0.0025
	Prunella_vulgaris	0.0044	0.009	0.0085	0.0101	0.0098	0.0104	0.0102	0.014	0.0056	0.0054	0.0052	0.0057	0.0082	0.0029
	Taraxacum_officinale	0.0029	0.0052	0.0047	0.0066	0.0063	0.0065	0.0062	0.0115	0.004	0.0038	0.0039	0.0084	0.0058	0.0024
	Trifolium_pratense	0.0051	0.0084	0.008	0.0101	0.01	0.01	0.0099	0.0138	0.0057	0.0053	0.0053	0.0069	0.0082	0.0027
	Trifolium_repens	0.0058	0.0077	0.0073	0.0096	0.0093	0.0101	0.0097	0.0141	0.0063	0.0057	0.0058	0.008	0.0083	0.0025
														0.0075	**0.0029**
RUDERAL	*Cirsium_arvense*	0.0032	0.0061	0.0059	0.0083	0.008	0.0076	0.0072	0.015	0.0039	0.0034	0.0035	0.0071	0.0066	0.0032
	Convolvulus_arvensis	0.0038	0.0049	0.0044	0.0061	0.0057	0.0063	0.0059	0.0163	0.0049	0.0047	0.0047	0.012	0.0066	0.0037
	Equisetum_arvense	0.0037	0.0067	0.0062	0.009	0.0089	0.0079	0.0075	0.0132	0.0047	0.0041	0.0041	0.0072	0.0069	0.0027
	Erigeron_annuus	0.0021	0.0051	0.0049	0.0067	0.0066	0.0066	0.0064	0.0171	0.0032	0.0029	0.0028	0.0082	0.0061	0.0040
	Galeopsis_tetrahit	0.0036	0.0105	0.0095	0.012	0.0116	0.0114	0.0107	0.0135	0.0049	0.0032	0.0032	0.0039	0.0082	0.0040
	Galium_aparine	0.0023	0.0054	0.0053	0.0064	0.0064	0.0064	0.0063	0.0169	0.0028	0.0028	0.0027	0.0089	0.0061	0.0040

	Geranium_robertianum	0.0022	0.0078	0.0074	0.0103	0.0103	0.009	0.0087	0.0131	0.0029	0.0029	0.0028	0.0054	0.0069	0.0036
	Plantago_major	0.0042	0.0074	0.0073	0.009	0.0087	0.0084	0.0083	0.0152	0.0042	0.0038	0.0037	0.0069	0.0073	0.0032
	Poa_annua	0.004	0.0066	0.0061	0.0097	0.0092	0.0089	0.0083	0.0158	0.0046	0.0038	0.0037	0.0073	0.0073	0.0034
	Potentilla_reptans	0.0027	0.0047	0.0044	0.0068	0.0066	0.0065	0.0063	0.017	0.0029	0.0026	0.0026	0.008	0.0059	0.0040
	Ranunculus_repens	0.004	0.0067	0.0062	0.0093	0.0086	0.0092	0.0087	0.0116	0.0044	0.0034	0.0034	0.0052	0.0067	0.0027
	Veronica_persica	0.0033	0.005	0.0046	0.0072	0.0068	0.0067	0.0064	0.0168	0.0046	0.0044	0.0045	0.0118	0.0068	0.0039
														0.0068	**0.0035**
WETLANDS	*Agrostis_stolonifera*	0.0037	0.0066	0.0062	0.0082	0.0079	0.0064	0.0059	0.0068	0.005	0.0043	0.004	0.0052	0.0059	0.0015
	Carex_flacca	0.0026	0.0103	0.0095	0.0115	0.011	0.0101	0.0094	0.012	0.0037	0.0033	0.0032	0.0033	0.0075	0.0038
	Deschampsia_cespitosa	0.0115	0.0126	0.0106	0.0128	0.0112	0.0125	0.0103	0.0097	0.0146	0.0116	0.0113	0.0077	0.0114	0.0017
	Eupatorium_cannabinum	0.0039	0.0096	0.009	0.0104	0.0098	0.0097	0.009	0.0143	0.0051	0.0032	0.0025	0.0054	0.0076	0.0036
	Festuca_arundinacea	0.0032	0.0059	0.0056	0.0088	0.0086	0.0061	0.0057	0.0136	0.0043	0.0039	0.0039	0.0096	0.0066	0.0030
	Filipendula_ulmaria	0.0106	0.0105	0.0098	0.0117	0.0111	0.0102	0.0091	0.0082	0.0112	0.009	0.0088	0.0044	0.0096	0.0020
	Gymnadenia_conopsea	0.0029	0.0119	0.0118	0.0118	0.0116	0.0114	0.011	0.0128	0.007	0.0073	0.0071	0.0069	0.0095	0.0031
	Linum_catharticum	0.0032	0.0132	0.0116	0.0146	0.0135	0.0129	0.0116	0.0144	0.0073	0.0068	0.0066	0.0073	0.0103	0.0038
	Listera_ovata	0.0059	0.0149	0.0139	0.0154	0.0146	0.0144	0.0133	0.0121	0.013	0.0119	0.0109	0.0095	0.0125	0.0027
	Platanthera_bifolia	0.0034	0.012	0.0108	0.0121	0.0109	0.0117	0.0104	0.0126	0.0069	0.0049	0.0036	0.007	0.0089	0.0035
	Rhinanthus_alectorolophus	0.0035	0.0081	0.0076	0.0116	0.0112	0.0081	0.0076	0.0075	0.0065	0.0062	0.0058	0.0069	0.0075	0.0022
	Solidago_gigantea	0.004	0.0073	0.0072	0.0091	0.009	0.0073	0.0073	0.012	0.0048	0.0044	0.0042	0.0085	0.0071	0.0024
														0.0087	**0.0034**
MEAN		**0.0038**	**0.0081**	**0.0074**	**0.0098**	**0.0092**	**0.0087**	**0.0081**	**0.0126**	**0.0054**	**0.0047**	**0.0045**	**0.0072**		
STDEV		**0.0021**	**0.0027**	**0.0024**	**0.0027**	**0.0026**	**0.0025**	**0.0023**	**0.0028**	**0.0025**	**0.0022**	**0.0022**	**0.0021**		

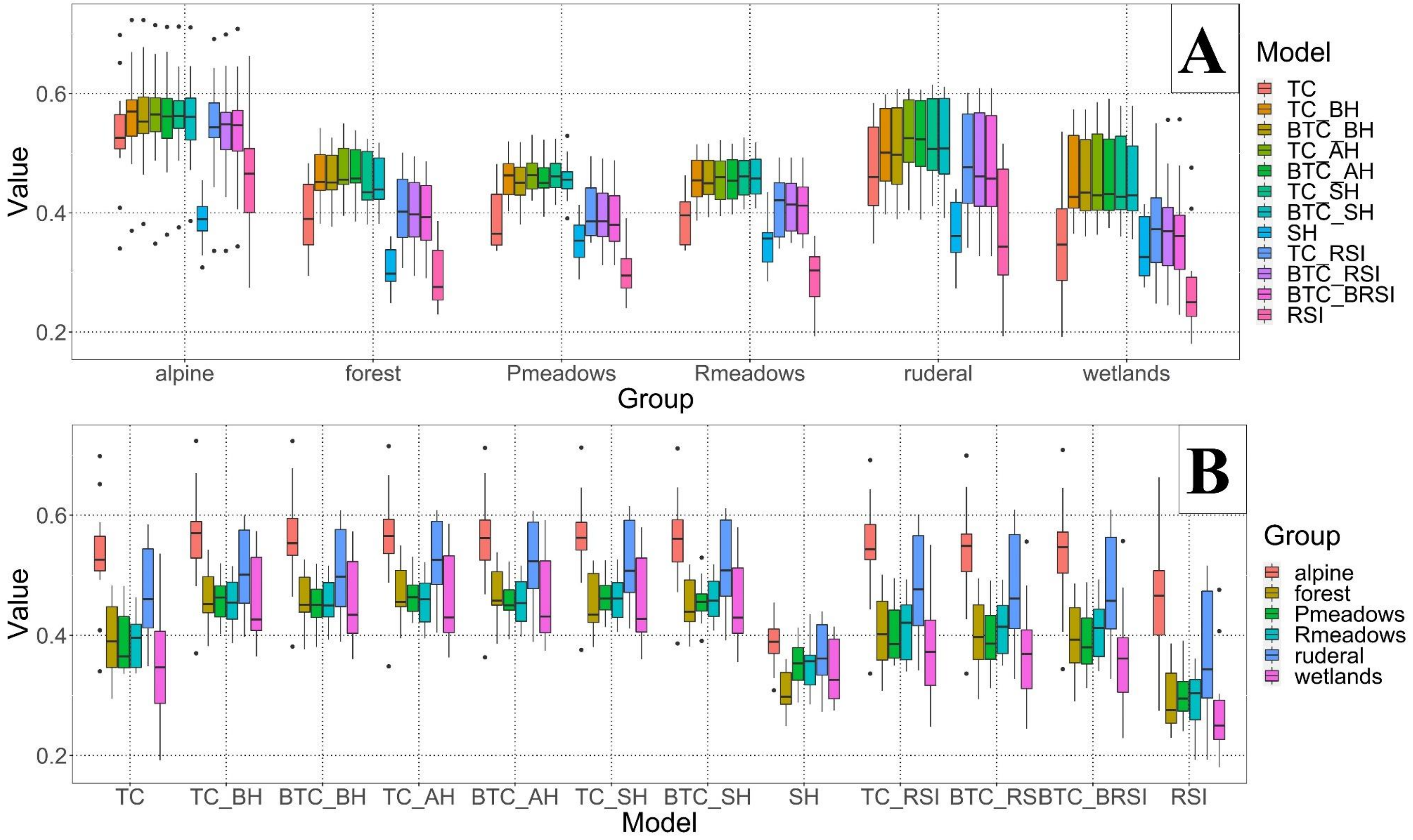


Fig. A1. Boxplots of TSS values of all models per ecological group (A) and of all groups per model (B).

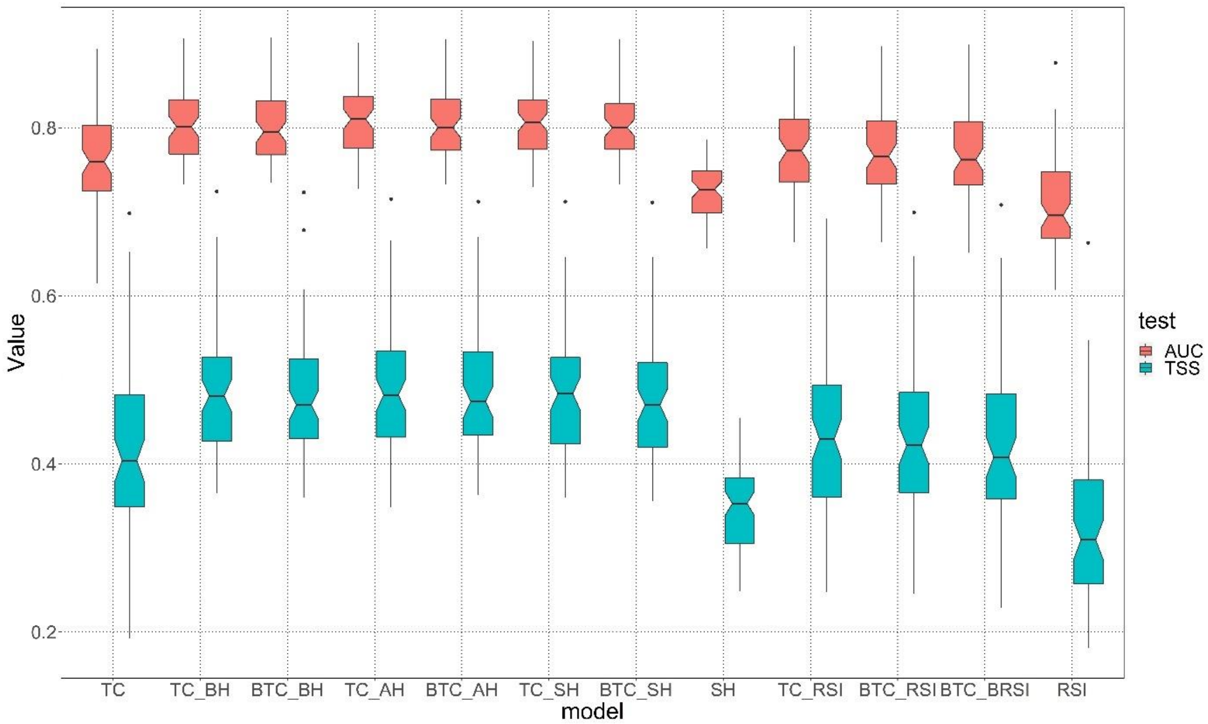
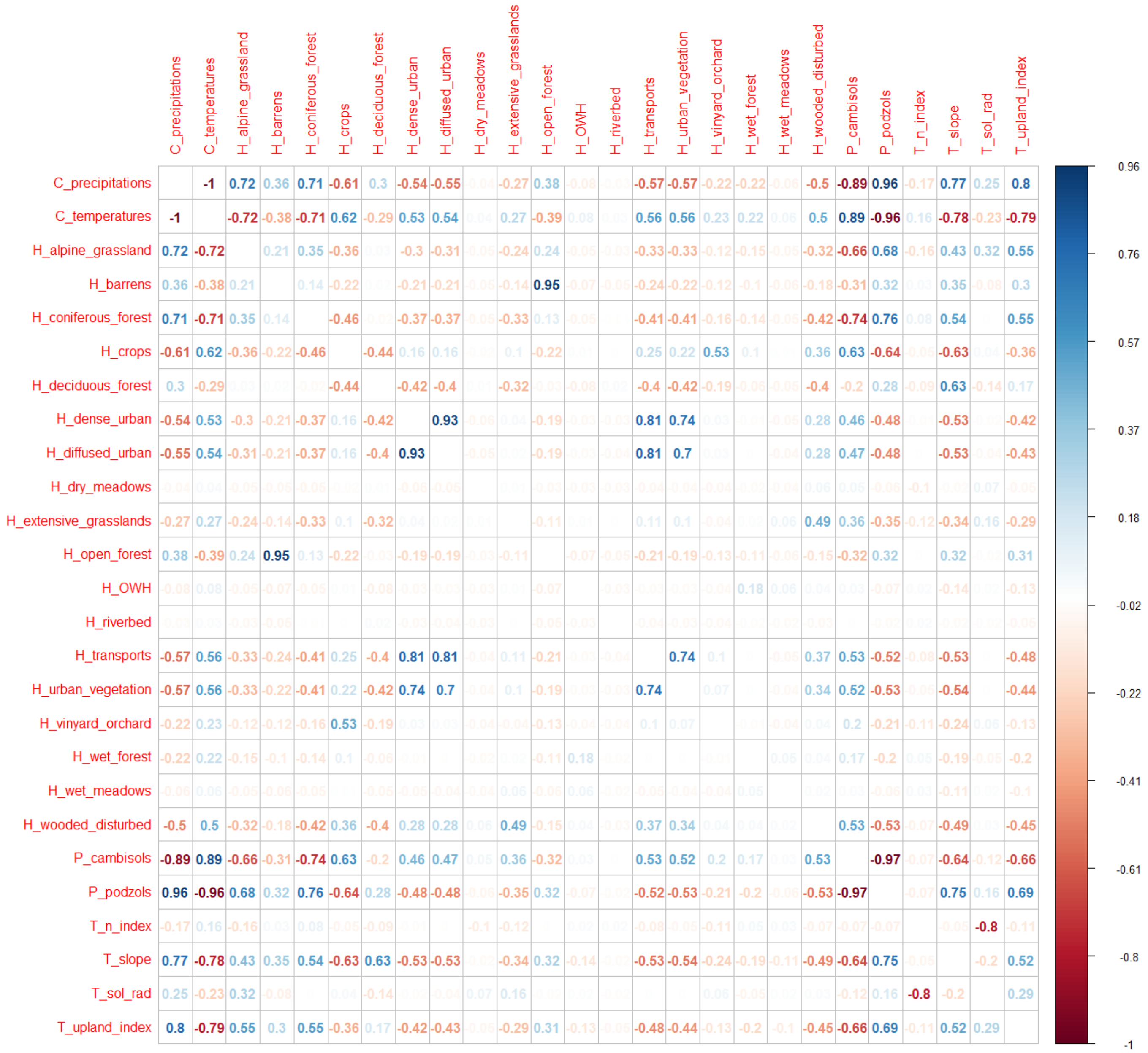


Fig. A2. Boxplot of AUC and TSS values for all models.



	C_precipitations	C_temperatures	H_alpine_grassland	H_barrens	H_coniferous_forest	H_crops	H_deciduous_forest	H_dense_urban	H_diffused_urban	H_dry_meadows	H_extensive_grasslands	H_open_forest	H_OWH	H_riverbed	H_transports	H_urban_vegetation	H_vinyard_orchard	H_wet_forest	H_wet_meadows	H_wooded_disturbed	P_cambisols	P_podzols	T_n_index	T_slope	T_sol_rad	T_upland_index
C_precipitations		-1	0.72	0.36	0.71	-0.61	0.3	-0.54	-0.55	-0.04	-0.27	0.38	-0.08	-0.03	-0.57	-0.57	-0.22	-0.22	-0.06	-0.5	-0.89	0.96	-0.17	0.77	0.25	0.8
C_temperatures	-1		-0.72	-0.38	-0.71	0.62	-0.29	0.53	0.54	0.04	0.27	-0.39	0.08	0.03	0.56	0.56	0.23	0.22	0.06	0.5	0.89	-0.96	0.16	-0.78	-0.23	-0.79
H_alpine_grassland	0.72	-0.72		0.21	0.35	-0.36	0.03	-0.3	-0.31	-0.05	-0.24	0.24	-0.05	-0.03	-0.33	-0.33	-0.12	-0.15	-0.05	-0.32	-0.66	0.68	-0.16	0.43	0.32	0.55
H_barrens	0.36	-0.38	0.21		0.14	-0.22	0.02	-0.21	-0.21	-0.05	-0.14	0.95	-0.07	-0.05	-0.24	-0.22	-0.12	-0.1	-0.06	-0.18	-0.31	0.32	0.03	0.35	-0.08	0.3
H_coniferous_forest	0.71	-0.71	0.35	0.14		-0.46	-0.02	-0.37	-0.37	-0.05	-0.33	0.13	-0.05	-0.01	-0.41	-0.41	-0.16	-0.14	-0.05	-0.42	-0.74	0.76	0.08	0.54	0	0.55
H_crops	-0.61	0.62	-0.36	-0.22	-0.46		-0.44	0.16	0.16	-0.02	0.1	-0.22	0.01	0	0.25	0.22	0.53	0.1	0.01	0.36	0.63	-0.64	-0.05	-0.63	0.04	-0.36
H_deciduous_forest	0.3	-0.29	0.03	0.02	-0.02	-0.44		-0.42	-0.4	0.01	-0.32	-0.03	-0.08	0.02	-0.4	-0.42	-0.19	-0.06	-0.05	-0.4	-0.2	0.28	-0.09	0.63	-0.14	0.17
H_dense_urban	-0.54	0.53	-0.3	-0.21	-0.37	0.16	-0.42		0.93	-0.06	0.04	-0.19	-0.03	-0.03	0.81	0.74	0.03	-0.01	-0.05	0.28	0.46	-0.48	-0.01	-0.53	-0.02	-0.42
H_diffused_urban	-0.55	0.54	-0.31	-0.21	-0.37	0.16	-0.4	0.93		-0.05	0.02	-0.19	-0.03	-0.04	0.81	0.7	0.03	0	-0.04	0.28	0.47	-0.48	0	-0.53	-0.04	-0.43
H_dry_meadows	-0.04	0.04	-0.05	-0.05	-0.05	-0.02	0.01	-0.06	-0.05		0.01	-0.03	-0.03	-0.03	-0.04	-0.04	-0.04	-0.02	-0.04	0.06	0.05	-0.06	-0.1	-0.02	0.07	-0.05
H_extensive_grasslands	-0.27	0.27	-0.24	-0.14	-0.33	0.1	-0.32	0.04	0.02	0.01		-0.11	0.01	0	0.11	0.1	-0.04	0.02	0.06	0.49	0.36	-0.35	-0.12	-0.34	0.16	-0.29
H_open_forest	0.38	-0.39	0.24	0.95	0.13	-0.22	-0.03	-0.19	-0.19	-0.03	-0.11		-0.07	-0.05	-0.21	-0.19	-0.13	-0.11	-0.06	-0.15	-0.32	0.32	0	0.32	-0.02	0.31
H_OWH	-0.08	0.08	-0.05	-0.07	-0.05	0.01	-0.08	-0.03	-0.03	-0.03	0.01	-0.07		-0.03	-0.03	-0.03	-0.04	0.18	0.06	0.04	0.03	-0.07	0.02	-0.14	0.02	-0.13
H_riverbed	-0.03	0.03	-0.03	-0.05	-0.01	0	0.02	-0.03	-0.04	-0.03	0	-0.05	-0.03		-0.04	-0.03	-0.04	-0.02	-0.02	-0.03	0	-0.02	0.02	-0.02	-0.02	-0.05
H_transports	-0.57	0.56	-0.33	-0.24	-0.41	0.25	-0.4	0.81	0.81	-0.04	0.11	-0.21	-0.03	-0.04		0.74	0.1	0	-0.05	0.37	0.53	-0.52	-0.08	-0.53	0	-0.48
H_urban_vegetation	-0.57	0.56	-0.33	-0.22	-0.41	0.22	-0.42	0.74	0.7	-0.04	0.1	-0.19	-0.03	-0.03	0.74		0.07	0	-0.04	0.34	0.52	-0.53	-0.05	-0.54	0	-0.44
H_vinyard_orchard	-0.22	0.23	-0.12	-0.12	-0.16	0.53	-0.19	0.03	0.03	-0.04	-0.04	-0.13	-0.04	-0.04	0.1	0.07		-0.01	-0.04	0.04	0.2	-0.21	-0.11	-0.24	0.06	-0.13
H_wet_forest	-0.22	0.22	-0.15	-0.1	-0.14	0.1	-0.06	-0.01	0	-0.02	0.02	-0.11	0.18	-0.02	0	0	-0.01		0.05	0.04	0.17	-0.2	0.05	-0.19	-0.05	-0.2
H_wet_meadows	-0.06	0.06	-0.05	-0.06	-0.05	0.01	-0.05	-0.05	-0.04	-0.04	0.06	-0.06	0.06	-0.02	-0.05	-0.04	-0.04	0.05		0.02	0.03	-0.06	0.03	-0.11	0.02	-0.1
H_wooded_disturbed	-0.5	0.5	-0.32	-0.18	-0.42	0.36	-0.4	0.28	0.28	0.06	0.49	-0.15	0.04	-0.03	0.37	0.34	0.04	0.04	0.02		0.53	-0.53	-0.07	-0.49	0.03	-0.45
P_cambisols	-0.89	0.89	-0.66	-0.31	-0.74	0.63	-0.2	0.46	0.47	0.05	0.36	-0.32	0.03	0	0.53	0.52	0.2	0.17	0.03	0.53		-0.97	-0.07	-0.64	-0.12	-0.66
P_podzols	0.96	-0.96	0.68	0.32	0.76	-0.64	0.28	-0.48	-0.48	-0.06	-0.35	0.32	-0.07	-0.02	-0.52	-0.53	-0.21	-0.2	-0.06	-0.53	-0.97		-0.07	0.75	0.16	0.69
T_n_index	-0.17	0.16	-0.16	0.03	0.08	-0.05	-0.09	-0.01	0	-0.1	-0.12	0	0.02	0.02	-0.08	-0.05	-0.11	0.05	0.03	-0.07	-0.07	-0.07		-0.05	-0.8	-0.11
T_slope	0.77	-0.78	0.43	0.35	0.54	-0.63	0.63	-0.53	-0.53	-0.02	-0.34	0.32	-0.14	-0.02	-0.53	-0.54	-0.24	-0.19	-0.11	-0.49	-0.64	0.75	-0.05		-0.2	0.52
T_sol_rad	0.25	-0.23	0.32	-0.08	0	0.04	-0.14	-0.02	-0.04	0.07	0.16	-0.02	0.02	-0.02	0	0	0.06	-0.05	0.02	0.03	-0.12	0.16	-0.8	-0.2		0.29
T_upland_index	0.8	-0.79	0.55	0.3	0.55	-0.36	0.17	-0.42	-0.43	-0.05	-0.29	0.31	-0.13	-0.05	-0.48	-0.44	-0.13	-0.2	-0.1	-0.45	-0.66	0.69	-0.11	0.52	0.29	

Fig. A3. Spatial correlation between topopedo-climatic set and specific habitats used in the SH sets. The first letter of the variables indicate its type and is followed by its name (C = climate, H = habitats, P = pedology and T= topography). Predictors highly correlated are colored in dark blue or dark red, respectively if they are showing a positive or negative correlation.

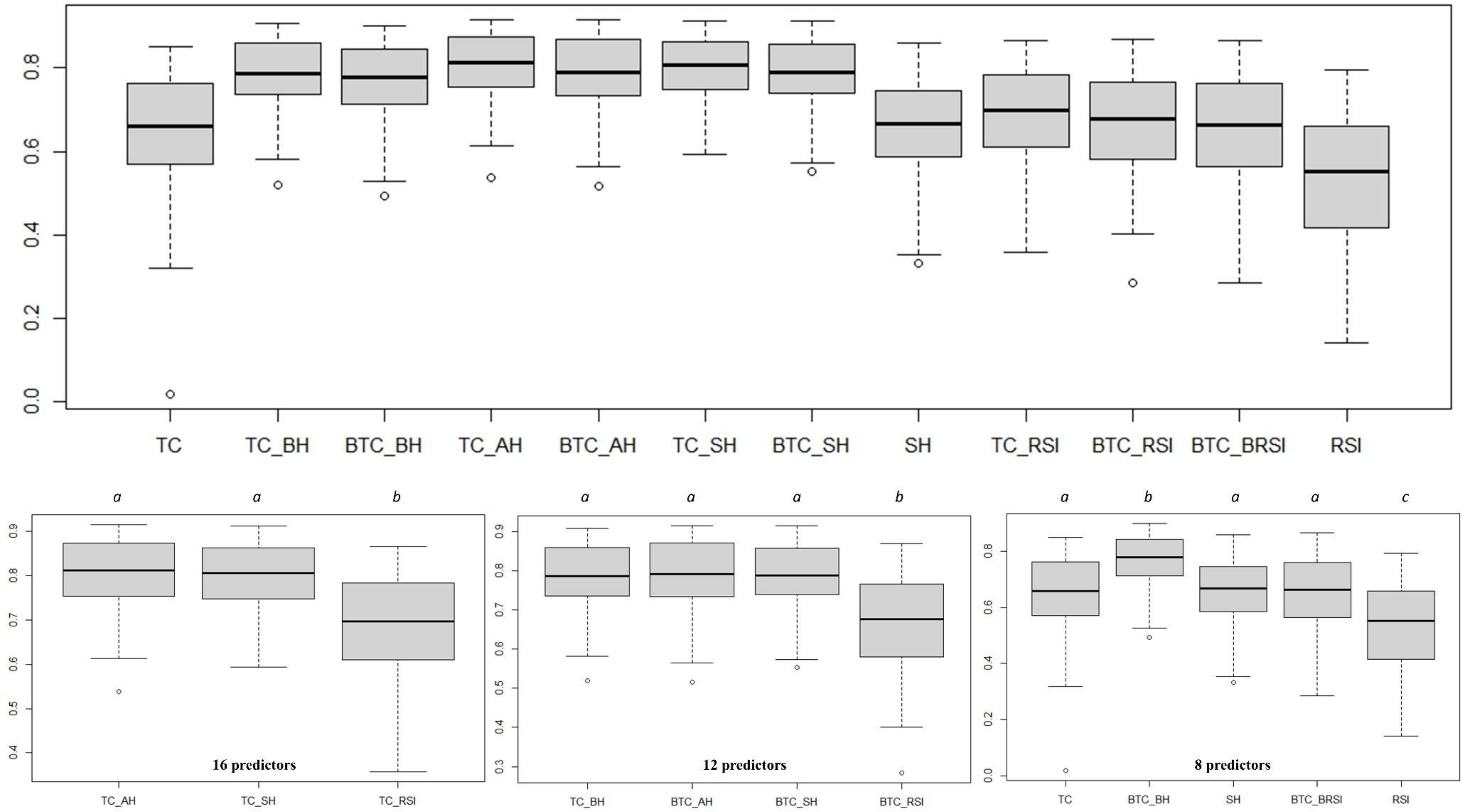


Fig. A4. Boxplots of calibration slope for all models (upper figure) and according to the number of predictors used (lower figures). The legends above the lower boxplots indicate differing calibration slope's values (different letter) according to a Wilcoxon paired data tests (p-value<0.05), while the same letters indicate no statistical differences.

Chapter 4

Effects of climate and land-use changes on plant distributions and vulnerability index assessment

From: Sanguet *et al.*, in prep

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In this paper, I participated to the conceptualization and to the methodology together with all the co-authors, and carried out the experiments and the writing of the original draft.

4.1. Context

Climatic and biotic predictors are key drivers influencing species distribution, as demonstrated in the previous chapter. Their predicted changes over the next decades are expected to cause drastic shifts in species and biodiversity distributions (Haines-Young, 2009; IPCC, 2018; IPBES, 2019; Nunez *et al.*, 2019; Pacifici *et al*., 2015; Thomas, *et al*., 2004). The effects of a warming climate on species distribution and phenology is already observed in many groups of species in the European Alps (Vitasse *et al*., 2021) and in Switzerland (Vittoz *et al*., 2013). In this context, it is essential to assess the range of possibilities of future species distributions in order to understand key patterns of changes regarding the evolution of biodiversity distribution. This eventually allows to identify, protect and restore areas with high ecological value in the long term. Some species might be more vulnerable to global changes than others and thus more likely to become locally extinct if no conservation actions are taken.

This chapter focuses on the impacts of global changes on species distributions using two different scenarios of climate change and one Land-Use-Land-Cover (LULC) business-as-usual scenario in 2050. Little is known on the methods for allowing the combination of prediction maps from models with different extent and resolution and two possible approaches are tested and discussed. The predicted distributional changes are assessed using several indicators such as the suitability, the relative size and fragmentation of species suitable areas, as well as their expected potential migration. Finally, these indicators were merged in order to create a vulnerability index for future environmental changes which was compared among the red list and native statuses of species, inspired by what has been done with breeding birds by Maggini *et al*., (2014). Assessing the vulnerability of plants to global changes is essential because the current health of their populations measured by their red list status might not be a reliable indicator of resilience under the future conditions.

4.2. Methods

4.2.1. Data

4.2.1.1. Predictor selection

Climatic predictors were downloaded from Worldclim (v.2.1, Fick & Hijmans, 2017) with a spatial resolution of 30 arc-seconds (~ 1km) and a European extent. They were selected according to their ecological potential and low level of collinearity and represent the maximum, minimum and variability of temperature and precipitation at different time scales (see Table 1). They were downloaded for six different general circulation models and two Representative Concentration Pathways (RCP) representing optimistic and pessimistic scenarios of climate change by 2050 (respectively RCP26 and RCP85 from CMIP5). The six general circulation models were selected according to their availability at the desired time period, the accessibility of all required predictors and data on Worldclim, but also according to their interdependency by selecting the most uncorrelated models in order to integrate the variability among climatic predictions into the modelling process, following the results of Sanderson *et al.,* (2015). The selected general circulation models are the following: MPI-ESM-LR, MIROC5, BCC-CSM1-1, CNRM-CM5, GISS+E2-R and MIROC-ESM-CHEM. An aridity index was then calculated for the three treatments (current, optimistic future and pessimistic future) and above-mentioned models. It was calculated using the ratio between the annual precipitations and the mean annual potential evapotranspiration (Eq. 1, 2) according to the method described in Karger *et al.,* (2017) and presented below.

$$pet = 0.0023 * r * (t + 17.8) * td^{0.5} \tag{1}$$

$$a = \frac{p}{pet} \tag{2}$$

Where *pet* is the mean annual potential evapotranspiration, *r* is the average annual solar radiation, *t* is the monthly mean daily temperature, *td* the daily temperature range, *p* the annual precipitations and a the aridity index.

Biotic predictors, extracted from LULC map categories, and topographic predictors were selected to maximize models' performances and according to their ecological relevance in the study area (Sanguet *et al.*, under review, see Table 1 for a complete list). Topographic predictors were calculated with ArcMap (v. 10.2.1) based on the local DEM at 25 meters resolution. From categorical, habitat and soil predictors were derived into continuous variables by applying a focal statistic with a 100-meters circle radius, corresponding to the length of four pixels. Hence, each variable has values between 0, corresponding to an absence of this habitat in the surrounding of the pixel, and 1 when all pixels in a 100-meters radius have the same class than the considered pixel. The value ranges between 0 and 1 with the proportion of neighbouring pixels belonging to the same class. This transformation has three consequences: 1) it hypothesizes that habitats have impacts on species distributions outside their spatial limits but within a close range; 2) the transition areas between two habitats are impacted by both the habitats allowing the consideration of the ecotone effect; and 3) a pixel located at the centre of one patch will have a higher value (i.e. a higher quality) than a pixel positioned at its margin, which somehow integrates habitat structure into the model. Habitat predictors were downloaded from the CORINE land-cover database and adapted to the local LULC map in order to create a covering map including the selected predictors. The LULC map was then projected in 2050 according to a projection of LULC changes observed between 2006 and 2018 and the integration of known projects on the territory using the TerrSet software (Rappaz, 2021, *not published*). Topographic, pedologic and biotic predictors have a resolution of 25 meters.

Table 1. Selected predictors for the climatic model at the European scale (climatic predictors) and the biotope model at the local scale in the study area (edaphic, biotic and topographic predictors).

Predictors	**Predictor's type**	**Source**
Aridity	Climatic	Calculated from Karger *et al.*, (2017)
Isothermality		Worldclim v 2.1
Maximum temperature of warmest month		Worldclim v 2.1
Minimum temperature of coldest month		Worldclim v 2.1
Precipitation of wettest month		Worldclim v 2.1
Precipitation of driest month		Worldclim v 2.1
Precipitation seasonality		Worldclim v 2.1
Cambisol proportion	Edaphic	Adapted from Hengl *et al.*, (2017)
Podzol proportion		Adapted from Hengl *et al.*, (2017)
Closed forests	Biotic	Adapted from CORINE land cover
Open forests		Adapted from CORINE land cover
Wetlands		Adapted from CORINE land cover
Crops		Adapted from CORINE land cover
Natural meadows		Adapted from CORINE land cover
Transportation		Adapted from CORINE land cover
Urban areas		Adapted from CORINE land cover
Anthropic vegetation		Adapted from CORINE land cover
Northness index (exposition)	Topographic	Local DEM at 25-meters resolution
Slope		Local DEM at 25-meters resolution
Annual solar radiation		Local DEM at 25-meters resolution
Upland index (TPI index Weiss, 2001)		Local DEM at 25-meters resolution

4.2.1.2. Species occurrences

Two separate datasets were created. The first one represents a compilation of local occurrences observed in the study area and downloaded from local botanical conservatories with a precision below 100 meters which corresponds to the range of the relative influence of habitat predictors as previously mentioned. Only recent occurrences between year 2000 and 2020 were kept because earlier observations might have been done in habitats that have now disappeared, increasing potential bias in model's fitting while not increasing the number of species in the data set. A selection was then made to keep only plant species with at least 20 occurrences to avoid low model's performances. Observations from the same species located in the same pixels were deleted in order to keep one occurrence per pixel per species maximum to consider the sampling spatial bias. After data cleaning, 755'259 occurrences were selected for 1692 plant species from all groups (Bryophytes, Pteridophytes, Gymnosperms and Angiosperms). Based on this list of selected species, a second dataset was created at the European scale with occurrences downloaded from the Global Biodiversity Information Facility (GBIF, accessed in August 2021) between 2000 and 2020 with a precision below five kilometres was used in order to integrate as many occurrences as possible. Finally, the dataset was filtered in order to smooth the distribution of occurrences and avoid spatial biases by keeping a maximum of one occurrence every two pixels per species, resulting in approximately 22 million occurrences when merged with the first set of regional occurrences. Red list statuses were downloaded from the three regions of the cross-border study area (*Geneva*, *Auvergne-Rhône-Alpes* and *Franche-Comté*) and the most endangered status from the three databases was selected for each species. Finally, the native status was also added, based on InfoFlora (accessed in 2021), and consists of three different groups of species: native or indigenous species, archaeophyte species that arrived more than 500 years ago and exotic or alien species introduced or arrived recently. Details of native and red list statuses are found in the Table 2.

Table 2 – Number of species according to the native or red list status

Red list status	**Number of species**	**Native status**	**Number of species**
Least Concern (LC)	1002	Native	1377
Near Threatened (NT)	146	Archaeophyte	116
Vulnerable (VU)	99	Exotic	173
Endangered (EN)	89	Unclear	26
Critically Endangered (CR)	88		
No data (NO)	268		
Total	1692	Total	1692

4.2.2. Modelling methods

Two models were created, one using the seven climatic predictors which was named the "climatic model" and one using biotic, edaphic and topographic predictors named "biotopo model" (Table 1). The first was calibrated at the European scale using all occurrences available (approximately 22 million) in order to fully capture the species realized climatic niche and avoid biases linked to a partial sampling (Scherrer *et al*., 2021). For each species, the occurrences were randomly split into data used for fitting the model (75%) and evaluation (25%), repeating this operation 10 times. Then, all occurrences available were used to fit a model and project it on the study area for current time and for the six future general circulation models of each scenario (optimistic and pessimistic). 10’000 background data were randomly created at the European scale for the evaluation workflow and another data set was created with background data distributed according to the density of occurrences for the projection workflow. This implies that more background data were attributed to areas with a high density of occurrences in order to take into consideration the spatial bias of the sampling data (Beck *et al*., 2014; Fourcade *et al*., 2014). The six future projections associated with each general circulation model were then stacked and the median value of each pixel was retained in order to create one optimistic and one pessimistic projections for each species. The projected map was then downscaled to a 25-meters resolution distribution using bilinear interpolation. The second model integrating biotic, pedologic and topographic predictors was calibrated and projected in the study area for current time and for a unique future business-as-usual scenario of LULC changes for 2050, following the same workflow described above except that only one set of randomly distributed background data was created and that the resolution of the predictors was already of 25 meters.

Models were calibrated and evaluated using Dismo (Hijmans *et al*., 2017) and ENMeval (Muscarella *et al*., 2014) packages in R (R core team, 2020) and MaxEnt algorithm (Phillips *et al*., 2004, 2006, version 3.4.1). Default settings were used except for the beta multiplier which was increased from 1.0 to 2.0 to avoid overfitting (Costa *et al*., 2010; Radosavljevic & Anderson, 2014). Performances were calculated using the Area Under the Curve of a receiver operating characteristics (AUC, Hanley & McNeil, 1982), Cohen's Kappa (Cohen, 1960) and the True Skill Statistic (TSS, Allouche, Tsoar & Kadmon, 2006; Peirce, 1884).

There is no general agreement on how to combine two models with different scales and resolution in the literature (McGarigal *et al*., 2016). The methods entail using the resulting map from the large scale model as an input for the local scale one (Bellamy *et al*., 2020; Mateo *et al*., 2019; Pearson *et al*., 2004), multiplying the biotic and climatic suitability maps only for areas where the climate is suitable (Fournier *et al*., 2017), or averaging the two predictions in the desired study area (Mateo *et al*., 2019). Here, the projections of the two models were combined using two different methods. First, the predictions were converted into binary maps using a threshold representing the suitability value allowing the integration of 90% of current occurrences. Areas above this threshold were thus considered as "suitable" while the rest was "not suitable". Then, the overlapping areas between suitable climatic and biotopo predictions were multiplied for current time and the two future scenarios. This model is named hereafter "biotopo U climate" because it represents the spatial union between the suitable areas from the two predictions. The second combination consisted on a multiplication of the two continuous predictions. The resulting map was then converted into a binary map following the same method for current time and future scenarios. This aggregation method is named hereafter "biotopo x climate". These two methods are further compared in the discussion section. A complete workflow of the modelling method is presented in Fig. 1.

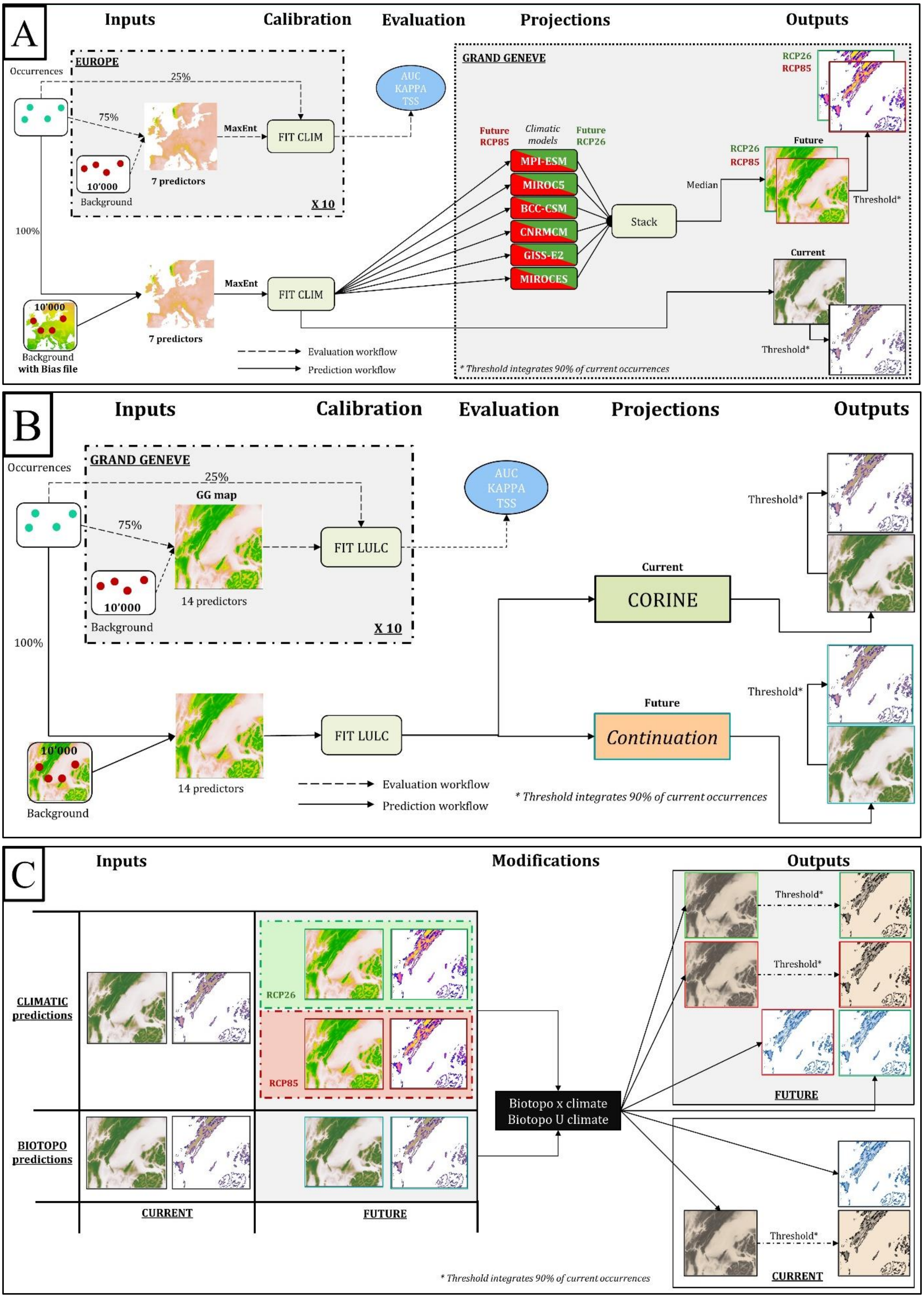

Figure 1. General workflow showing the method used for: A) the climatic models; B) the biotopo models; and C) the combination between the two previous predictions where the maps outlined in green represent optimistic scenarios and in red pessimistic scenarios.

4.2.3. Vulnerability index

The vulnerability of a species to global changes is composed of three main aspects: the exposure, the sensitivity and the adaptive capacity of the species (Williams *et al.*, 2008). The exposure quantifies the extent of changes predicted that will be experienced by a species; the sensitivity indicates how a species would tolerate such changes regarding its fitness and other physiological traits such as its thermal tolerance; and the adaptive capacity represents the ability of a species to adapt to new conditions by migrating or through phenotypic plasticity (Butt *et al.*, 2016; Dawson *et al.*, 2011). Six indicators were used to measure species' distributional changes between current and future conditions. These indicators encompass the changes of species' habitats quality through the measure of the average suitability of the suitable areas (*Su*), the expected gain or loss of suitable surface (*G*), the proportion of the surface occupied by a species compared to the total surface of the study area (*Si*), the habitat persistence measured by the overlap between current and future suitable areas (*H*), the colonization potential through the proportion of new suitable area in future conditions (*C*), and the fragmentation of the suitable areas (*F*) by measuring its MESH size index using the package "landscapemetrics" (Hesselbarth *et al.*, 2019; see Table 3). The three aspects of species vulnerability are, at least partially, assessed through the use of several scenarios of global changes in the study area corresponding to the exposure, their impacts on various spatial features of species distribution which correspond to the consequences of species' sensitivity, and the consideration of an unlimited migration which does not represent a compromising assumption regarding the relative small size of the study area, representing the adaptive capacity (Crossman *et al.*, 2012; Maggini *et al.*, 2014).

These indicators were calculated for the climatic and biotopo predictions as well as for the two combinations of climatic and biotopo predictions ("biotopo x climate" and "biotopo U climate") for the optimistic and pessimistic scenarios. The change of habitat suitability (*S*) was calculated as presented below (Eq. 3).

$$S = \left(\left(\frac{s_x}{s_c + s_x}\right) - 0.5\right) * 2 \tag{3}$$

Where s_x is the average future suitability of suitable areas, s_c the average suitability of current suitable areas. This indicator theoretically ranges between -1 if the future suitability s_x equals 0, and tends toward +1 if s_c is negligible compared to the future suitability. The same modification has been made for the gain or loss of suitable surface (*G*) and for the fragmentation (*F*). Habitat persistence (*H*) was measured as the overlap between current and future suitable surface and was calculated as presented below (Eq. 4).

$$H = \frac{n_x * 100}{n_c} \tag{4}$$

Where n_x represents the overlapping surface between current and future suitable areas, n_c the surface of current suitable areas. It ranges between 0 if there is no overlap and +100 if all current suitable areas stay suitable under future conditions. The colonisation potential (*C*) is measured as the proportion of the suitable surface that is new and was calculated as presented below (Eq. 5).

$$C = 100 - \frac{(n_x * 100)}{n_f} \tag{5}$$

Where n_x represents the overlapping surface between current and future suitable areas, n_f the surface of future suitable areas. It ranges between 0 if no new suitable areas are predicted in the future and +100 if all future suitable areas are new. Finally, the proportion of suitable surface occupied by a species (*Si*) is a ratio between the suitable surface and the total surface of the study area.

The six indicators calculated for the four modelling treatments based on climatic, biotopo, biotopo x climate and biotopo U climate predictions were then averaged and normalized in order to keep one value per indicator, scenario and species. The four modelling treatments were considered together in order to avoid a biased estimation of impacts of global changes that would be derived from a unique approach. The indicators were averaged by the following formula presented below (Eq. 6) for each scenario and time-step.

$$I = \frac{I_{clim} + I_{bio} + I_{cxb} + I_{cub}}{I_{max}} \qquad (6)$$

Where I is the final indicator's value, I_{clim} the value for climatic predictions, I_{bio} the value for biotopo predictions, I_{cxb} the value for biotopo x climate predictions, I_{cub} the value for "biotopo U climate" predictions, I_{max} the absolute maximal value reached by the sum of the indicator's values from the four modelling treatments ($I_{\text{clim}} + I_{\text{bio}} + I_{\text{cxb}} + I_{\text{cub}}$) across the whole data set. This operation was necessary in order to consider the six indicators equally in the vulnerability index calculation. A summary of the six indicators' code, metric, calculation and range is available in Table 3.

Table 3 – Details and summary of the six indicators.

Code	Metric	Calculation	Range
Su	Change of average suitability (habitat quality)	Gain or loss of average habitat suitability for suitable areas in future conditions compared to current	-1 ; 1
G	Change of suitable surface	Gain or loss of suitable surface in future conditions compared to current	-1 ; 1
Si	Proportion of suitable surface occupied	Ratio between the suitable surface and the total surface of the study area	0 ; 1
F	Change of MESH size (fragmentation)	Gain or loss of MESH value for suitable areas using eight directions (Queen's case) in future conditions compared to current	-1 ; 1
H	Suitable areas' overlap (habitat persistence)	Overlap between current and future suitable surfaces	0 ; 1
C	Colonisation potential	Proportion of the future suitable surface not currently suitable	0 ; 1

Finally, the six indicators were added in order to create a vulnerability index to global changes per species and per scenario as presented below (Eq. 7).

$$V = 3 + Su + G + Si + F + H + C \qquad (7)$$

Where V is the global vulnerability index for future conditions (optimistic or pessimistic scenarios), Su the changes of average suitability (habitat quality), G the changes of suitable surface, Si the proportion of suitable surface occupied, F the changes of MESH size (fragmentation), H the suitable areas' overlap (habitat persistence) and C the colonization potential. This vulnerability index V theoretically ranges between 0 if all currencies have their minimum values, indicating that the species are highly vulnerable to global changes, to 9 if they all have their maximum value, indicating that the species is benefiting from them.

If a species has a vulnerability index below 3, it is vulnerable to global changes because the six indicators have very low values. This limit is purely mathematical because it implies that the sum of the six indicators equals zero or less, indicating detrimental average effects on species distributions. It is assumed that above a vulnerability index of 5, the species is resilient to global changes and even benefits from them in some aspects because it implies that the sum of the six indicators equals at least 2 indicating average positive effects on species distribution.

These indicators could be correlated and the increase or decrease of one of them might affect others although they were selected because of their complementarity and because they cover different aspects of distributional changes. For example, if a species is modelled to gain suitable surfaces in the future (*G*), its proportion of suitable surface occupied (*Si*) will inevitably increase. However, if the current range of this species is very narrow but expected to double in the future, *G* will be high while *Si* will remain low. However, in the event where the disappearance of a species is modelled, all indicators will inevitably show strongly negative effects, indicating a (justified) high vulnerability.

4.3. Results

4.3.1. Modelling methods

Models show good performances on average and similar scores were observed for climatic and biotopo models with the exception of the KAPPA value which was higher for biotopo than climatic models (Fig. 3A in Appendix). An example of predictions from the four modelling treatments are presented in Fig. 2. Climatic predictions show important changes in size or shifts of suitable areas in 2050, especially under the pessimistic scenarios. However, only small scattered changes are observed for future biotopo predictions. This was expected because of the high similarities between current and future LULC in the study area. Hence, biotopo predictions were excluded from the following figures. The two combinations of climatic and biotopo predictions show different patterns. The predictions from the “biotopo U climate” approach show higher spatial shifts between current and future scenarios indicating a greater correlation with climatic predictions while the “biotopo x climate” predictions are less influenced by climatic or biotopo predictions and show less dramatic changes over time.

As presented in Fig. 3., climatic predictions exhibit large variations of indicator values compared to the other modelling treatments. It shows that species future realized climatic niche might be more versatile suggesting that climate is the main driver of distributional changes in plants. However, it is important to note that the tremendous difference of average suitability (*Su*) between the climatic and the two combined approaches shown in the Fig. 3. is only due to the method used to create the “biotopo x climate” and “biotopo U climate” predictions, based on the multiplication of the climatic and biotopo maps with values ranging between zero and one. Thus, the average suitability can only be compared between the two combined approaches but not with climatic models for this specific indicator. The suitable surface occupied (*Si*) is drastically smaller for the two combining approaches indicating that not considering biotic, edaphic and topographic predictors leads to a high overestimation of species ranges, and that the climatic niche alone might not be very representative of species habitat suitability.

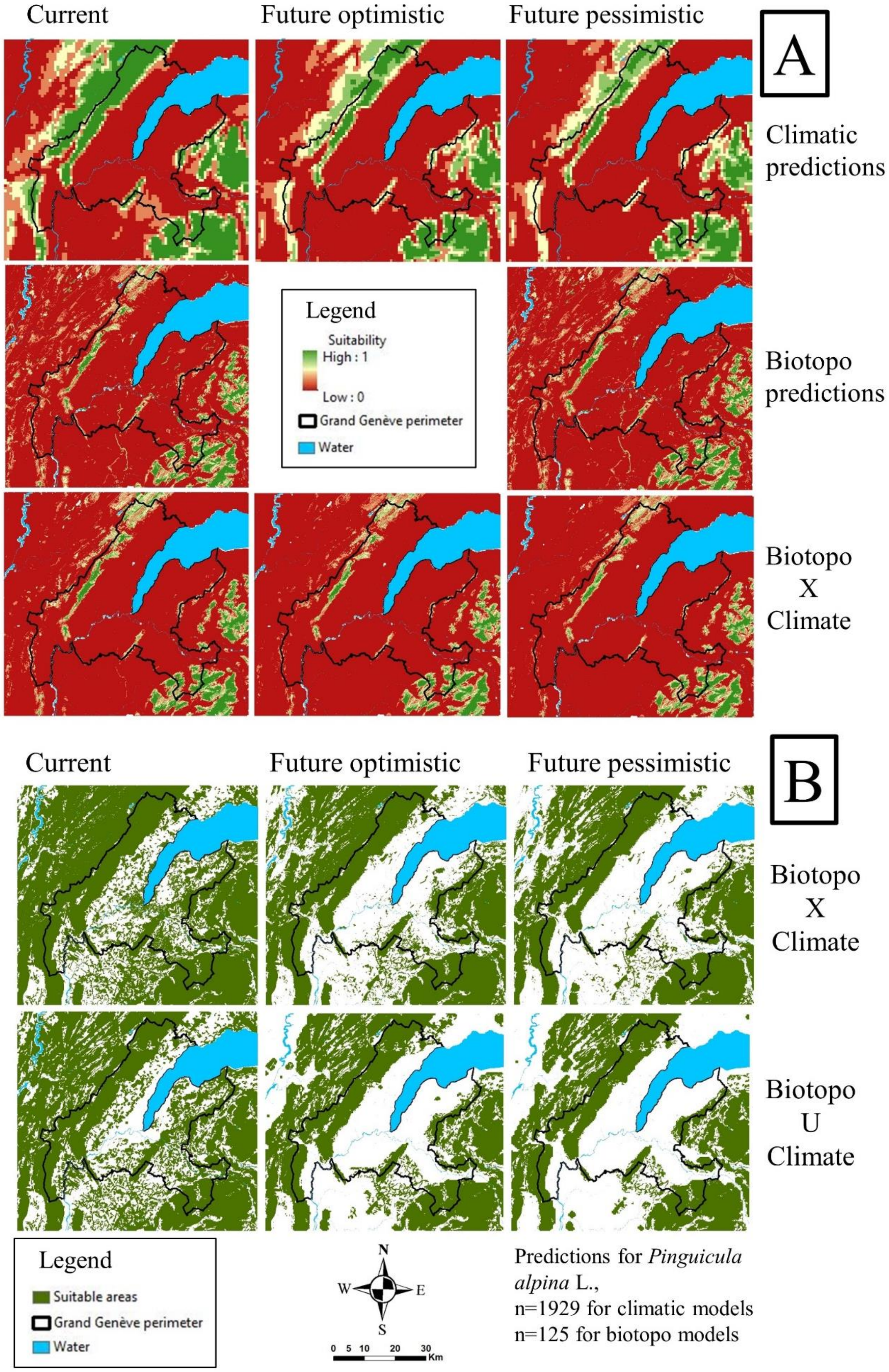

Figure 2. Predicted maps of Pinguicula alpina L. showing the differences between the modelling treatments and the time-steps and scenarios considered. A) continuous maps resulting from climatic, biotopo predictions and the "biotopo x climate" approach. B) binary prediction maps from the two combining approaches.

When comparing the values of indicators according to the modelling treatment, “biotopo x climate” predictions significantly differ from climatic ones for eight over 11 tests (two or three tests per indicator), without considering the tests associated with the three values of average suitability as developed above (Fig. 3). Regarding the differences between “biotopo U climate” and climatic predictions, only six tests show significant values, confirming that “biotopo U climate” predictions are more similar to climatic ones than “biotopo x climate”. Finally, the two combined approaches show 11 significantly different values among the 14 indicators calculated (the suitability values can be compared here because the two combined approaches are calculated following the same method, Fig. 3). This result shows that despite having a comparable calculation approach, the modelling method has tremendous impacts on the final predictions and thus on the six indicators measured for the different time-steps and scenarios. In order to avoid over-interpretation and for ecological reasons developed in the discussion, the main focus will be addressed on the “biotopo x climate” predictions for the rest of this article because “biotopo U climate” predictions are too correlated with climatic ones.

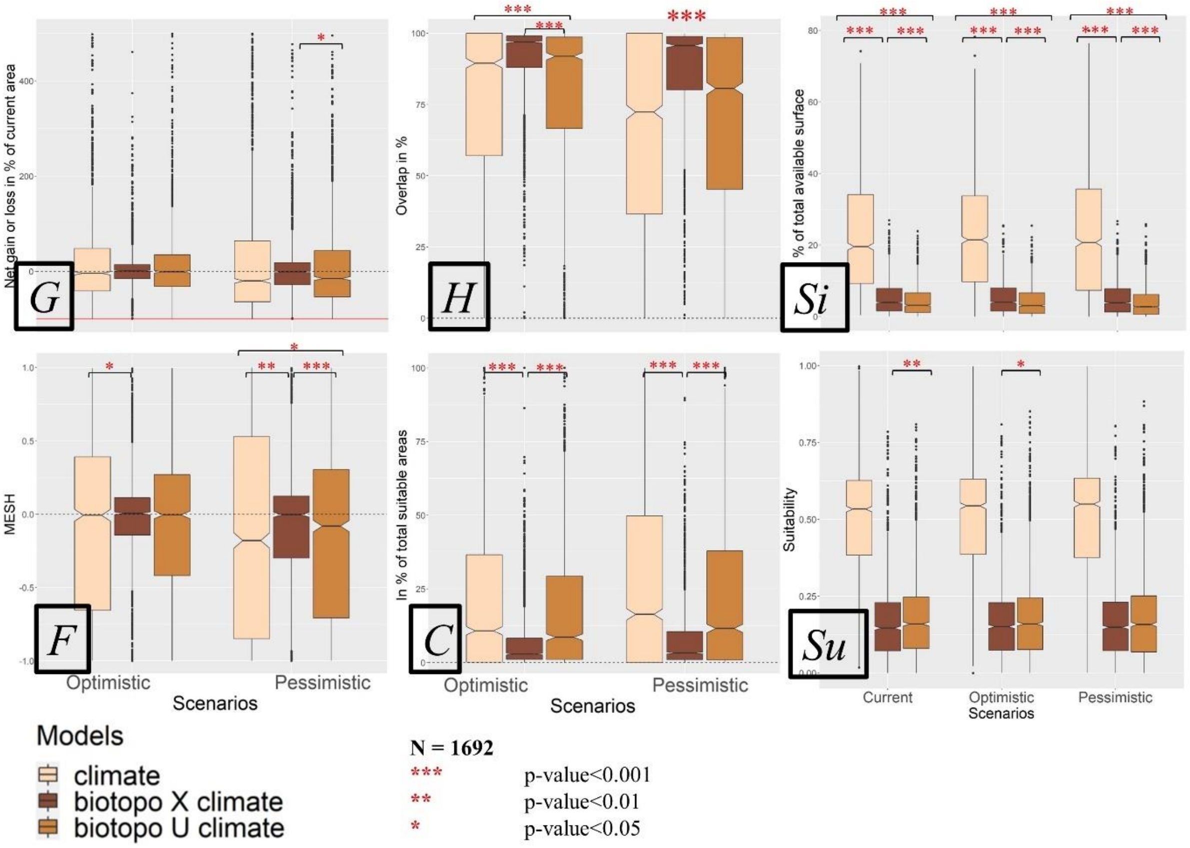

Figure 3. Boxplots of all indicators for climatic, “biotopo x climate” and “biotopo U climate” predictions with the p-value score corresponding to a Wilcoxon mean test. (G) Gain or loss of suitable surface in percentage of current suitable surface, the red line indicates -100% (loss all of its suitable surface), the dashed line indicates 0 (no change); (F) Mesh size rate (or habitat fragmentation), the dashed line indicates 0 (no change), below it the distributions are more fragmented in the future, above it they are more continuous than the current one; (H) Overlap between current and future suitable surfaces (habitat persistence), the dashed line represents 0 (no overlap) indicating that all suitable areas either shifted or disappeared; (C) Proportion of new suitable areas (colonisation potential), the dashed line indicates 0 (no new suitable areas in the future); (Si) Proportion of suitable surface occupied and (Su) average suitability of suitable areas. More details about the indicators could be found in Table 3.

4.3.2. Impacts of global changes on plant distribution

No clear trends emerge regarding the evolution of indicators according to the scenarios when all the species are considered without partitioning (Fig. 3 and 3B in Appendix). However, taking the example of the expected gain or loss of suitable surface (*G*), the intensity of change differs between climatic and "biotopo x climate" predictions. Results for climatic predictions show that 27 species are modelled to lose their entire climatic suitable areas by 2050 and 152 of them are expected to lose more than 75% of their current surfaces in optimistic scenarios, representing 1.60% and 8.99% of all species assessed respectively. These numbers increase to 50 and 288, respectively 2.96% and 17.02% of all species in pessimistic predictions (Table 3B in Appendix). On the contrary, 277 species are expected to gain at least +100% of their current extent in future optimistic scenarios and 377 in pessimistic ones, representing respectively 16.37% and 22.28% of all species assessed, with a maximum of +5190% for *Chaenomeles japonica* (Thunb.) Lindl. ex Spach, an introduced planted shrub found in the dense urban areas where the temperatures are the highest. These results indicate that many more species might gain in climatic suitability in the future than lose. However, results from "biotopo x climate" predictions show that four species from both scenarios are expected to disappear, 20 species are expected to lose at least 75% of their current surface for optimistic scenarios and 69 for pessimistic ones, respectively representing 0.24%, 1.18% and 4.08% of all species assessed, showing less dramatic impacts than climatic predictions only but indicating major differences between optimistic and pessimistic scenarios even by 2050. In addition, 69 (4.08%) and 105 (6.21%) species are expected to gain at least +100% of their current surface respectively in optimistic and pessimistic scenarios with a maximum gain of +1401% for *Gleditsia triacanthos* L., also an introduced species, followed by *Himantoglossum robertianum* (Loisel) P.Delforge a Mediterranean orchid located at its distribution margin in the study area with +704% (Table 3B in Appendix). It is important to note that it is easier for a species to expect a gain of +100 of its current surface if it is currently narrow, than losing all of its suitable areas, this is the reason why it is important to consider several indicators. The results for "biotopo U climate" predictions are not presented here but show comparable results to the climatic ones (table 3B in Appendix 3). The results for the other indicators are found in Tables 3A, 3B and 3C in the Appendix 3.

Focusing on "biotopo x climate" predictions, major differences are found between native species and the two other groups (Fig. 4.). Compared to archaeophyte and exotic species, native species demonstrate a lower gain of suitable surface (*G*), lower habitat persistence (*H*), lower colonisation potential (*C*) and higher fragmentation (*F*; p-value<0.001; Fig. 4.1). Although current suitability (*Su*) is higher for native species compared to exotic ones (p-value<0.001), this is not the case for both future scenarios because of the increasing habitat suitability of exotic species. The same reasoning could be made regarding the proportion of suitable surface occupied (*Si*) by native species which is significantly higher today than for the exotic ones (p-value<0.001), but not in future pessimistic scenarios, indicating a net expansion of exotic species ranges in the future and/or a reduction of native species distributions, confirmed by the values of the indicators *G* and *C*. Furthermore, exotic species are expected to retain the majority of their current distribution which is not the case for the native species (*H*; p-value<0.001; Fig. 4.1). Archaeophyte species have intermediate results between native and exotic species for all indicators except for *Su* and *Si* where they significantly outperform indigenous and exotic species for most measures (Fig. 4.1).

The Figure 4.2 presents the values of each indicator according to the native status and scenarios considered. Pessimistic scenarios always exacerbate the trends observed for optimistic ones. Indeed, native species show a net decrease of *G*, *F* and *H* between optimistic and pessimistic scenarios (p-value<0.001, Fig.4.2). The indicator *Si* shows a significant drop in pessimistic scenarios but not in optimistic scenarios (p-value<0.01). However, *Su* and *C* show no significant change. Globally, archaeophyte species show no major change between the two future scenarios except for an increase of *C* and *Si* (p-value<0.05). Exotic species on the contrary show an increase of suitable surface (*G*; p-value<0.01) also visible in *Si* (p-value<0.05). However, no major change is expected regarding *F* and *H*. Interestingly, the average suitability (*Su*) is expected to increase for exotic species when compared to the current situation (p-value<0.001) but there is no significant difference between the two future scenarios (Fig. 4.2).

4.3.3. Vulnerability index

The vulnerability index did not show significant change according to the red list status of species (Fig. 3C in Appendix). However, major differences were found among the species' native statuses with indigenous plants showing lower values than archaeophyte and exotic species, indicating that the former are more vulnerable to global changes than the latter two (p-value<0.001; Fig. 5). These results are exacerbated in pessimistic scenarios because the vulnerability index is lower than for optimistic ones, corresponding to an increased vulnerability, while exotic species show higher values suggesting better resilience or higher benefits to global change (p-value<0.001; Fig. 5.).

Species considered as vulnerable to global changes (vulnerability index < 3) are composed of 15 exotic, 16 archaeophyte and 577 indigenous species respectively representing 8.67%, 13.79% and 41.90% of their group for optimistic scenarios, with an additional 13 species with an unknown native status raising the total number of vulnerable species to 621, corresponding approximately to one-third of assessed plants (36.70%). For pessimistic scenarios, 9 exotic, 16 archaeophyte and 714 indigenous species are considered vulnerable which correspond to 5.20%, 13.79% and 51.85% of their respective groups, with an additional 14 species with an unknown status raising the total number of vulnerable species to 753, almost half of all assessed plants (44.50% of all species). On the opposite side, 37 exotic, 5 archaeophyte and 31 indigenous species representing 21.39%, 4.31% and 2.25% of their group respectively, were shown to benefit from global changes for optimistic scenarios (vulnerability index > 5), which correspond to 73 species or 4.31% of all species assessed. These numbers rise to 67 exotic, 13 archaeophyte and 51 indigenous species representing 38.73%, 11.21% and 3.70% respectively for pessimistic scenarios representing a total of 132 species (one has an unknown status) or 7.80% of all species. These results confirm that native species are more vulnerable to global changes than exotic ones which are, on the contrary, more likely to benefit from them. Pessimistic scenarios exacerbate this trend and compared to optimistic ones, an additional 10% of all indigenous species are considered vulnerable while an additional 17% of all exotic species would benefit from them. Details are available in Table 3D in Appendix.

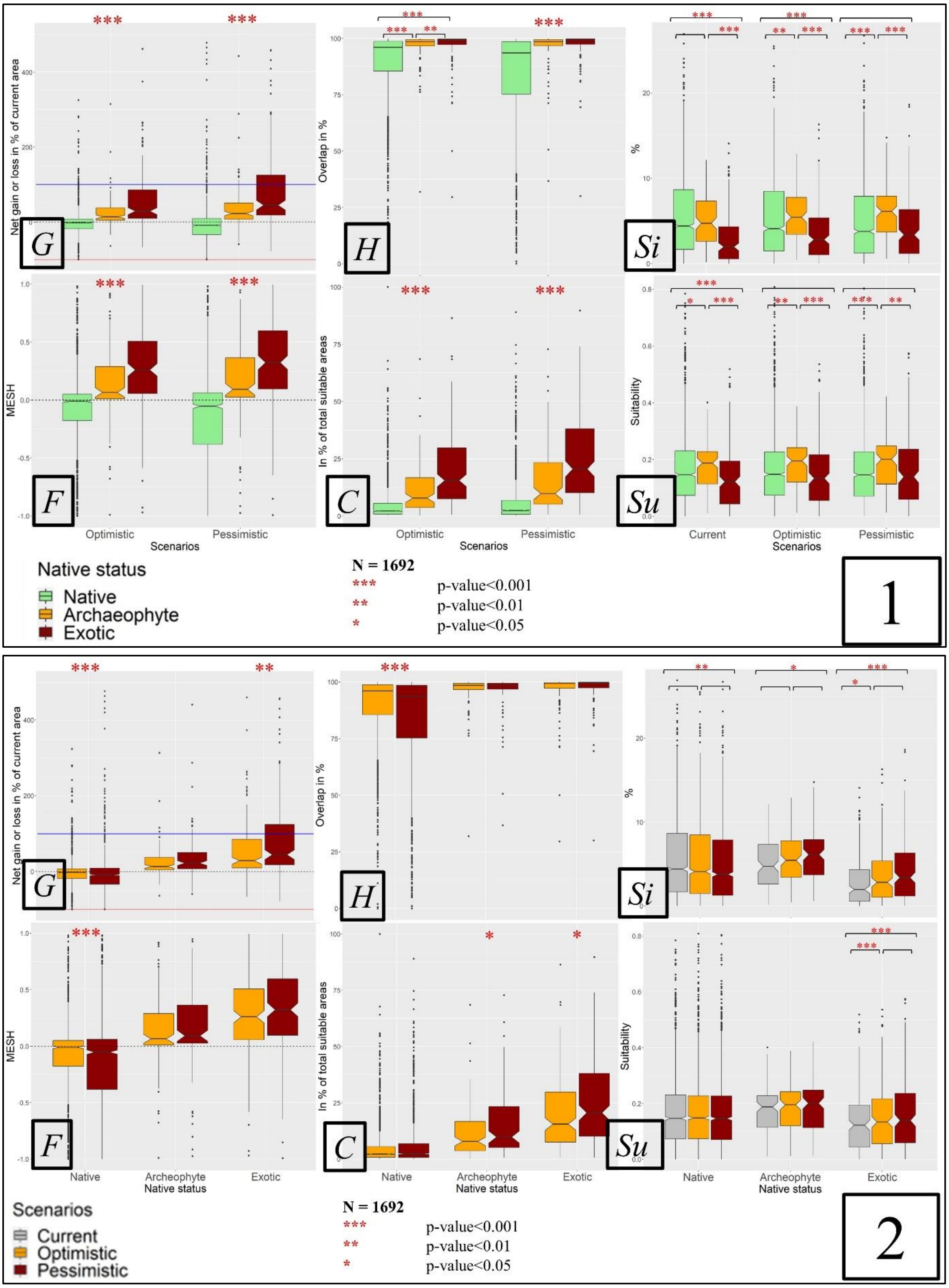

Figure 4. Boxplots showing the six indicators according to their native status for the "biotopo x climate" predictions. (1) Evolution of the six indicators according to the native status and (2) according to the time-steps and scenarios. Red stars represent the p-value score corresponding to a Wilcoxon mean test. (G) Gain or loss of suitable surface in percentage of current suitable surface, the red line indicates -100% (loss all of its suitable surface), the blue line +100% (gain of a new suitable surface

the size of the current distribution), the dashed line 0 (no change); (F) Mesh size rate (or habitat fragmentation), the dashed line indicates 0 (no change), below it the distributions are more fragmented in the future, above it they are more continuous than current time; (H) Overlap between current and future suitable surfaces (habitat persistence); (C) Proportion of new suitable areas (colonisation potential); (Si) Proportion of suitable surface occupied and (Su) average suitability of suitable areas. More details about the indicators are given in Table 3.

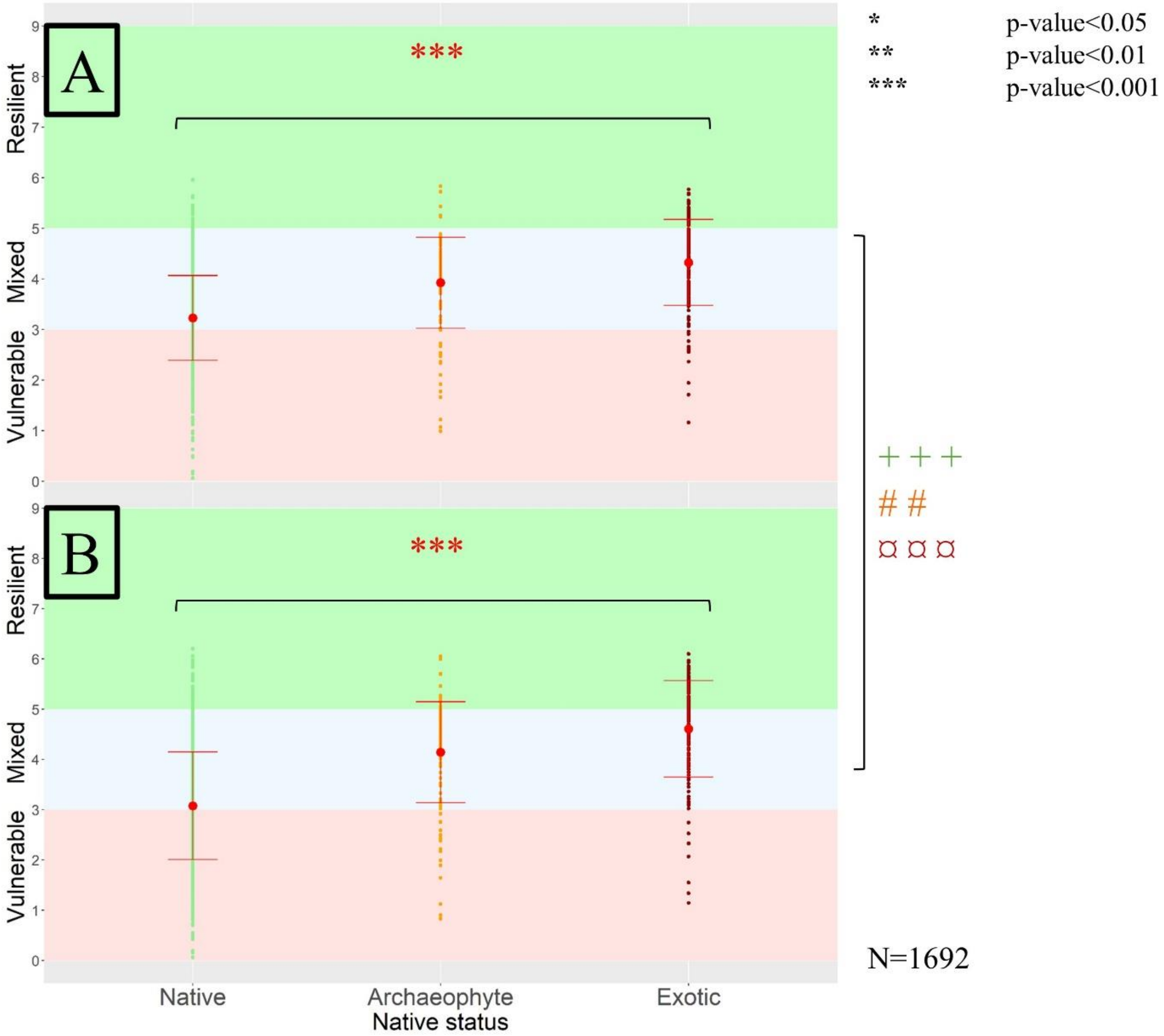

Figure 5. Vulnerability index according to the native status of species for both future scenarios. The upper green part of the figures represents values between five and nine which indicates that species located in this range are resilient to global changes, even benefiting from them. The central blue part represents values between three and five indicating mixed results with neutral, beneficial or detrimental impacts depending on the indicator. The lower part in red indicates values between zero and three corresponding to the vulnerability. A) Results for optimistic scenarios and B) for pessimistic scenarios. Stars located above the values represent the p-value associated with a mean Wilcoxon test between each native status. Symbols located on the right side represent the p-value associated to a Wilcoxon mean test between the values of the two future scenarios for native (+)*, archaeophyte* (#) *and exotic species* (¤)*.*

4.4. Discussion

4.4.1. Modelling method

LULC and climate changes are among the most important threats to biodiversity because they are major drivers determining species distributions, operating at different time and geographical scales. Indeed, while changes in LULC will induce a rapid and localized impact on species distributions, climate change repercussions will be visible on a broader scale and over a longer time span (Soberón, 2007). Combining these two aspects is thus essential to assess species vulnerability to global changes and, even if various methodologies exist, there is no precise workflow (Fournier *et al.*, 2017; McGarigal *et al.*, 2016; Santos *et al.*, 2021; Pearson, Dawson & Liu, 2004). For this analysis, predictors have been used at multiple geographical and time scales with different resolutions, and both methods used to combine the predictions from climatic and biotopo models have their limitations and assumptions. One common limitation is that the separate assessment of the climatic and the biotic/pedologic/topographic niche does not allow the models to account for the interactions between these two types of predictors. In this work, the predictors from the two models could not be merged in the same model fitted at the European scale for several reasons: 1) The biotopo predictors were initially selected and calculated for their high modelling importance and ecological meaning in the study area (Sanguet *et al.*, under review) and were not available at a larger scale; 2) Habitats from CORINE land-cover were modified to better fit the local LULC map and projected according to the local context of protected areas and planned urban projects; and 3) A broad resolution is not a major problem for climatic predictors at large scale but habitat ones would not be as relevant if used at broad resolution. Although climatic predictors could have been downscaled to fit the resolution of habitat predictors, the computational time of each model would have been greatly increased.

The method “biotopo U climate” selects the overlapping surface between suitable areas from both predictions. This approach hypothesizes that suitable areas and, by extension, the distribution of plant species, are located where both the climate and the habitat & topography are simultaneously fully appropriated even when considered separately. It also means that if only one of the two parameters is suitable (or one is not) the area is thus not considered as part of the species’ distribution. This method could be seen as being the result of successive environmental filters delimiting species distribution. One limitation of this approach is the choice of the threshold to identify suitable areas from both climatic and biotopo predictions. Indeed, the creation of binary maps, the threshold selection and even the ecological meaning of this operation are highly debated (Liu *et al.*, 2013, 2016). The second method “biotopo x climate” partially accounts for the interaction between the two predictions and does not fundamentally require binary maps. This approach hypothesizes that suitable areas are found where a factor calculated from the interaction between the climatic and the biotic & topographic niches have a sufficiently good value. Contrary to the first method, one prediction can actually compensate for the other but if one of them is highly unsuitable for a given area, the probability that it would be considered as “suitable” in the final map is low. This means that plants could grow in regions located at the margin of their climatic niche if their optimal habitat is available, and *vice-versa*.

The results from “biotopo x climate” predictions were on average quite similar to the ones from the “biotopo U climate” method but the formers were less dependent on the strong climatic shifts and variations predicted for future scenarios. The strong correlation between “biotopo U climate” and climatic predictions is explained by its methodological approach. Indeed, because the predicted LULC changes on the study area in 2050 are trivial compared to climatic ones, assessing the magnitude of change from a spatial overlap between nearly fixed LULC predictions and highly variable climatic predictions, in a sense corresponds to assess climatic prediction changes in a fixed subset of the study area. However, when the climatic and biotopo continuous maps are multiplied before the creation of binary maps this effect is more diluted, although it does not change the fact that climate drives the expected changes of species distributions. Thus, the “biotopo x climate” method appear to have more methodological and ecological benefits than the “biotopo U climate” one and in order to avoid potential over-interpretation or to concede too much importance to climatic results, the former was selected for the rest of the analysis. Methods combining various predictions at different geographical scales should be further discussed and tested, especially for the assessment of local scale impacts of climate and LULC changes on species distributions.

4.4.2. Plant distributions

Optimistic and pessimistic scenarios of climate change lead to similar trends for 2050 with no regard for the modelling approach (Fig. 3B in Appendix). It could be explained by the relatively high resilience of the climatic system and its low capacity of rapid change. More importantly, it also suggests that even if we were following the most optimistic scenarios, which is not the case, significant climatic and species distribution changes might occur as soon as 2050, and should be seriously discussed. In regards to the current evolution of greenhouse gas emissions and knowing that climatic models from the CMIP5 have been corrected to a faster and greater magnitude of climate change in the CMIP6 models, the predictions from this experiment that are assumed to be closer to future conditions might be pessimistic ones, according to the current knowledge. Indeed, CMIP5 models do not include all existing Earth system feedbacks and are thought to underestimate both rates and extents of changes (IPCC, 2018; Knutti & Sedláček, 2012). The scenarios together with the modelling method are the most important sources of uncertainties regarding the final predictions (Thuiller *et al.*, 2019) and this conclusion is confirmed here. This experiment could thus be further improved by using an ensemble forecasting modelling approach in order to integrate model’s variability and uncertainty in the final predictions.

In the study area, future LULC is highly similar to current one and this is explained by the local context. Indeed, the canton of Geneva is quite small but highly dynamic, and territorial legislations avoid urban sprawl and the loss of agricultural lands. Most changes are thus expected on the French side of the study area and the urbanization and densification are already high on the plateau. However, the steep slopes of mountain ranges positioned on both sides of the plateau (the Jura and the Alps) do not allow urban expansion, concentrating it in the lowlands. Furthermore, natural parks and protected areas located on mountain ranges prevent a strong modification of the LULC on these locations. But the major reasons are the small size of the study area and the short-term projection which allow only a relatively small portion of pixels to be changed. We did not consider that climate change might induce “natural” changes of vegetation type or habitat distributions in less than three decades, especially because the landscape is already highly managed in the study area. However climate change might actually induce changes in habitat distribution or quality in the long term and should be further investigated.

The results show that the integration of habitats, as well as the pedologic and topographic predictors drastically modifies the predictions as well as the magnitude of expected change between current and future distributions compared to predictions using only climatic predictors. This confirms their relevance for SDM, especially at small scale and in mountainous landscapes (Chauvier *et al.*, 2021; Oliveira *et al., 2021;* Sanguet *et al*., under review). Assessing only the climatic niche might lead to an overestimation of expected shifts and changes in species distributions. These results also suggest that biotic and topographic factors might help increase plant resilience against climate change and might locally help reducing the impacts of warming temperatures allowing species to grow outside of their climatic range by modifying nearby abiotic conditions. Consequently, conserving (semi-)natural areas of high ecological value might locally increase our capacity to mitigate the effects of climate change on local biodiversity.

4.4.3. Plant species vulnerability

There are no standard ways to assess species vulnerability to global changes and the information needed or available mostly determines which approach is the most appropriate (Pacifi *et al.*, 2015). The Climate Change Vulnerability Index (CCVI, Young *et al*., 2012) is a widely used method using a trait-based tool mostly used by resource managers which has been applied to a large number of species, especially in North America, but only considers changes of climatic conditions (Young *et al.*, 2015). Most studies taking into account LULC in calculating species vulnerability to global changes consider that climate influences species distributions while LULC affects dispersal ability, reproduction and population viability (Santos *et al*., 2021). Other approaches quantify population changes and could be based on the observations of species' abundance, comparable to the IUCN red list methodology to determine vulnerability statuses (IUCN, 2010). Other methods estimate the extinction probability based on population viability analysis, demographic or evolutionary models (Maschinski *et al*., 2006). However, these two methods were mostly used for animals and rarely for plants (Pacifi *et al*., 2015). To complete the vulnerability index proposed here, the sensitivity and adaptive capacity should be further investigated and, as examples, the dispersal capacity assessment, the magnitude of phenotypic plasticity, as well as the study of the eco-physiological limits of all species and their potential evolutionary response to global changes could be assessed (Dawson et al., 2011). In this work, the emphasis is placed on defining global trends of plant vulnerability in the Grand Genève region derived from potential distributional changes.

The index calculated in this work is better suited for identifying vulnerable species than resilient/benefiting ones, although increasing values corresponds to a decreasing vulnerability. Indeed, the lower threshold of 3 indicating the vulnerability is calculated based on the hypothesis that the sum of all indicators is equal or inferior to zero (inducing detrimental or neutral effects). However, fixing an upper limit that would indicate clear benefits to global change is more difficult. While the threshold of 5 used in the vulnerability index indicates clear positive average effects, it is still open to discussion and ultimately depends on the considered species. It is important to note that in practice, the value of 9 is not reachable because it would require that one unique species has the maximum value for all indicators which is not the case here. Thus, the identification of species vulnerability is better supported than their resilience/benefits. In practice, all indicators can compensate one for the other and a vulnerable species could actually experience positive effects according to certain indicators even if the rest of them are highly detrimental, inducing negative average impacts of global changes and *vice-versa* for resilient species. The vulnerability or resilience of a species ultimately depends on its characteristics, history and ecology, and this index could be further adapted to better fit specific groups of plants.

Interestingly, results show that there is no major pattern when considering species all together without grouping them according to their native status which suggests that global changes will have variable impacts on species distributions and the same statement could be made when considering species according to their red list status (Fig. 3B and 3C in Appendix). On average, endangered species are not more threatened by global changes than those with other red list statuses which might seem counter-intuitive, although it has already been found for cacti where endangered species benefitted more from climate change than non-endangered ones (Benavides *et al*., 2021). On the contrary, some studies have shown that threatened species had high risk of extinction while others have shown that half of studied plants would benefit from climate change (Dudley *et al*., 2019; Garcia *et al*., 2013). This demonstrates that global changes have unpredictable *a priori* effects that might depend on the plant's ecology and the local context and scale, which justifies the necessity of assessing species vulnerability. Furthermore, it could also indicate that the main threats are not fully understood and could be related to other factors that are not considered here such as soil or water pollution and quality, direct impacts of human activities, habitat quality and availability, access to resources, interactions with other species etc.

Some hypothesizes could explain why exotic species are modelled to be resilient to global changes while native species are more vulnerable. Many introduced species are cultivated plants used for ornamental purposes in private garden or public green spaces. These plants are often cultivated in containers or planted in city centres where the temperatures are warmer than in the less urbanized areas due to the heat absorption and restitution of concrete and wind protection named the “urban heat island phenomenon” (Ackerman, 1985; Taha, 1997). The substrate is also drier due to the low water permeability of urban soil and individuals planted in containers are even more exposed to a rapid drying substrate. Thus, the selected species have to resist to drier and warmer conditions than indigenous ones. Future temperatures are expected to increase and inevitably, areas located at higher altitude will offer more suitable conditions for the development of these species, demonstrated here by their great range expansion, especially because in the study area, the city-centre is located at the lowest elevation and thus, the warmest area. Following the same reasoning, some indigenous species growing at high elevation in the mountain summits are supposed to be particularly vulnerable to global changes because they cannot migrate at higher elevation to find cooler temperatures in the study area. Focusing this analysis on ecological groups would help better understand the trends identified here, linking the vulnerability to the ecology of species.

4.5. Conclusion

Using two distinct approaches, climatic predictions at the European scale and biotopo predictions at the local scale were combined in order to assess the distributional changes of 1692 plant species in Grand Genève for 2050. We found that multiplying climatic and biotopo continuous suitability maps was a better method than using the union of binary maps for ecological and methodological reasons. We used six indicators to assess the effects of climate and LULC changes on species distributions, referring to habitat suitability, expansion or reduction of range size, habitat fragmentation and potential migration. It was found that the magnitude of global changes’ impacts mainly depends on the climatic scenario and the group of species considered. Indeed, while no clear effect was found when assessing distributional changes of all species or according to their red list status, native species have been found to be more vulnerable than exotic ones. This result was further confirmed by the assessment of a vulnerability index based on the six indicators. Finally, it was found that pessimistic scenarios exacerbated the trends identified for optimistic ones.

This work demonstrates the absolute need of integrating biotic, pedologic and topographic variables in vulnerability assessments, especially at the regional scale where these predictors are highly relevant, because the use of climatic predictors alone might overestimate the magnitude of global change and species’ exposure. The assessment of optimistic and pessimistic scenarios of climate change helps understand the possible influence of political and individual decisions for reducing greenhouse gas emissions on species distributions and although the trends are similar for both scenarios in 2050, the impacts on plants are highly exacerbated in pessimistic ones which demonstrates the urge of taking rapid and effective environmental policies. The vulnerability index developed here could be used as a complement to the red list status for local conservation authorities, ultimately helping understand the evolution of plant diversity and increasing our capacity of taking effective conservation actions.

Chapter 5

Assessment and improvement of conservation areas effectiveness under climate and land-use changes

From: Sanguet *et al.*, in prep

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In this paper, I participated to the conceptualization and to the methodology together with all the co-authors, and carried out the experiments and the writing of the original draft.

5.1. Context

The distribution of species diversity is part of the identification of one of the three pillars of the Green Infrastructure (GI)(biodiversity pillar). Aligning with the biodiversity strategy of the Canton of Geneva, the European Commission strategy and the United Nation Convention on Biological Diversity, the GI should represent 30% of the territory (DETA *et al.*, 2018; European Commission, 2013; FOEN, 2017). The previous chapter presented the evolution of 1692 species distributions modelled using 22 million occurrences according to several scenarios of climate change and one scenario of Land-Use-Land-Cover (LULC) change. However, the distribution of several aspects of plant diversity has not been assessed neither has the role and ability of Conservation Areas (CA) in protecting species distributions. In order to identify a reliable Green Infrastructure, each of the three pillars described in Chapter 2 should be assessed separately and the results from this chapter can be used as a “biodiversity pillar”.

In this chapter, the ability of CA to protect species distribution was assessed using the species distributions modelled for three time treatments (current, optimistic future and pessimistic future) in the previous chapter in order to test their relevance in conserving the plant diversity under several scenarios of global changes. A particular emphasis is made on species native status, knowing that native species are more vulnerable than exotic ones. Then, the “Biodiversity Pillar” (BP) composed of the most interesting areas according to the specific richness and the ranking maps from a prioritisation process was proposed. Finally, the CA and the BP were compared, and the interesting patterns of plant diversity distribution were discussed. This last chapter is in the continuity of the previous one and represent an example of the concrete application of the results developed during the PhD. It aims at proposing new outputs that could be used by local authorities to expand current areas dedicated to biodiversity conservation and better understand the distribution of plant diversity.

5.2. Methods

5.2.1. Data

The distribution of 1692 plants species was used for current and two future scenarios in 2050. They were modelled using the multiplication of the two resulting maps from: 1) climatic predictions at the European extent projected in and downscaled to the study area for the current time and two climate change scenarios in 2050 (optimistic and pessimistic), and 2) predictions using biotic, pedologic and topographic predictors at the local scale for the current time, and projected according to a business-as-usual scenario of land-use-land-cover change map for 2050. The modelling method is further described in Sanguet *et al.*, in prep (Chapter 4). As a result, each species has three different habitat suitability maps according to the time-step and scenario considered: current, future optimistic and future pessimistic. These maps have values ranging between 0 and 1 according to the suitability of the pixel, 0 meaning that the pixel is not suitable for the species and 1 that it is highly suitable. They were summed for each treatment to create a richness map in order to highlight interesting areas suitable for many species, commonly named “hotspots”. The term “hotspot” used here does not refer to the global hotspots concept developed by Myers *et al.*, (2000) but rather to a spatial area where many species are able to grow compared to the rest of the study area (Lehmann *et al.*, 2002; Scherrer *et al.*, 2018). These maps do not show exactly the number of species able to grow in each pixel but rather a general suitability of its habitat for all species assessed. In order to avoid confusion, the metric measured by the specific richness maps was named “suitability value”. Hence, the hotspots represent the areas with a high suitability value for many species and will be named “suitability hotspots”.

Focusing on the strict perimeter of the cross-border territory of Grand Genève, all areas with a strong environmental conservation status were identified (Fig. 1). They represent protected areas and natural reserves designated by Swiss and French local, cantonal, regional or national authorities, as well as priority habitats recognized for their conservation value. Because the legislation is not the same for all included areas they are named hereafter "Conservation Areas" (CA). They are distributed across the whole study area and represent 13.69% of the surface, which is similar to the proportion of protected surface in Switzerland (OFEV, 2021). Areas with low conservation status such as part of the Natura200 network, natural areas of ecological interest as well as the natural regional park of the Haut-Jura, were not incorporated in this experiment because they would collectively represent around 80% of the territory which would not be relevant for this experiment. However, some areas of the natural regional park are included in the CA selection because they are considered as natural reserves.

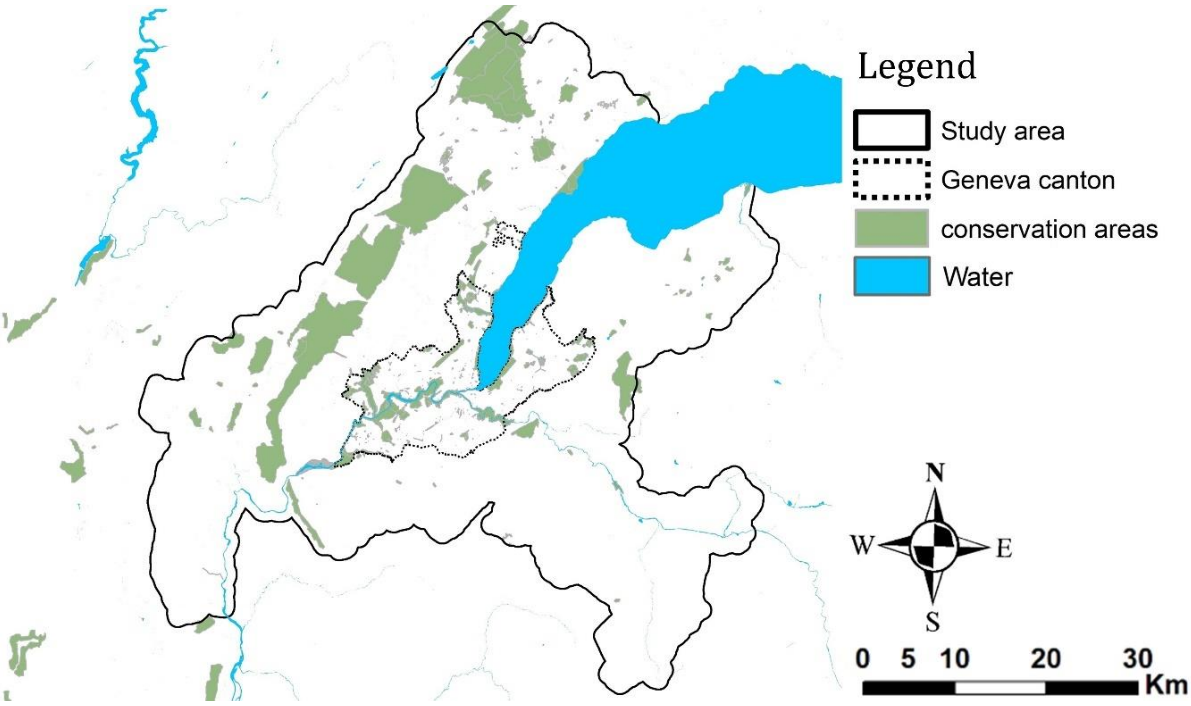

Figure 1. Extent of the study area (Grand Genève), the canton of Geneva and location of the selected CA. The great patches located on the western side of the study area correspond to the natural reserves of the Regional Park of the Haut-Jura.

5.2.2. Spatial Conservation Prioritization

Spatial Conservation Prioritization (SCP) is widely used in systemic conservation planning because it allows to find the right compromise between conservation targets and a spatially optimized priority area network (Moilanen *et al.*, 2009a). The software Zonation (Moilanen *et al.*, 2009b) produces a hierarchical prioritization map across the landscape, iteratively removing pixels with the lowest aggregation value according to the desired result and tuhs, providing maps supporting and informing spatial conservation planning by identifying the most interesting areas of a territory from a conservation perspective (Di Minin *et al.*, 2014; Lehtomäki & Moilanen, 2013). Several settings are available. The Core-Area Zonation (CAZ) allows the identification of priority areas that have a high interest for a single rare feature while the Additive-Benefit Function (ABF) gives more importance to pixels with many features (Di Minin *et al.*, 2014). Although having access to the distribution of the suitability hotspots is of great benefit to inform decision planning, selecting the ABF setting would lead to an over-representation of hotspots in the biodiversity network which might lead to important features being overlooked (Marchese, 2015; Orme *et al*., 2005). Thus, the CAZ setting was used because it selects priority areas where rare species are growing which offers a complementary input into systematic conservation planning.

The Zonation software was run using current and future species distributions, weighting twice as much the species identified as vulnerable to global changes in a previous study (Chapter 4) according to their expected changes in suitability, habitat fragmentation, size of suitable surfaces and migration potential (Sanguet *et al.*, in prep). The continuous maps of habitat suitability were used in order to avoid biases (Muscatello *et al*., 2021). Among the 1692 species assessed, 621 are considered vulnerable for optimistic scenarios and 753 for pessimistic ones and they are almost entirely composed of native species, respectively representing 92.91% and 94.82% of vulnerable plants (Sanguet *et al.*, in prep, chapter four). Strict urban areas were excluded from this assessment because GI are supposed to integrate only natural and semi natural areas (Benedict and McMahon, 2006; European Environment Agency, 2014). The resulting map represents a prioritised ranking of pixels (named hereafter "ranking map") where the highest values determine the most valuable areas for species conservation named "priority areas".

5.2.3. Relevance of CA and biodiversity pillar assessment

The Canton of Geneva, the Helvetic confederation, the European Commission strategy on biodiversity and the United Nations Convention on Biological Diversity recommend using a GI covering 30% of the territory (DETA *et al.*, 2018; European Commission, 2013; FOEN, 2017). The top 30% of areas with the highest values from the richness and the ranking maps were extracted for each treatment and represent, respectively, the suitability hotspots and the priority areas. The spatial patterns of these maps are compared and the most interesting areas were identified and discussed. Finally, suitability hotspots and the priority areas were merged together through a spatial union and the top 30% of areas were extracted to create the Biodiversity Pillar (BP), one of the three pillars to be assessed for the Green Infrastructure (GI) identification (Honeck *et al*., 2020a, 2020b). This BP could also be seen as a similar network to that for the GI but for plant diversity only.

The relevance of CA in conserving plant diversity was assessed using their ability to integrate a significant proportion of species distribution, suitability hotspots and priority areas in current time as well as in the two future scenarios. A focus was placed on the effectiveness of CA to integrate species distributions according to their native and red list statuses and the results were compared and tested across the three treatments (current, future optimistic and future pessimistic) using a Wilcoxon mean test. The ability of CA to integrate at least a part of all species distributions was also verified. Furthermore, the composition of CA was assessed in order to describe the important natural habitats included. Finally, the same assessments were applied for the BP and the results were compared to CA's. Recommendations were proposed to improve CA reliability in facing future conservation challenges.

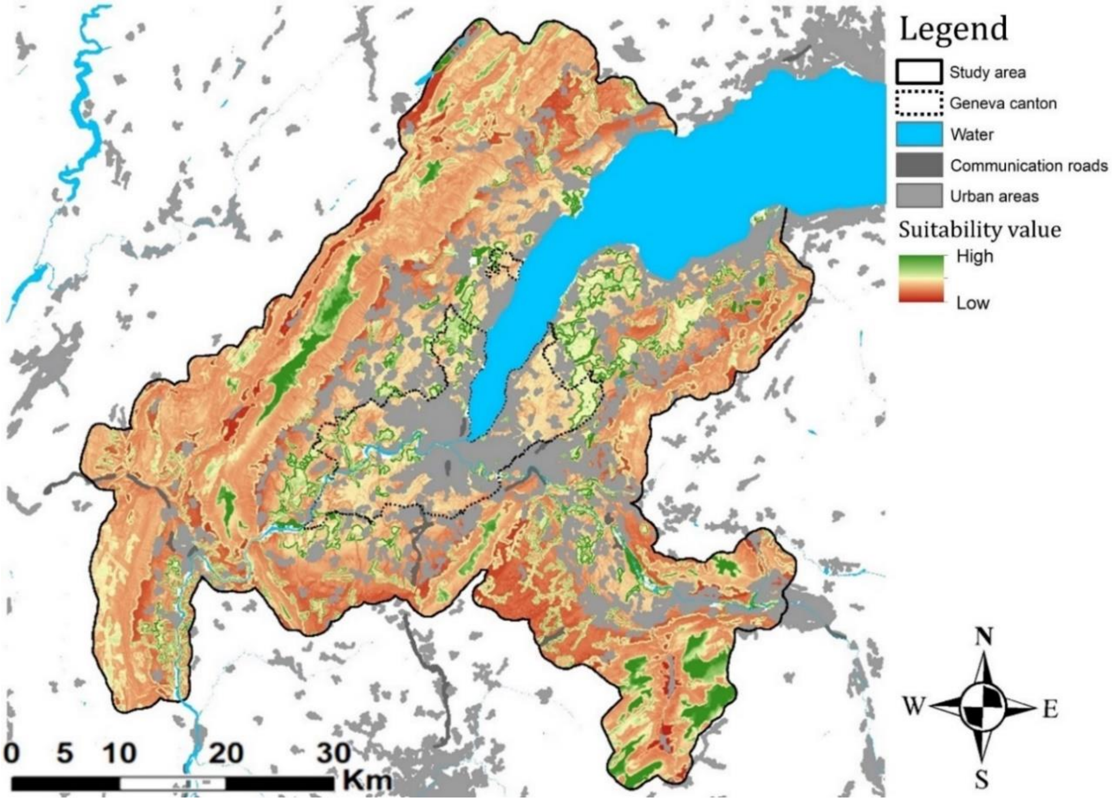

Figure 2. Richness map for current time showing the distribution of the global suitability. Areas in green have a high suitability value for many species and represent interesting inputs for conservation planning.

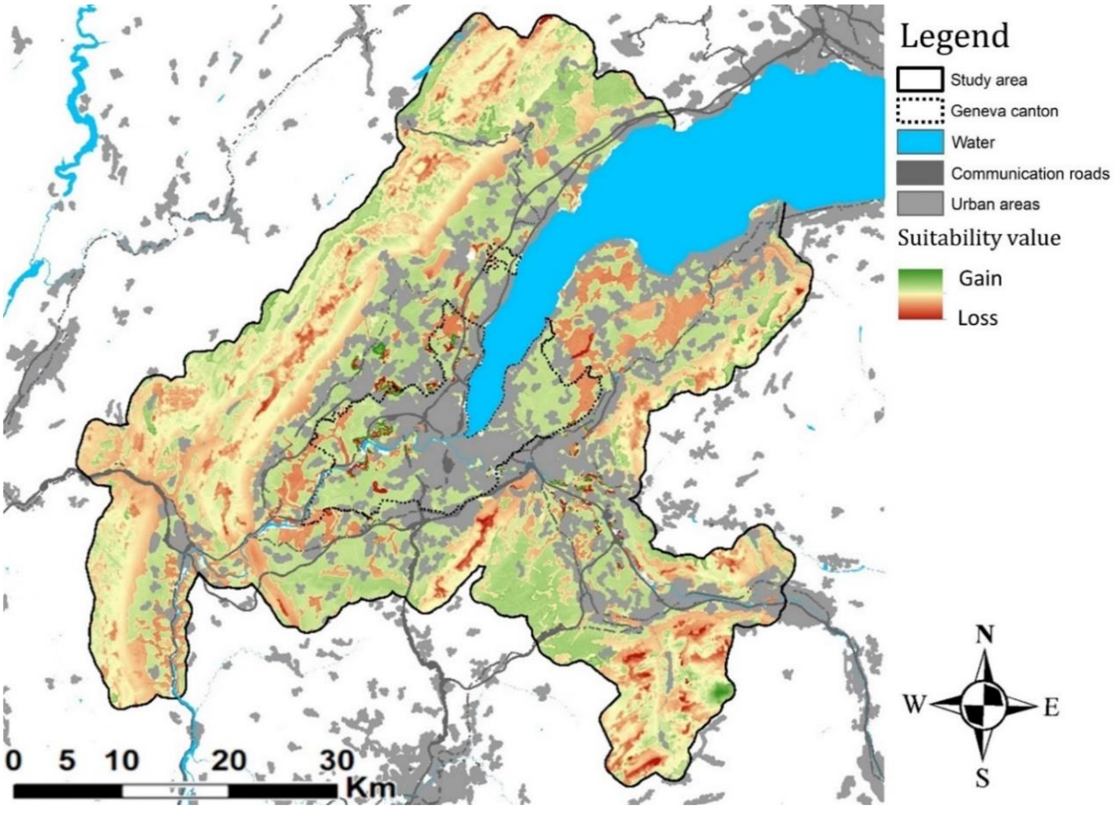

Figure 3. Changes of suitability value between current's and future pessimistic scenario. Areas in green show a potential gain of suitability in future conditions while areas in red show a potential loss of suitability in future conditions.

5.3. Results

5.3.1. Priority areas and suitability hotspots distribution

The richness maps show highly similar spatial patterns for current time and the two future scenarios (Fig. 4A in Appendix 4). The most interesting areas represent great patches mostly located in the mountainous habitats on both sides of the plateau, in the South-eastern corner and the western side of the study area (Fig. 2), corresponding to alpine pastures. In the lowlands, located all around the lake and further South, some forested habitats also show an interesting suitability, although it appears that the margins of these habitats have a higher suitability than the core, which is attributed to the ecotone effect and further debated in the discussion. Thus, the suitability of habitats varies depending on the altitude and the location in the territory, which is a useful finding for applications in conservation planning. Some isolated patches show an important change of suitability especially in the lowlands mainly due to future changes in the LULC (Fig. 3). Indeed, areas projected to become more "natural" in the future are automatically modelled as suitable for more species than disturbed areas such as crops and *vice-versa*. The magnitude of change is similar when comparing current global suitability with optimistic or pessimistic future scenarios, although the trends are accentuated in the second (Fig. 4B in Appendix 4). Interestingly, areas with high current suitability values are mostly expected to lose suitability in the future while the quality of areas with a current low suitability value will increase. The comparison between the specific richness maps from future optimistic and pessimistic scenarios shows an important decrease of global suitability in the highlands, especially in the areas considered as highly suitable in the three treatments indicating that these areas are vulnerable to global change and to warming temperatures in particular (Fig. 4B in Appendix 4). On the contrary, a general increase is observed at lower elevation. The average suitability value of the territory is, respectively, 113.66, 110.30 and 106.56 for current time, future optimistic and future pessimistic scenarios, indicating a slow decrease of the global suitability of the study area. This decrease is even more accentuated for the suitability hotspots with an average value of respectively 172.36, 166.70 and 161.68, which coincides with the previous observation of a decrease of suitability in these areas (Fig. 3; Fig. 4B in Appendix 4).

The ranking maps show similar patterns for the three treatments (Fig. 4C in Appendix 4). Areas located in the highlands, and especially alpine pastures, have a high priority as well as some disparate patches located in the plateau, but mid-elevation forests seem to show the opposite (Fig. 4). These patterns remain similar in future conditions (Fig. 4C in Appendix 4). The priority changes between current and future ranking maps are sporadically distributed across the territory without a clear trend (Fig. 5 and 4D in Appendix 4). However, it appears that areas located in the highlands show a gain of priority while important patches of forested habitats in the plateau show a drop of priority in the future (Fig. 5).

The suitability hotspots and the priority areas are presented in Fig. 6. Interestingly, while priority areas tend to be located in the highlands, the suitability hotspots on the contrary show a wide distribution in the lowlands, demonstrating their complementarity in identifying different aspects of plant diversity and thus for conservation planning. The overlapping surfaces are located all over the study area and represent alpine pastures and lowlands deciduous forests, but the most important patches are found in the highlands. The evolution of the suitability hotspots, the priority areas and their overlap for the three treatments is presented in Fig. 4E in the Appendix 4. The suitability hotspots show a great overlap, of 93.70% and 88.30% respectively between current and future optimistic and pessimistic scenarios. Priority areas, however, show a lower overlap rate over time of 80.81% and 77.61%, respectively, indicating a greater shift of interesting areas for rare species in the future. These results show that valuable areas for plant diversity conservation will shift more with warmer temperatures leading to a lower effectiveness of conservation measures in pessimistic scenarios.

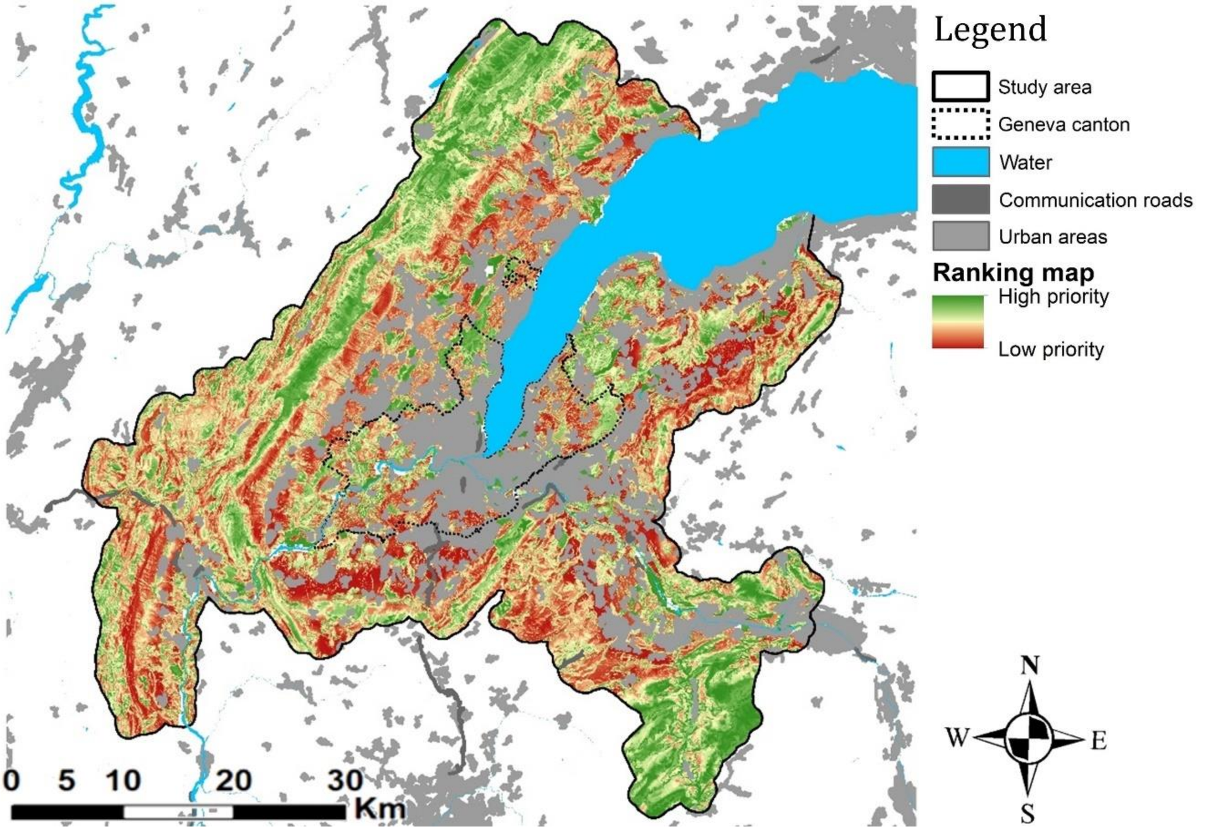

Figure 4. Ranking map for current time. The green areas indicate a high priority for rare plant species conservation.

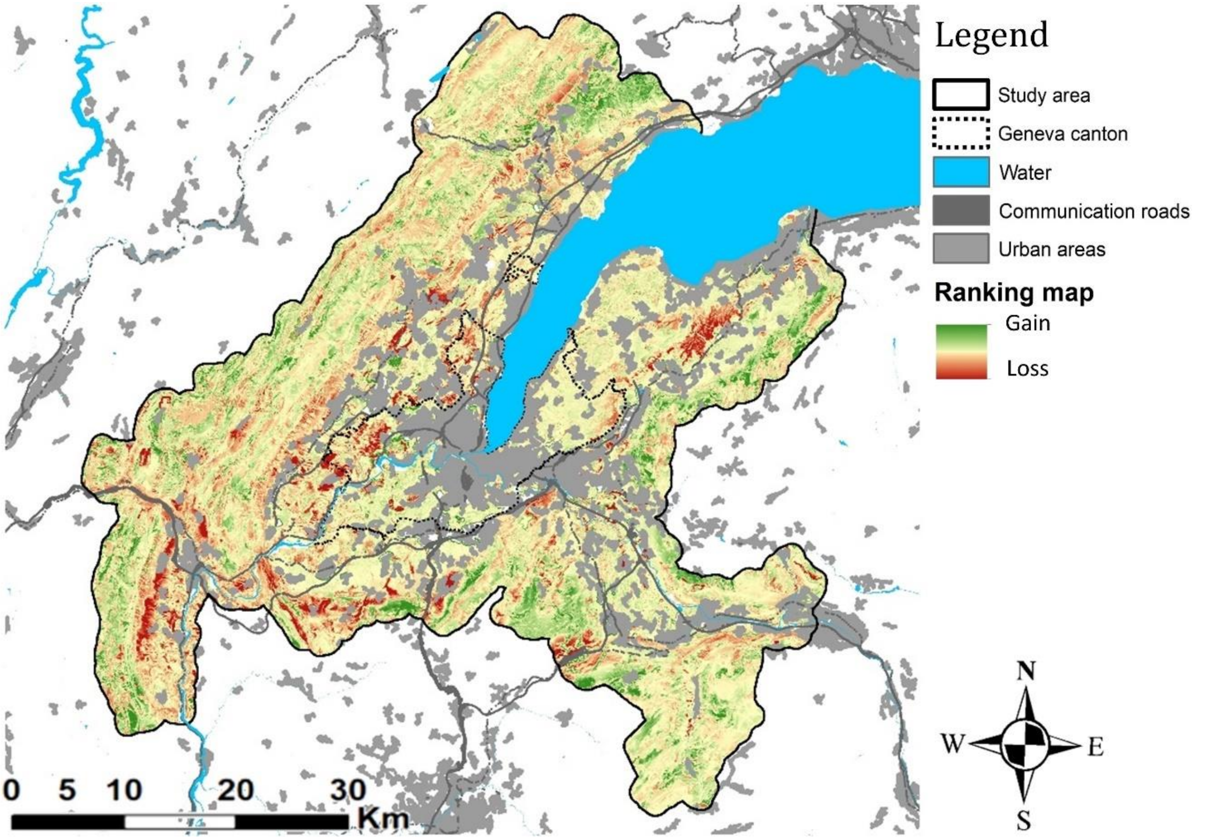

Figure 5. Changes between the ranking maps of current time and future pessimistic scenarios. Areas in green show an increased priority in the future and areas in red a decrease.

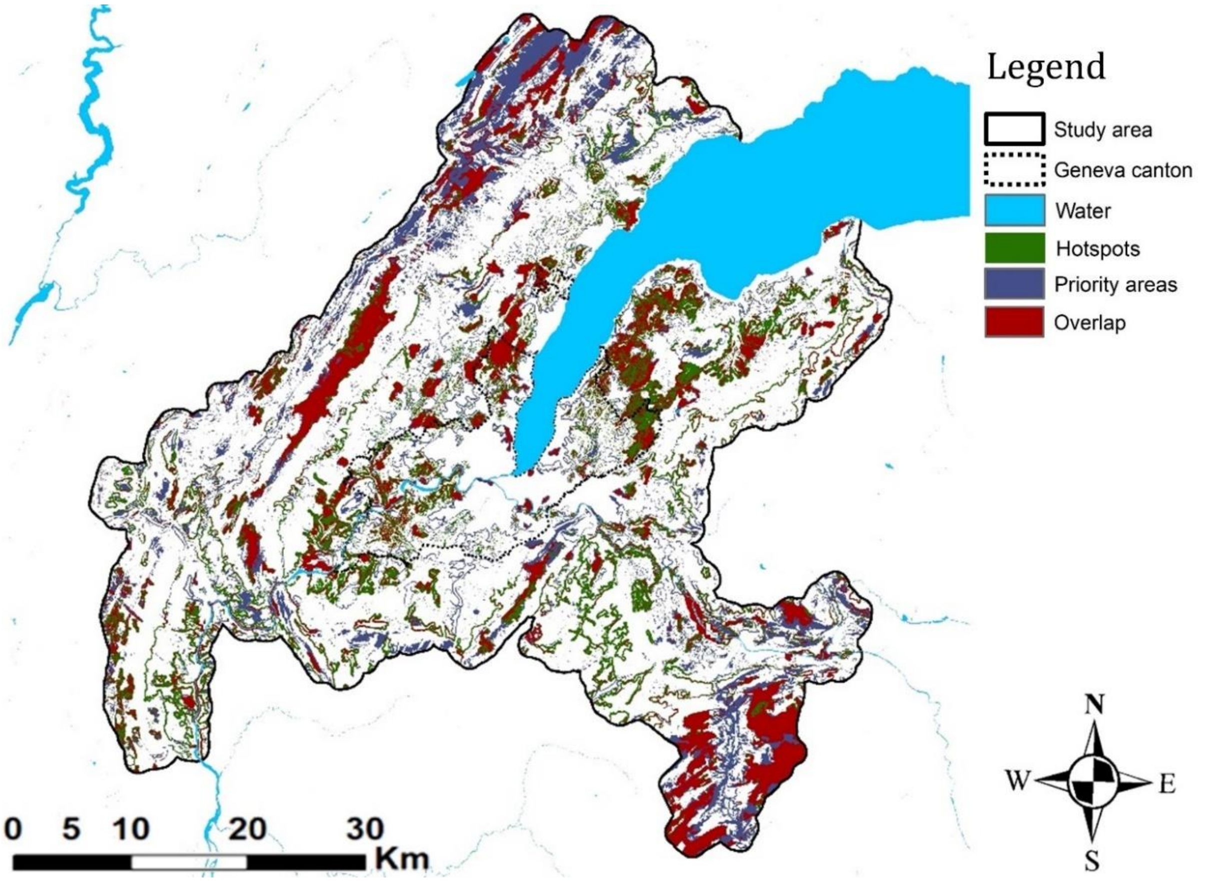

Figure 6. Distribution of suitability hotspots (in green), priority areas (in purple) and the overlap between them (in red) for current time.

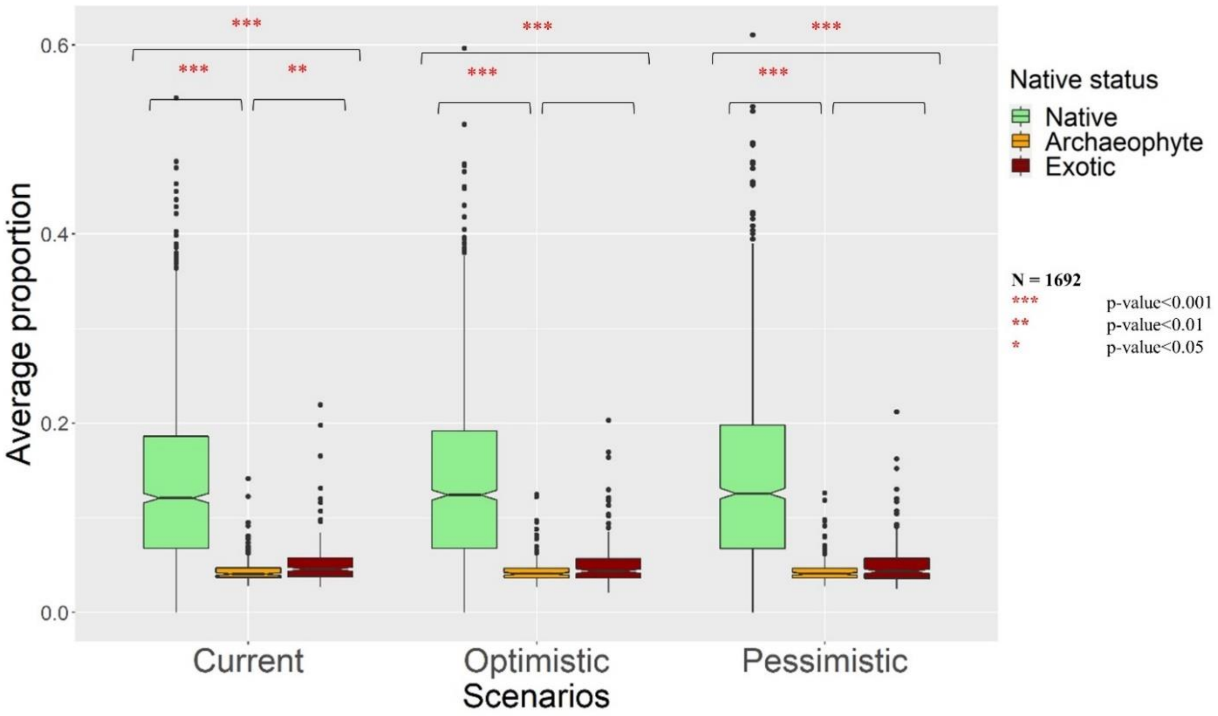

Figure 7. Effectiveness of CA to conserve species distribution according to their native status. The red stars indicate the p-value of a Wilcoxon mean test between native groups within each treatment. Precise mean values are found in the Table 1.

5.3.2. Effectiveness and relevance of CA

Areas with a conservation status represent 13.69% of the natural and semi-natural surface of the study area, excluding urban categories. CA show a tremendous disparity in its habitat composition. Indeed, they are mostly composed of closed forest (68.55%), followed by meadows (14.99%) and crops (6.38%), while open forests and wetlands only represent a small proportion, respectively of 1.74% and 2.01% of CA's surface. The remaining proportion is made of disturbed habitats. However, the integrated habitats represent 18.42% of all closed forests of the study area, 17.87% of open forests, 14.95% of wetlands, 11.30% of meadows and only 3.60% of crops, showing a more balanced representativeness of all natural habitats in the territory, which is valuable in a conservation perspective.

Interestingly, CA are not very effective in conserving the suitability hotspots. Only 14.84% of the hotspots are integrated into CA for current time and this proportion stays relatively similar in future conditions (14.23% for optimistic scenarios and 13.53% for pessimistic ones). This result is surprisingly low, especially considering that these hotspots only represent 30% of the territory. CA effectiveness in conserving priority areas is slightly higher with integration values of 17.98% for current time, 17.59% and 17.23% in future optimistic conditions and pessimistic ones, respectively. Results suggest that while current CA are not very effective in conserving plant species hotspots and priority areas according to these results, their effectiveness remains broadly the same in the future. It is important to note that due to their relative surfaces covered, CA cannot conserve more than 45% of the suitability hotspots and the priority areas.

Most species have at least a part of their current distribution integrated in CA with the exception of four specie for current time. This number is expected to increase to 18 species in optimistic future scenarios and 26 in pessimistic ones. They are only native species, mostly alpine plants that are not threatened with the exception of two critically endangered species for future scenarios (Table 4A in Appendix 4). On average, 12.30% of all current species distribution is integrated into CA and this number stays relatively similar in future conditions (see Table 1 for details). A greater proportion of native species distributions is integrated in CA compared to the other statuses for current and future scenarios (p-value<0.001; Fig. 7).

5.3.3. Biodiversity pillar characteristics and comparison with CA

The BP represents the most interesting areas regarding the current distribution of hotspots and priority areas and covers 30% of the study area (Fig. 8). It is composed of closed forests (49.40%), natural or extensively managed meadows (24.18%), crops (10.99%), wetlands (3.51%), open forests (3.25%) and disturbed vegetation (1.91%), the rest being urban areas and roads. However, the BP represents 29.97% of all closed forests in the study area, up to 75.56% of open forests, 58.91% of wetlands, 41.15% of natural meadows, 14.20% of crops, and 10.68% of disturbed vegetation. Although BP covers more than twice the CA's surface, it is interesting to note that the BP only integrates a proportion of closed forest that is 1.5 time larger than that in the CA, indicating that they have a lower ecological value or that a sufficiently large surface is considered. However, the BP integrates around four times more open forests, wetlands, crops and meadows than CA suggesting that these specific habitats are important for plant diversity and should be further integrated into conservation planning.

The BP integrates up to 83.78% of the suitability hotspots and 72.73% of the priority areas for current time and 80.00% of hotspots and 67.86% of priority areas in optimistic scenarios and respectively 77.15% and 66.20% for pessimistic ones. The high proportions observed here were expected because these metrics were the inputs used to calculate and map the BP. However, these results show that the suitability hotspots and the priority areas will somehow remain in the same location in the future despite great expected shifts of species distributions (Sanguet *et al*., in prep, chapter 4). This result is confirmed by the high overlap between current and future BP (89.54% for optimistic scenarios and 84.99% for pessimistic ones). It also suggests that the most interesting areas for current time will mostly stay relevant under the future conditions, which is an encouraging element in a conservation perspective. Finally, around 40% of CA are integrated into the BP, indicating that, with this methodology, 60% of CA are currently protecting areas that are not identified as relevant for plant diversity conservation, suggesting that there is still room for improving CA.

Almost all species have at least part of their current distribution integrated into the BP. Only two species (*Laurus nobilis* L. and *Lavandula angustifolia* Mill.) are not covered by the BP for current time, but they are mostly planted and are not found outside city green spaces and gardens. However, all species included in this analysis have at least a part of their distribution covered by the current BP in future conditions, indicating an increased effectiveness in the future. It indicates that the current BP is still highly relevant in the future, suggesting that the methodology used for its identification is effective for conservation purposes. Native species have a larger proportion of their distributions covered by the BP compared to archaeophyte and exotic species, for the three treatments considered ($p\text{-value}<0.001$; Fig. 9). In addition, the proportion of native species distributions included is significantly higher in future pessimistic scenarios ($p\text{-value}<0.01$). This observation could be explained by a greater reduction of species range outside the BP, leading to a higher proportion covered by the BP, which suggests that the habitats integrated in the BP have a higher quality than those located outside of it.

5.4. Discussion

5.4.1. Spatial distribution of plant diversity

Areas located at high elevations appear to be of greater interest for plant diversity showing a high conservation priority for all treatments but a loss of global suitability in the future. These observations could be explained by the expected altitudinal shift of species distributions as they follow their optimal climatic conditions. Indeed, mountain plants living in subalpine pastures and open habitats do not have many possibilities to migrate higher in altitude in the study area because the mountain summits reach around 2’000 m.a.s.l., which corresponds to the beginning of the altitudinal range of their habitat and the upper limit of montane forests. Alpine species’ habitat is rare and they are highly vulnerable to global changes which induce a priority selection by the prioritization ranking process. Although most of them will still find suitable conditions by 2050, an increased competition with forest species shifting higher in altitude combined with less suitable climatic conditions might contribute to increase their local risk of extinction. However, although rising temperatures are expected to allow more species to grow at higher elevations, the loss of alpine plants and the lower suitability observed for these locations seem to outstrip the potential gain of new species. While these subalpine meadows are highly diverse, mid-elevation forests show a lower priority and a lower global suitability according to their specific richness and conservation priority observed in this work,. Thus, the loss of alpine species might not be balanced by the gain from forest plants. Higher elevations mountain ranges are found outside the study area and species might thus be able to migrate at these locations, despite expected difficulties due to the landscape fragmentation and the unprecedented rapidity of change (Corlett & Westcott, 2013; Leimu *et al*., 2010; Perry, 1994). Nevertheless, all indicators seem to point to the conclusion that subalpine meadows are highly important for plant diversity, especially in a context of climate change, and might represent potential candidates for the expansion of natural reserves to better cover this habitat. It also demonstrates that the landscape and habitat management of these areas are highly beneficial to plant diversity.

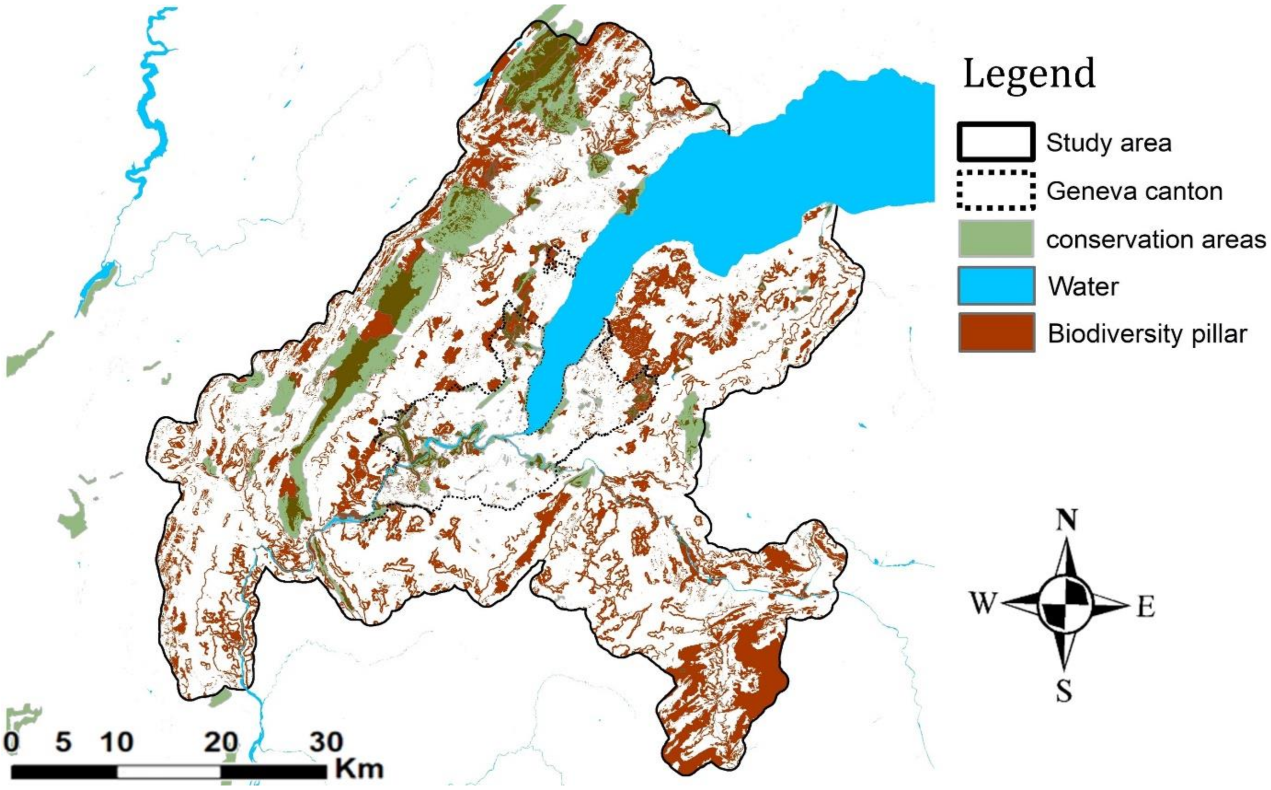

Figure 8. Distribution of the BP (in red) and of the CAs in the study area.

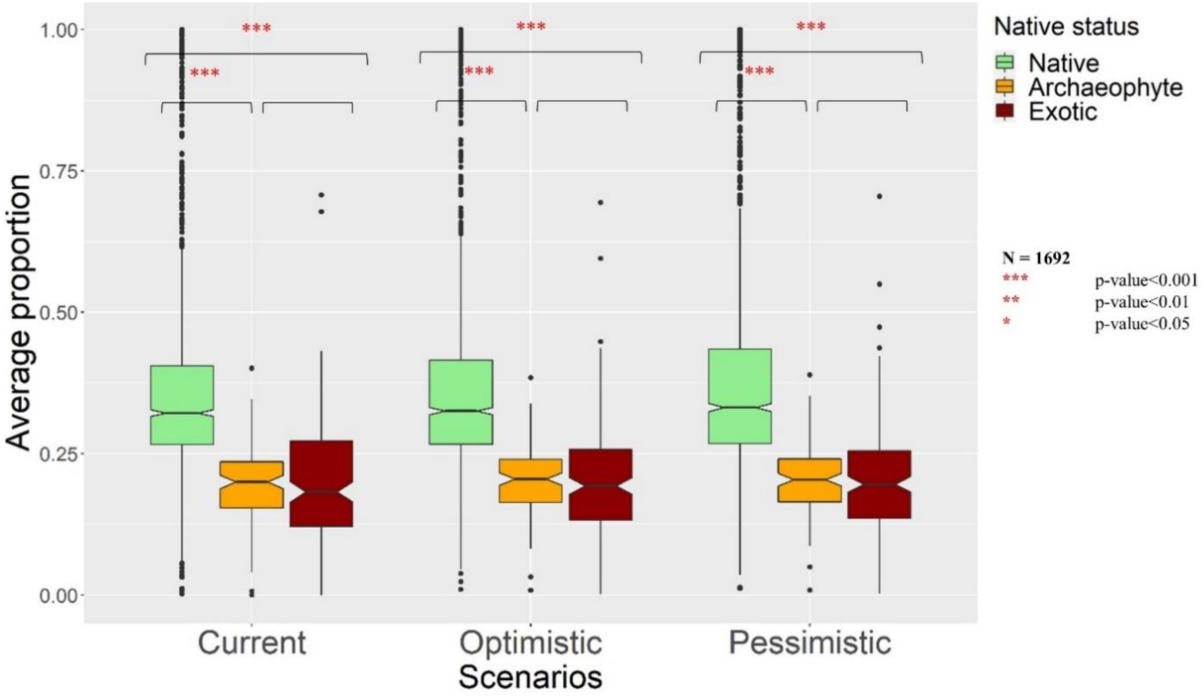

Figure 9. Effectiveness of the BP to conserve species distribution according to their native status. The red stars indicate the p-value of a Wilcoxon mean test between native groups within each treatment. Precise mean values are found in the Table 1.

Table 1. Average effectiveness of CA and the BP in integrating species distribution. The numbers are expressed in % of the total distribution.

Group of species	Treatment	Conservation Areas (CA)	Biodiversity Pillar (BP)
All	Current	12.30	34.89
All	Optimistic	12.61	35.82
All	Pessimistic	12.85	36.71
Native	Current	13.77	37.78
	Optimistic	14.22	38.86
	Pessimistic	14.52	39.93
Archaeophyte	Current	4.57	19.45
	Optimistic	4.59	20.27
	Pessimistic	4.62	20.42
Exotic	Current	5.21	19.26
	Optimistic	5.06	19.49
	Pessimistic	5.08	19.61
Not endangered	Current	12.90	36.78
	Optimistic	13.04	37.56
	Pessimistic	13.18	38.36
Endangered	Current	10.54	34.40
	Optimistic	11.13	33.89
	Pessimistic	11.58	34.13

The suitability is expected to slightly increase in the lowlands which could be explained by the rising temperatures in the plateau leading to more suitable conditions for species usually found growing in urban environments where temperatures are warmer compared to the countryside due to the urban heat island phenomenon (Ackerman, 1985; Taha, 1997). Furthermore, rising temperatures would allow more Mediterranean species to expand their current range within the study area or to colonize it in the near future since latitudinal shifts are expected and are already observed in Mediterranean habitats (Benito Garzón *et al*., 2008; Penuelas & Broada, 2003; Resco de Dios *et al*., 2007; Vogiatzakis *et al*., 2016). It suggests that the richness map might even underestimate the potential increase of suitability in the lowlands because the models were only developed for species that are currently growing in the study area without considering potential future arrivals. However, some of the new exotic species could outcompete native ones and become invasive which in turn would lower net richness. Although an increase is expected in the future, the level of suitability is still low to average in the lowlands. The expected gain of suitability in the plateau might participate in explaining why this area has less priority in the prioritization ranking process than subalpine meadows. Thus, the results show an interesting complementarity between the richness and the ranking maps. Indeed, suitability hotspots alone might not be able to capture the whole diversity of a landscape, especially for rare or threatened species (Marchese, 2015; Orme *et al*., 2005), but could be very useful when used in association with other aspects of biodiversity distribution. Interestingly, while subalpine meadows are the focus for plant diversity conservation at high elevation, deciduous forests seem to be the main focus in the lowlands. However, mid-elevation forests are not selected by the method employed here and this should be further investigated. Nevertheless, these results indicate that the intrinsic conservation value of a given area does not only depend on the type of habitat but also on the context (altitude for example).

While climate seems to drive shifts of species distributions in the study area (Sanguet *et al.*, in prep), very localized changes of specific richness are on the contrary induced by the changes in habitats, although the LULC distribution is not expected to vary much in the study area by 2050 (Sanguet *et al.*, in prep, chapter four). Habitats with a more "natural" constitution are expected to host more species than disturbed or highly managed land-cover types and thus, the replacement of forested areas by crops leads to a greater decrease of global suitability locally, and *vice-versa*, as presented in Fig. 10. Although natural habitats have a higher biodiversity level than anthropogenic/urban ones, on average, the magnitude of gain or loss of global suitability a simple change of habitat could induce is demonstrated here. These results indicate that restoring, re-naturing and rewilding green spaces are highly valuable conservation actions accessible at the smallest scale with tremendous benefits to the local biodiversity. A deep knowledge of its landscape and an effective systematic conservation planning thus favour making better conservation decisions.

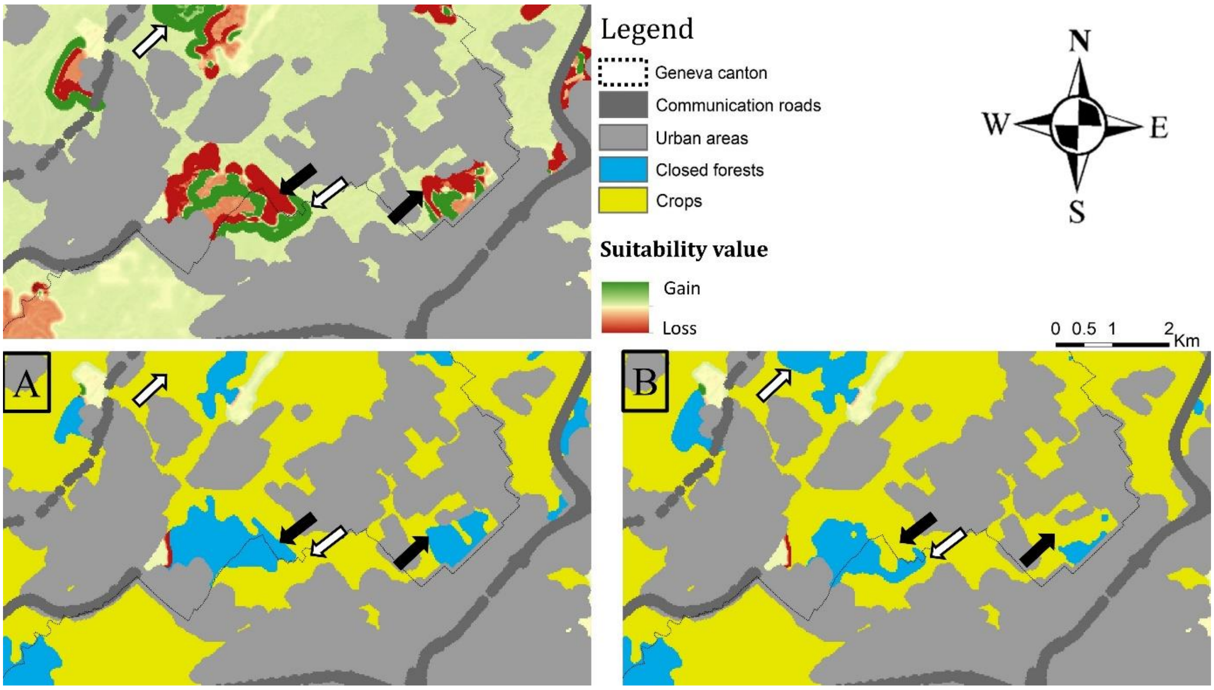

Figure 10. Gain or loss of suitability according to changes in Land-Use-Land-Cover. (A) Current habitats distribution; (B) Future habitats distribution. Black arrows show areas modelled to transit from forests to crops inducing a loss of suitability and white arrows show areas modelled to transit from crops to forests inducing a gain of suitability.

5.4.2. Relevance of CA and biodiversity pillar

CA are not always spatially congruent with species distributions or biodiversity hotspots, nor are they necessarily relevant for future spatial shifts, suggesting that assessing their long-term effectiveness is essential (Araújo *et al.*, 2011; Vieilledent *et al.*, 2013). In this study, CA are not expected to lose relevance in the future because they include similar levels of species distributions but struggle to effectively conserve the suitability hotspots and the priority areas identified in this work. It might be explained by the fact that they mostly integrate large patches of mid-elevation forests that do not hold a great interest for plant diversity conservation. Less than half of CA are integrated into the BP which is again surprisingly small considering that this pillar covers 30% of the whole study area. The BP identified here show promising results and the methodology used for mapping it would benefit from being tested in different contexts and against other methods. Indeed, despite having a surface around twice as large as CA, it integrates an average proportion of species distribution three times larger, and allows for the identification of highly valuable habitats for plant diversity. These results show that there is still room for improvement regarding current CA effectiveness in conserving plant diversity. The areas covered by the BP serve as a reservoir of candidate for increasing the surface of CA and reach the aim of 30% of the territory, especially since the results have shown that the most valuable areas for plant diversity will mostly remain at the same location in future conditions. It is difficult to predict if the same observation would be made in other territories and further investigations should be done. However, it demonstrates that systematic conservation planning is a highly effective method to reach conservation objectives and describe the conservation value of a territory, especially in a context of climate change (Critchlow *et al.*, 2022; Moilanen *et al*., 2011).

Although plants are at the bottom of all trophic chains and constitute the habitats upon which all animals depend, the BP should be complemented with a similar assessment using animal species. Indeed, while some habitats are not essential for plant diversity conservation, they might be highly relevant for animal movements, migrations, feeding habits or reproduction. This would also increase the reliability of the BP allowing it to reach a higher level of effectiveness as described in Honeck *et al*., 2020a (chapter 2). Furthermore, the Green Infrastructure does not only consider the distribution of biodiversity but also landscape and species connectivity as well as ecosystem services supplies (Honeck *et al*., 2020a, 2020b). Thus, CA should also include other important features of the biosphere that were not assessed in this study. The current and future relevance of CA should thus be assessed using a complete Green Infrastructure network created using several aspects of biodiversity distribution. Another limitation is that many areas modelled to have a high ecological interest might not be available for protection because they might rely on other legislation, integrate private lands or have other purposes. These factors were not considered in this work. CA identification thus depends on complex trade-offs between many aspects occasionally in conflict between each-other.

Using models has been proven to be useful in biodiversity conservation (Addison *et al*, 2013; Baker *et al*., 2021; Guisan *et al*, 2013; Honeck *et al*, 2020b; Lehmann *et al*. 2002a; Mateo *et al*, 2013; Pullin *et al*, 2004). However, biases exist at each step of the process from the quality and selection of inputs, to the methods and settings used as well as arbitrary choices. They could induce large spatial variations in the resulting maps, especially if there are numerous modelling steps. Hence, deciding to protect areas solely based on results originating purely on models might lead to non-optimal solution. In this work, the habitats used to model species distribution were transformed from discrete to continuous values using a focal statistic. This permits the consideration of habitat structure and the ecotone effect in the models. However, this method might have led to an exceeding high-quality interpretation of habitat margins. Indeed, the models might have considered these locations as suitable for both habitats (and hence, both plant communities) creating a spatial artefact visible on the richness maps as well as on the Zonation's outputs, where the margins of some habitats appear to be more valuable than the habitat itself. Whether or not the ecotone effect might be over-estimated, this result demonstrates that methodological choices could lead to specific features even when many modelling steps have been done before the final results. Results from models should be interpreted with care and should not replace field observations and local knowledge, especially on highly sensitive topics, but should rather be used as a supplementary and complementary input in the decision-making processes of local authorities.

5.5. Conclusion and perspectives

The results of this work have shown that CA are expected to keep their current quality in the future although they could be further improved by integrating more suitability hotspots and priority areas to increase their effectiveness in conserving long-term plant diversity. The distribution of suitability hotspots and of priority areas have shown an interesting complementarity and their use to identify a biodiversity network has been revealed to be particularly effective. The BP has allowed for the identification of essential habitats for the conservation of plant diversity, mainly composed of subalpine meadows and lowlands deciduous forests. The BP identified is highly relevant in future conditions and thus represents a set of interesting areas that could be further included in current CA.

Several aspects of this work merit further investigations to expand and confirm the trends identified. For example, using several prioritisation settings such as different weights allowed to vulnerable species, and/or rare species or endangered ones, would reveal which areas are always selected and thus essential conservation assets, but would also show the areas specifically important for one or another group of species. The comparison of the ranking maps from the ABF and CAZ methods of Zonation may also reveal interesting features of the landscape, especially when comparing them with the distribution of hotspots. The results found in this experiment are also very interesting because they fully describe the territory through a plant diversity prism and provide covering maps that help understand the spatial patterns of biodiversity distribution, and its evolution, in the near future while taking into consideration global changes. This work has shown that systematic conservation planning is a powerful method to evaluate the effectiveness of CA and helps reaching conservation targets. It also shows that SDMs could produce highly valuable outputs for conservationists and local authorities.

Chapitre 6

Discussion and Conclusions

« Alors je crois que s'il est une exemplarité que nous devrions tenir, c'est peut-être celle *du sérieux. Aujourd'hui, être sérieux c'est être révolutionnaire, être sérieux c'est défier les* règles et critères implicites. *[…] Mais je* crains que bien souvent, derrière nos calculs et nos expériences, nous ne soyons pas très *sérieux nous autres chercheurs. »*

« I think that if there is an exemplarity that we should keep, I believe it might be seriousness. Today, being serious is being revolutionary, being serious is defying the rules and implicit criteria. […] However I fear that behind our calculations and experiments, we are not so serious, we researchers. »

- Aurélien Barrau, "Sur l'exemplarité du monde académique face à la catastrophe écologique.", publié le 11 Mars 2022.

6.1. Foreword

The global discussion is articulated in three sections. First, the relevance of the use of models to determine species distribution is debated. While these models are essential tools to understand the impacts of global changes on local plant diversity, the limits inherent in these methods are also presented. Second, a thorough evaluation on the territory of the study area is done, showing that this work has brought important elements for consideration in local conservation practices by highlighting ecologically rich areas and crucial trends regarding the evolution of species distributions and plant diversity, especially for mountain species and exotic plants. Third, key ideas derived from this work are discussed on a global scale, and a particular emphasis is placed on how to limit our impacts on the natural world as well as on how to manage natural ecosystems in order to favour a global biodiversity rebound. Finally, a conclusion is made regarding the outcomes of this PhD project and presents the main contributions of this thesis to the local authorities and to the scientific fields of biological conservation and habitat suitability modelling, as well as giving potential perspectives and ameliorations concerning what has been done.

6.2. About the use of models in conservation

The use of models, and specifically SDMs, represents a considerable asset in biodiversity conservation and management because they allow the extrapolation of point information across space and time. Modelling and projecting species distributions in various environmental conditions improves knowledge about species ecology and gives insights on their vulnerability to global changes. Being able to forecast how species may respond to future environmental changes is interesting because current snapshots of population health might not be sufficient for conservation agencies to take rapid, adequate measures to prevent local extinctions. Furthermore, knowing that a species expects a shrink of its range or a decrease in its habitat suitability, ensures that conservation efforts and monitoring can be focused on these vulnerable species. In this context, knowing in advance how disturbances or abiotic modifications could affect species enables conservationists to take better proactive decisions to ensure the long-term survival and prosperity of species.

Results from SDMs are, however, highly dependent on several factors and might lead to limited or even counterproductive decisions if they are not discussed, correctly understood and integrated. One reason is that we cannot precisely predict how the climate will evolve, nor how species or our societies may actually respond to these changes. Random events (pandemics, war, political decisions, resource supply, natural catastrophes etc.) could completely change the magnitude and rapidity with which these aspects are evolving and that cannot be fully measured, quantified or integrated in future scenarios. Furthermore, the evaluation of the intrinsic biases and quality of models is essential and must be understood before using their outputs. Indeed, there are no agreed-upon standards in SDM and the quality of their outputs may vary according to the methodology used (Araújo *et al*., 2019).

6.2.1. Biases and quality of predictions

Before using any results from models, it is essential to understand all possible biases at each step of the modelling process. Most biases appear at the early stages of model development indicating that preliminary arbitrary choices or small imperfections can have noticeable consequences on the final results. For example, potential human mistakes regarding species identifications, imprecision and imperfections in the data (spatial precision of occurrences, predictor's resolution and quality), and arbitrary choices (model's algorithms and settings, set of species and predictors, indicators selected, etc.) alter the final results, although most of the arbitrary choices are supported by ecological and methodological evidence.

The first biases occur at the very early stages of data acquisition and concern the geographical precisions of the observations, the survey method, the right taxonomy being used to describe the taxa (synonymy and taxonomy are real issues when dealing with data from different countries) as well as potential mistakes regarding determination (Anderson, 2012; Araujo *et al.*, 2019; Tessarolo *et al.*, 2014). Identically, the creation and calculation of predictors raster map might be biased by the intrinsic quality and selection of general circulation models as well as scenarios for climatic predictor forecasts, the predictions of edaphic explanatory variables, the ability of GIS software to create ecologically meaningful topographic predictors, the capacity and relevance to map habitat distribution (the difficulty of this has been demonstrated in this work for wetlands in Chapter 3), the ecological relevance of delimiting habitat in space and if species do "perceive" habitats the way we think they do. As an example, the differences between the coupled model intercomparison project phase five or six (CMIP5 or CMIP6) result in different interpretation of global climatic circulation models and ultimately lead to different SDM predictions. It is essentially impossible to verify these biases and the models were run under the hypothesis that the input data were of sufficiently good quality for the purpose.

The set of occurrences integrates species from all major taxonomic groups of plants but only represents a subset of all plants growing in the study area for which a sufficient number of occurrences were available in order to calibrate reliable models (Stockwell & Peterson, 2002; Wisc *et al.*, 2008). Spatial biases occur in these occurrences as areas that are easier to access are more surveyed than remote places, which raises the question over the representativeness of inputs for the study area (Barbet-Massin *et al*., 2010, 2012; Elith *et al.* 2006, 2011; Phillips *et al*. 2009; Zaniewski *et al*. 2002). This is also visible on GBIF with some countries participating intensively in the data contribution efforts while others do not (Beck *et al*., 2014). This spatial bias is avoided, as much as possible, in the methodology used for the Chapters 3 and 4 by using a subset of all available data according to their spatial distribution and quality, as well as with the use of refined spatial distribution of background data (Beck *et al.*, 2014; Fourcade *et al*., 2014).

The choice of predictors influences predictions. Indeed, their ability to correctly describe the study area environment and correctly capture species ecology, according to the relevant geographic scale, is essential. Spatial auto-correlation, data quality, adequate resolution, choice of habitat classes and their level of detail all play an important role in model's performances (as demonstrated in chapter 3), and therefore can have potential repercussions. Here, predictors were selected according to their ecological meaning for the study area and the considered taxa, and were tested for correlation with Pearson's correlation rate and the variable inflation factor in order to identify a set of independent explanatory variables covering as many aspects of species' ecological niche. However, many predictors cannot be used because digital data on them do not exist, cannot be modelled or is not available (access issues). Biotic interactions and other random events, known to play a significant role in explaining species distributions, remain difficult to use as predictors and thus, only a partial sample of species realized ecological niche could be used in models (Austin & Van Niel, 2011; Guisan *et al.*, 2017; McGill, 2010; Pearson & Dawson, 2003).

The choice of the modelling algorithm also induces variations in the final results. In this project, MaxEnt was chosen because its interface allows local conservationists to run the same models in the future in order to follow the evolution of species distributions or to improve them. In addition, the predictors were actually the varying factors tested and therefore, using a unique modelling approach limits the variability of resulting maps. However, other algorithms would have probably produced slightly different results (Li & Wang, 2013). The number of replicates, the degree of freedom, the number and spatial distribution of background data and the model settings are also sources of variability (Araújo *et al*., 2019; García-Callejas & Araújo 2016; Hallgren *et al*., 2019; Merow *et al*., 2014). In this project, the median value of several replicates was selected for the final predictions and 10 replicates were always run to test their models' performances in order to integrate model's variability in the evaluation. In the Chapter 4, the threshold used to create the binary maps, the approaches used to combine climatic and biotopo predictions and the indicators selected to calculate the vulnerability index, are sources of variation in prediction maps and were discussed therein. Finally, in the Chapter 5, the settings of the prioritization software Zonation and the choice of plant diversity aspects integrated into the biodiversity pillar could also be further discussed and expanded.

6.2.2. Difficulties of modelling species distribution under global changes

The integration of new climates in SDM raises many questions and has been widely discussed in the literature (Araújo *et al*., 2019; Pearson & Dawson, 2003; Sinclaire *et al*., 2010; Thuiller *et al*., 2008). As climate and land-cover change over time, new predictor combinations appear in the projected space which forces models to make predictions outside the range of calibration data. This issue, known as the "non-analog climate", comes from the prediction that future climatic conditions might be different from those that exist today which would alter models' ability to predict future species distributions (Faurby & Araújo, 2018; Fitzpatrick & Hargrove, 2009; Peterson *et al*., 2018; Thuiller *et al*., 2004). The same problem is raised when projecting the realized ecological niche of an invasive species to a new geographical space (Petitpierre *et al*., 2017). This issue could lead to low predictive accuracy and an over or under-estimation of future species distributions (Veloz *et al*., 2012). However, this issue can be limited if the species' realized climatic niche is fully sampled, for example using occurrences from the whole spatial range of species, especially if they integrate identical climatic conditions to the ones predicted in the study area (Guisan *et al*., 2014, 2017). This is why the climatic models have been fitted at the European scale in the Chapter 4.

The use of climatic variables representing mean seasonal or annual values might lead to a misestimation of the distributional shift of species. Indeed, these predictors do not always reflect the physiological response of species to their changing environment, and a single heatwave might have dramatic impacts on plant individuals as it has been shown in Switzerland (Vittoz *et al*., 2013). This suggests that rare, extreme events might play a major role in delimiting species distributions, and their frequency is expected to rise in the future (Beniston, 2004). Extreme events are difficult to integrate in SDM because they are stochastic. The methods to integrate them in SDM should be further studied (Gardner *et al*., 2019). Other types of predictors could be ameliorated and, for example, the use of annual precipitations could benefit from being replaced by water availability which better corresponds to the physiological use of water by species (Gardner *et al*., 2019). This is what has been partially done in this work by using an aridity index, together with classic climatic predictors in the third chapter. Finally, other methods propose different sets of predictors depending on the habitats considered because various habitats could occur within the same climatic conditions depending on biotic interactions (i.e. forest and meadows; Pausas & Bond, 2021).

Modelling species distributions under climate change also raises ecological questions. Indeed, rapid changes in climatic conditions lead to an overlooking of species ability to evolve and adapt. Yet, some species might actually be able to adapt to new conditions if their populations have local genetic variability (Atkins & Travis, 2010; DeMarche *et al*., 2019; Hoffmann & Sgrò, 2011). SDMs consider species as a single, ecologically uniform entity, but the variations of adaptations of species populations to a partial portion of its ecological niche lead to different projections under climate change (Hällfors *et al*., 2016). Many research gaps were identified to better understand the role of rapid adaptation and evolution of plants in a context of global changes and how to integrate this knowledge into models (Anderson & Song, 2020). It suggests that having access to a mapping of species' genetic diversity might help in creating more performant models leading to a better understanding of species responses to global changes, which represents exciting possibilities for future research.

Biotic interspecific interactions might change in intensity and quality along with the climate, leading to an accelerated spatial shift or mitigated effects of climate change on species distributions (HilleRisLambers *et al*., 2013). Additionally, global changes could alter the magnitude, frequency and direction of biotic interactions directly causing major changes in species distributions, and ultimately to ecosystem functions and services' supply (Blois *et al*., 2013; Montoya & Raffaelli, 2010). While climate is thought to be the main driver of species' distribution at a large spatial scale and the leading factor for future distributional shifts, as presented in the third chapter, biotic interactions might represent a catalyst or a buffer, either accelerating or reducing climatic effects on species distribution (Araújo & Luoto, 2007). Thus, a better knowledge of species interactions and their evolution according to a climatic gradient would help determine the magnitude of species' spatial shift that could be expected in the near future.

Other factors such as the questionable equilibrium between a species and its environment (Alexander *et al*., 2017; Sax *et al*., 2013), the potential mismatch between cause and correlation in explaining species distribution with climatic data, or the potential future changes of species ability to migrate, are further developed in Sinclair *et al.*, (2010) and Urban *et al*., (2016), while additional climate change metrics are reviewed and discussed in Garcia *et al*., (2014). These discussions represent the limits of our knowledge and of the modelling methods available to predict future species distributions. As George EP. Box and Norman Draper said in 1987, "essentially, all models are wrong, but some are useful". It is thus essential to understand the inherent limits of the methodology applied and to discuss them, but they also represent exciting scientific challenges over the coming decades.

6.3. Insights for local conservation planning

Despite having some limitations, the use of models represents a unique opportunity to forecast 1) the impacts of global changes on species distributions and 2) our capacity to act and take the appropriate decisions to prevent potential damage to biodiversity and human societies (IPCC, 2021, 2022a, 2022b). Indeed, when used to predict future distributions, SDMs represent an essential asset to help conservationists take proactive measures to conserve biodiversity and focus on the most vulnerable species (De Kort *et al*., 2020; Rowland *et al*., 2011). These predictions could be used as a justification for conservation actions, in association with on-the-ground observations, or as a supplementary input into decision-making process. As an example, they could be particularly useful in identifying the drivers of rare species distributions and to spot new areas to survey in order to find new populations (Fois *et al*., 2018), ultimately leading to the identification of new areas that are interesting for conservation (Hamilton *et al.*, 2022).

According to Abrahms *et al*., (2017), successful long-term conservation planning has to follow five key steps, that were respected in this thesis, encompassing the assessment of: 1) the magnitude of climate change expected in the study area, which has been done through the use of two scenarios for 2050; 2) other elements susceptible to change and playing a role in explaining species distribution such as biotic factors or changes in LULC; 3) the vulnerability of species to the above-mentioned new conditions; 4) the expected changes in species distribution responding to the new environmental conditions, and finally 5) the potential management strategies which have been estimated through the evaluation of the effectiveness of current conservation areas and by proposing a network of key areas for the long-term conservation of plant diversity. The results of this thesis have shown that climate is expected to drive the shifts of species distributions, leading to potential migration and extinction events that are further discussed below. They have also shown that highly restricted increase in specific richness is caused by the switch of LULC anthropogenic category to a more “natural” one and *vice-versa*, which represents a powerful leverage tool for the people and the authorities to increase the biodiversity level at the very local scale. Some of the key trends this work has brought regarding the impacts of global changes on species’ ecology are discussed in this section for a better understanding of the evolution of local plant diversity.

6.3.1. Species migration

Species are expected to shift their distributions following their optimal climatic conditions which raises fundamental questions about their conservation in a changing environment. Indeed, if species are expected to migrate, it might be counter-productive to put effort into conserving them in places where the climate will not be as suitable as it once was. Following this reasoning, it might be beneficial to let natural migration induce a gradual and partial replacement of species communities by new ones, while original species will colonize new areas at higher latitude and/or altitude. This proposition might be comforting and attractive but has many limitations. First, as hypothesized in this work, habitats and biotic interactions might increase species resilience to climate change allowing them to grow outside of their supposed climatic range (Hargreaves *et al*., 2014; Louthan *et al*., 2015), at least for some time. This “lag” in species response to environmental change has been identified for alpine plants (Alexander *et al*., 2018). Climate is not the only driver of species distribution and the micro-climatic niches induced by habitats or topography might play an important role in preserving current plant communities in future conditions (Körner & Hiltbrunner, 2021). Second, species might not be able to migrate to their new suitable areas because of the highly fragmented landscape, poor habitat quality or simply because their ability to migrate might be outpaced by the rapidity of climate change (Corlett & Westcott, 2013; Leimu *et al*., 2010; Perry, 1994). While the first limit is theoretical, the second one is functional and can be overcome by providing connected natural areas, emphasizing the absolute need for a functional GI network to allow species movements and reinforce their resilience. Finally, the new species might not be able to replace the full range of biotic interactions and ecosystems functions that the old ones provided which might induce cascading effects on local biodiversity although this assumption is not always verified depending on the context (Hulme & Bernard-Verdier, 2018; Loiola *et al*., 2018; Pyšek *et al*., 2020). These limitations represent valuable arguments against a “do nothing” strategy regarding plants conservation in the context of global changes especially because these limits could also interact with each other increasing the magnitude of the consequences.

On the contrary, some authors have proposed the deliberate translocation and introduction of species in places outside their natural range in order to help them find new suitable areas and prevent them from becoming extinct. This action is named “assisted migration” and the pros and cons are highly debated in the literature (Thomas, 2011; Vitt *et al*., 2016; Williams & Dumroese, 2013). Assisted migration might be an interesting option for the survival of a few species but it also raises ecological issues related to the introduction of new non-native species, such as the potential large-scale invasions, among others (McLachlan *et al*., 2007). Some authors suggest creating hybrids or selecting adaptive parts of the genome to increase species resilience and adaptive capacity to global changes (Charles & Stehlik, 2021; Chen *et al*., 2022). Although it currently seems impossible to successfully translocate all species to their new suitable environment, which also raises strong ethical questions, the collection of wild seeds might represent an interesting intermediate option to prevent current extinction while enabling for future *ex-situ* reintroductions (Vitt *et al*., 2010). Nevertheless, some species sold in garden-centres and plant nurseries are already benefiting from unintentional assisted migration, as they are sold and planted largely outside their naturally occurring ranges (Van der Vekens *et al*., 2008).

The ”do nothing” and the “assisted migration” approaches both represent extreme solutions with limited support in the literature. However, conserving as many natural areas as possible and identifying corridors could help species use them as stepping stones to reach new suitable places without interfering too much with natural processes (Christmas *et al*., 2016). The identification and improvement of this important ecological process are some of the main purposes of GI, and represent another argument for its development. The impacts of our way of living and producing goods have detrimental effects on natural habitats. Indeed, the pollution by the excessive use of biocides, the lighting of our infrastructures and the fragmentation of natural spaces should also be reduced to increase the quality of semi-natural and anthropogenic land-covers favouring the return of species (IPBES, 2019). Global scale solutions promoting the return of biodiversity are discussed in the third part of the discussion.

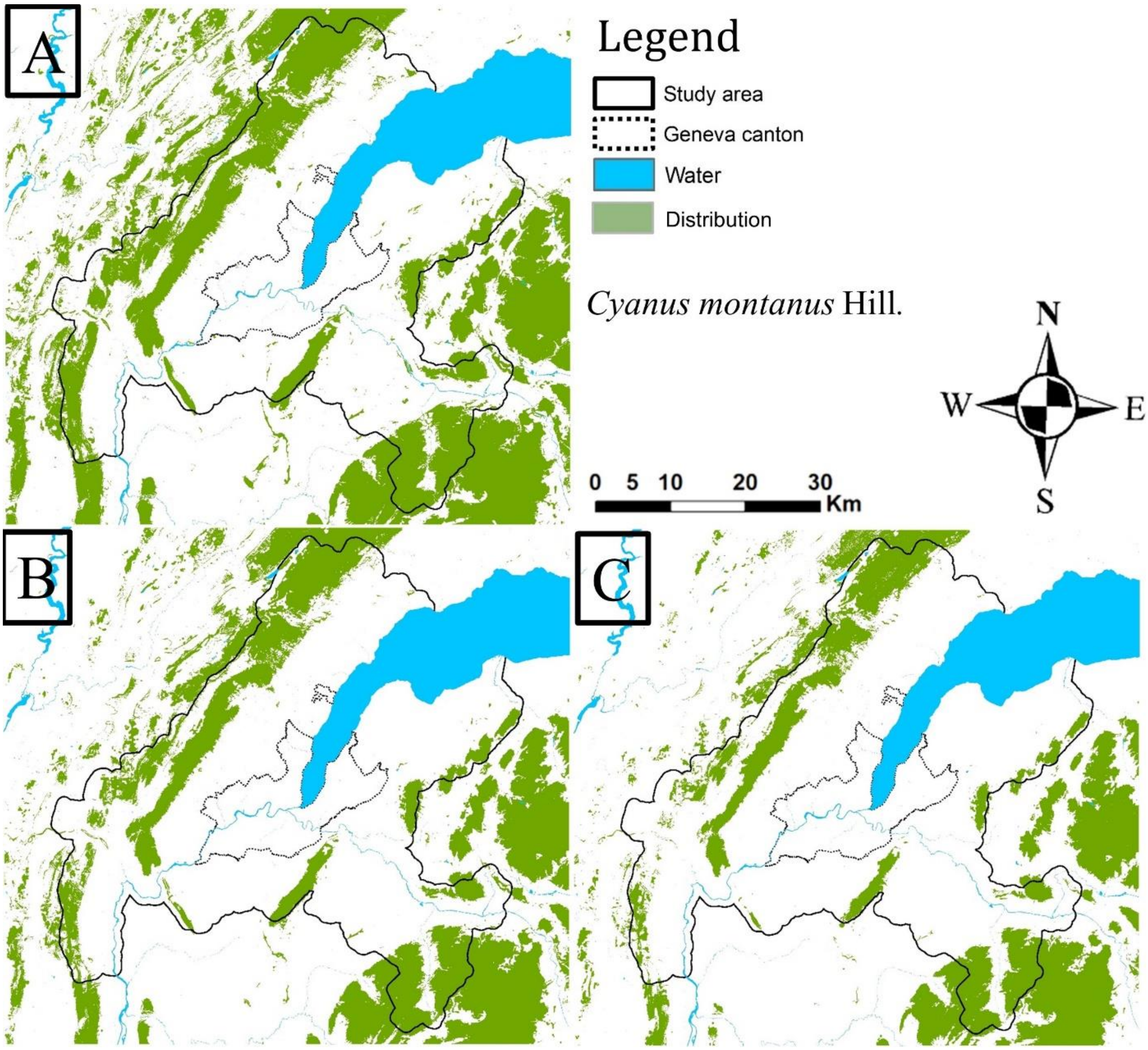

Figure 1. Evolution of the predicted distribution of Cyanus montanus *Hill. (=* Centaurea montana *L.), with the biotopo x climate modelling method. A) current distribution, B) distribution in 2050 for optimistic scenarios and C) distribution in 2050 for pessimistic scenarios. We can see a drastic reduction of its distribution in 2050 with no regards to the scenario considered, and a concentration toward the areas located at high elevation.*

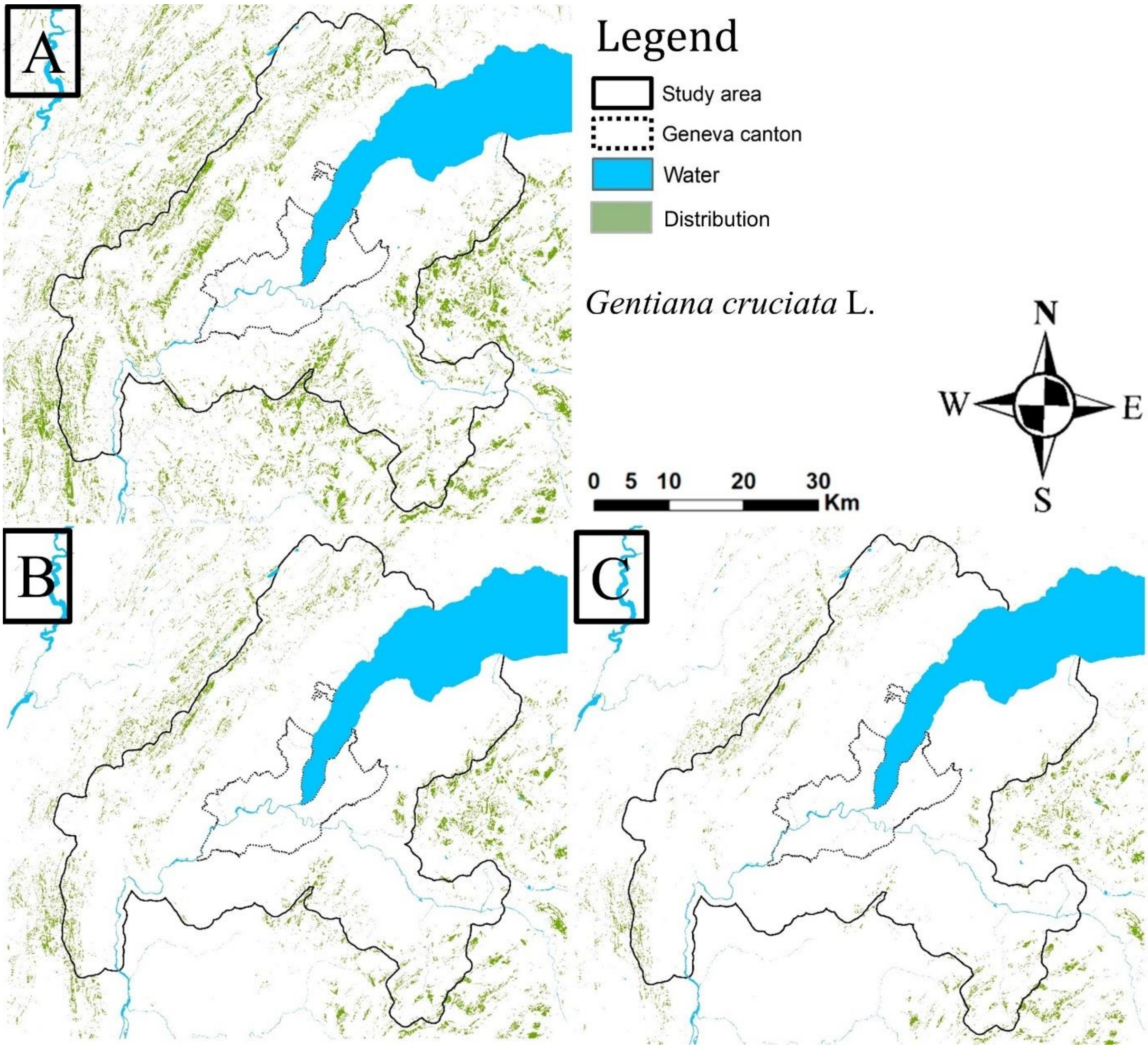

Figure 2. Evolution of the predicted distribution of Gentiana cruciata *L., an alpine species with the biotopo x climate modelling method. A) current distribution, B) distribution in 2050 for optimistic scenarios and C) distribution in 2050 for pessimistic scenarios. We can see a drastic reduction and fragmentation of its distribution in 2050, especially in pessimistic scenarios.*

6.3.2. The case of mountain species

Mountain ecosystems are in the frontline facing climate change and a close monitoring of alpine plant communities helps understanding key ecological responses to global changes (Tito *et al.*, 2020). We hypothesized in this work that alpine plants, or mountain species living in the highlands of the study area, might be more threatened by global changes due to their particular ecology and habitat, as discussed in the Chapter 4 and 5. This hypothesis is illustrated in Fig.1. and Fig. 2., showing a drastic reduction and an increased fragmentation of species distributions in future scenarios, especially in pessimistic ones. The distributions also tend to concentrate toward higher elevations. When comparing the vulnerability index of seven ecological groups in the study area, alpine plants show the highest vulnerability and represent the only group with average values below the vulnerability threshold. Among the 121 species belonging to this ecological group, 87 are vulnerable in optimistic scenarios and 97 in pessimistic ones representing, respectively, 71.90% and 80.17% of this group as presented in the Tables 1 and 2 Therefore, they by far represent the most vulnerable group in the study area. The reason why they are so vulnerable might be accentuated by the geographical limits of the study area that do not allow potential migration to higher elevation because higher mountains are located outside of the study area, as discussed in the Chapter 5.

However, alpine species are *de facto* vulnerable to global changes because alpine environments represent islandic ecosystems difficult to reach, and because altitudinal migration automatically reduces the surface area of habitats available, due to the conic shape of mountains (Alexander *et al*., 2017; Engler *et al*., 2009; Grabherr *et al*., 2010; Harrison, 2020; Riebesell, 1982). A previous study in Switzerland revealed that the first extinction of alpine species would not occur before 2080-2100 (Engler *et al*., 2009). However, among the four species projected to disappear from the study area using the biotopo x climate approach, two of them are alpine species (*Ranunculus sartorianus* Boiss. & Heldr. and *Scorzoneroides pyrenaica* (Gouan) Holub., also named *Leontodon pyrenaicus* Gouan) that are already found in their range limit in the study area. These local extinctions demonstrate that unsuitable conditions might induce a slow decrease in the global population of species ultimately leading to their extinction after a certain “time-lag” where they survive in unsuitable conditions. This “extinction debt” has been shown for high-mountain species (Dullinger *et al.*, 2012). Finally, when considering only climatic models, many more species are expected to lose their entire climatic niche in the study area by 2050, 27 in optimistic scenarios and 50 in pessimistic ones, most of these are mountain species.

Despite these alarming numbers, alpine plants might as well be more robust than lowland species facing changing climate because of the microclimatic conditions availability at small scale (Körner & Hiltbrunner, 2021). Indeed, the strong topographical variations in alpine environments might help species find new suitable areas within a close range without the necessity of migrating higher in altitude. This potential resilience might also be explained by their close biotic interactions with other plant species and especially by the facilitation mechanism observed in mountain plant communities where nurse plants buffer microenvironmental conditions ensuring the persistence of other species (Anthelme *et al*., 2014). These hypothesises together suggest that risks to alpine species regarding climate change may be overestimated by models (Scherrer & Körner, 2011).

These contradictory reasonings suggest that the impacts of future changes might depend on the location, the topography, the local context and the species considered, and no general trend may be identified. Microclimatic niches are difficult to integrate in models and might play a major role in determining species vulnerability to global changes. However, the results of this thesis show a higher vulnerability of alpine species compared to other ecological groups. Interestingly, their habitat, mostly composed of subalpine meadows, is highly diverse in terms of specific richness and priority ranking for conservation purposes. This specific habitat has been massively selected in the biodiversity pillar assessed in the Chapter 5, demonstrating that the method used to identify key areas for plant diversity conservation is effective, and more globally that systematic conservation planning represents useful tools for conservationists.

Table 1. Average vulnerability index according to the ecological group of a subset of the original dataset. This table was made using the 978 plant species for which information about the ecological group was available in the InfoFlora database. This subset is composed of 820 indigenous, 77 exotic and 81 archaeophyte species. As a reminder, the vulnerability index has low values for vulnerable species (3 being the threshold of vulnerability) and high values for resilient ones. The ranking columns show the ecological group vulnerability from the most vulnerable (close to 1) to the most resilient (close to 7).

ECOLOGICAL GROUP	OPTIMISTIC SCENARIOS		PESSIMISTIC SCENARIOS		N
	Average vulnerability index	Ranking	Average vulnerability index	Ranking	
ALPINE	2.79	1	2.46	1	121
FOREST	3.42	3	3.29	3	271
POOR MEADOW	3.37	4	3.29	2	126
PIONEER	3.66	5	3.65	5	51
NITROGEN RICH MEADOWS	3.77	6	3.81	6	51
RUDERAL	3.93	7	4.11	7	215
WETLAND	3.33	2	3.30	4	143

Table 2. Proportion of vulnerable species according to their ecological group using the same dataset described in Table 1. The ranking columns show the ecological group vulnerability from the most vulnerable (close to 1) to the most resilient (close to 7).

ECOLOGICAL GROUP	PROPORTION OF VULNERABLE SPECIES			
	Optimistic scenarios	Ranking	Pessimistic scenarios	Ranking
ALPINE	71.90%	1	80.17%	1
FOREST	28.41%	4	44.28%	2
POOR MEADOW	30.16%	3	38.89%	4
PIONEER	19.61%	5	25.49%	5
NITROGEN RICH MEADOWS	9.80%	7	13.73%	6
RUDERAL	10.70%	6	12.56%	7
WETLAND	39.16%	2	43.36%	3

6.3.3. The spread of exotic species

New species are expected to naturally reach the study area and colonize it in the near future, especially Mediterranean species that are migrating North as temperatures rise (Parmesan & Yohe, 2003). Indeed, warming temperatures are expected to be more suitable for thermophilous species allowing them to potentially outcompete local species, further expanding their ranges in the study area. This is illustrated by the predicted distributions of a Mediterranean orchid *Himantoglossum robertianum* (Loisel) P. Delforge. whose recent range expansion is well-documented (Ramos Gutierrez *et al*., 2018) and that has been observed for the first time in Haute-Savoie (France) in 2017 and in Geneva in 2007 (Société Française d'Orchidophilie Rhône-Alpes SFO & Monitoring de la Flore Genevoise MonGE). The modelled distributions of this species are presented in the Fig.3 and show a great expansion in the study area which could be representative of other thermophilous species.

Global changes have been found to ease the spread of invasive species that are already threatening local biodiversity (Bellard *et al.*, 2013). Using the results of the third chapter, we can evaluate if invasive exotic species are expected to take benefits from global changes in the study area. In the database used for this work, 19 species are blacklisted, which indicates that they are recognized as exotic invasive species, and eight are on a watchlist, signifying that they have a high potential for propagation in Switzerland (InfoFlora, 2022). Blacklisted and watchlisted species have a lower vulnerability than the average value of all species, 4.17 and 4.29 respectively from the vulnerability index calculated in the Chapter 4, while the average value excluding these two groups is 3.37 for optimistic scenarios and 4.44 in pessimistic ones. This indicates that they will on average benefit from global changes, especially in pessimistic scenarios, as presented in the Fig. 4. It is important to note that two of the blacklisted species are considered as vulnerable (*Bunias orientalis* L. (Brassicaceae) and *Heracleum mantegazzianum* Sommier & Levier (Apiaceae)), meaning that their vulnerability index is below 3. Even if these two species are not considered, the average vulnerability index of black listed species would be “only” of 4.41 for optimistic scenarios and 4.73 for pessimistic ones. These values are not higher than the average values of exotic species (respectively 4.33 and 4.61) suggesting that the predicted expansion of invasive species due to global changes is not greater than the other exotic plants in the study area. This does not significate that exotic invasive species are not modelled to cause troubles to the local biodiversity, but shows that this group does not seem better suited to thrive in future climatic conditions than any other exotic species.

The hypothesises about why exotic species are expected to benefit from future conditions in the study area have been discussed in Chapter 4 and 5. Although their suitability will undoubtedly increase under future conditions, exotic plants are not expected to fully replace native ones in the study area. Indeed, many of exotic species are planted and managed in urban green spaces and the risk for them to escape and propagate in the natural habitats seems low, as shown in Fig. 4. However, this risk will probably increase gradually as temperatures increase. In this regard, plants that have recently colonized the study area naturally might be more inclined to undergo a rapid expansion of their distributions, as shown in Fig. 3. It is thus difficult to draw general conclusions regarding the impacts of species migration on local biodiversity because it is highly dependent on the context and the species considered. Nevertheless, it seems highly probable that plant distributions will undergo strong modifications in the near future. Findings regarding alpine and exotic plant distribution dynamics consolidate what has already been found in the region (Nobis *et al.*, 2009; Theurillat & Guisan, 2001; Vittoz *et al.*, 2013; Walther, 2002).

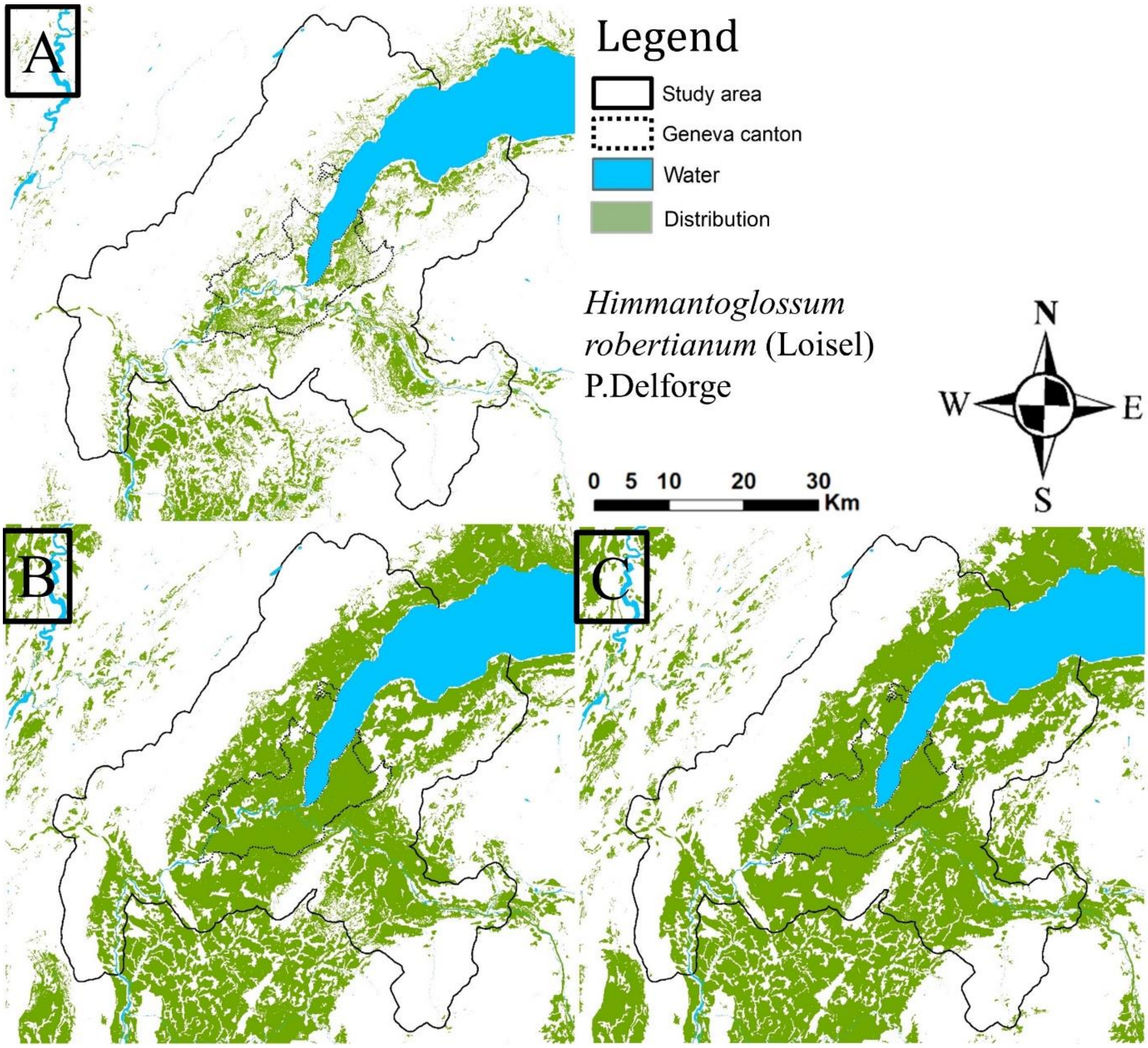

Figure 3. Evolution of the predicted distribution of Himmantoglossum robertianum (Loisel.) P. Delforge (Orchidaceae)*, a naturally arrived Mediterranean species observed the first time in Geneva in 2007, for current time (A), optimistic scenarios in 2050 (B) and pessimistic scenarios in 2050 (C) according to the biotopo x climate modelling method. A tremendous expansion of its distribution is expected in the next decades, with a potential colonization of the whole lowlands.*

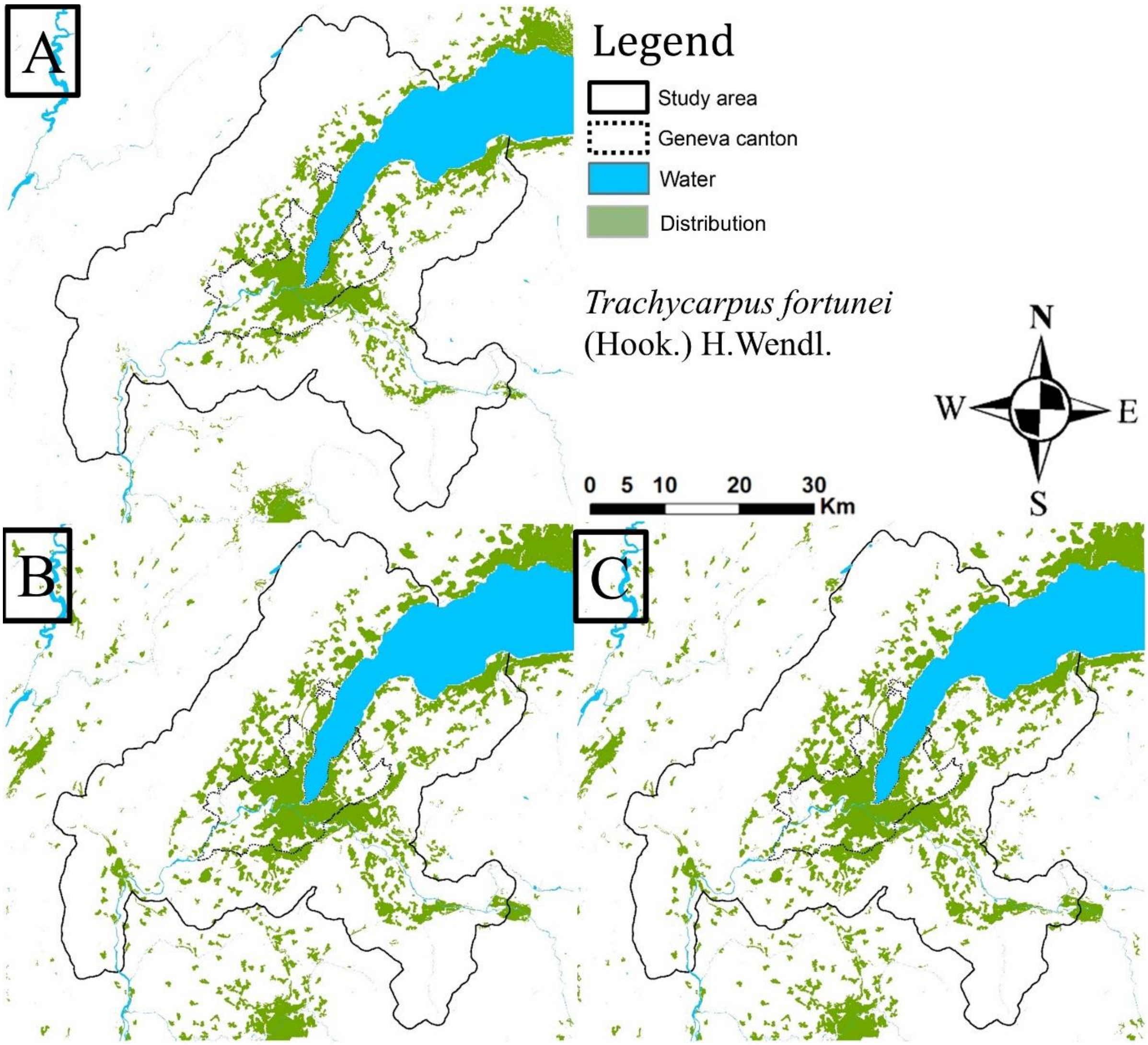

Figure 4. Evolution of the predicted distribution of Trachycarpus fortunei (Hook.) H.Wendl. (Arecaeae), *an introduced species black listed and considered as invasive, for current time (A), optimistic scenarios in 2050 (B) and pessimistic scenarios in 2050 (C) according to the biotopo x climate modelling method. An expansion of its distribution is expected in the next decades, especially in urban environment because it is mostly a planted species in urban gardens and green spaces.*

6.3.4. Species' vulnerability index

Previous research has shown that using many approaches and several indicators helps taking more effective decisions than relying on one single aspect or method, ultimately leading to more successful adaptation planning processes (Dawson *et al*., 2011; Rowland *et al*., 2011). In the Chapter 4 of this thesis, a vulnerability index to global changes has been developed using six indicators of future distributional changes, revealing that some species were more vulnerable than others and that pessimistic scenarios of climate change resulted in a higher vulnerability for these species. Using a vulnerability index to inform conservation decisions and management strategies, or to identify priority areas, has been widely discussed in the literature, although most of the articles were only assessing climatic shifts with no consideration of the changes of LULC (Cross *et al*., 2012; Crossman *et al*., 2012; Young *et al*., 2015). However, the consideration of LULC information drastically changes the associated prediction maps and thus represent an indispensable input to develop SDMs, especially on a small scale. LULC data also provide interesting information for conservation planning such as the importance and contribution of habitats in the modelling process. These ideas once again argue for the development of a precise LULC for each territory with the aim of understanding the distribution and evolution of its diversity. Thus, the vulnerability index developed in this work is well adapted to the regional context and more reliable than other methods used in the literature.

This index could be used to complement red list statuses to evaluate species vulnerability by local authorities in the study area. Although some ecological aspects are integrated in both indexes, such as species' fragmentation and distribution, they are assessed in divergent, yet complementing ways. Red list statuses evaluate current population health of species and past dynamics using punctual, field-based surveys and observations, as well as expert knowledge. On the other hand, the vulnerability index developed in this thesis evaluates potential future changes of species distributions using covering geographical information, statistical and spatial analyses. Thus, the vulnerability index could be particularly interesting for reinforcing current efforts regarding the most endangered and vulnerable species under future conditions. It could also be used to help local red list index assessments, especially for species located at the limit between two statuses. The assessment of species vulnerability to global changes represents an essential asset when used to take rapid proactive conservation measures.

6.4. Insights about biodiversity conservation

6.4.1. Systematic conservation planning

Meeting the increasing needs and desires of human societies without damaging natural systems and reducing biodiversity levels represent one of the greatest challenges facing humanity, especially when the good functioning of our societies is directly threatened by climate change (IPCC, 2021, 2022a, 2022b). This context suggests that we need to consider the natural world together with societal development in our Systematic Conservation Planning (SCP) in order to implement reliable long-term protected areas and understand the dynamics in play. Climate change also represents a major challenge in conservation biology because of the expected shift of species distributions and therefore a potential decrease of conservation areas effectiveness in the near future. Some authors even suggested the creation of temporary and dynamic conservation areas (CA) to answer critical needs, especially for migrating animal species, or achieve specific objectives not reach by the traditional permanent CA approach (D'Aloia *et al*., 2019).

There are still many areas on the planet with low anthropogenic impacts, which may be as much as 56% of the terrestrial surface minus permanent ice, as found by Jacobson *et al*., (2019). Although they are not homogeneously distributed among biomes and are highly fragmented, they still represent a great reservoir of wilderness and potential new areas to conserve. Evaluating the quality of the remaining (semi-)natural habitats is essential to optimize and expand CA, and prioritization approaches represent a great asset in SCP. Projecting priority areas under future climatic conditions has been widely done to test the potential shift of CA, identify potential ecological actions (restoration, protection), set spatial and temporal protection priorities or test the uncertainties and trade-offs between several options (Reside *et al*., 2018). However, the projections mostly focus on the distributions of a few groups of species and more overlooked taxa should be considered, as well as other features of biological diversity, to build a resilient and reliable conservation network, especially in a context of global changes (Pollock *et al*., 2020). Furthermore, SCP globally lacks clarity around its theories, definitions and effectiveness (McIntosh *et al*., 2017). Effective conservation planning should use highly qualitative and representative input data (Arponen, 2012; Honeck* *et al*., 2020a; Loiselle *et al*., 2003; Velazco *et al*., 2020), set a realistic implementation of the CA in adequation with stakeholders' needs (Game *et al*., 2013; Pienkowski *et al*., 2021), and take into account uncertainties linked to the methods used (Margules & Pressey, 2000; Reside *et al*., 2018). The use of GI is, therefore, a particularly effective SCP because it encompasses many aspects of biodiversity, nature's contribution to people as well as the connectivity of the landscape (Honeck* *et al*., 2020a).

New conservation approaches are emerging and new theories show promising results. For example, the modern portfolio theory is based on the assessment of the benefits and estimated risks of an ensemble of assets, instead of assessing one feature at the time (Eaton *et al*., 2019; Sierra-Altamiranda *et al*., 2020). Artificial intelligence could be used to optimize trade-offs between biodiversity protection and economical loss (Silvestro *et al*., 2022) and ensures the integration of phylogenetic information into the design of conservation planning implementation has also been proposed (Carvalho *et al*., 2017). Other methods named Land System Science call for a better integration of social aspects to the use of SCP to enhance the legitimacy of conservation plans (Iwamura *et al*., 2018). These promising new approaches rely on the strong cooperation between the academic, conservation and decision-making worlds, which is an essential element in biodiversity conservation. SCP is, by definition, an interdisciplinary field and we would all benefit from increased assessments of on-the-ground implementation of conservation actions (Mair *et al*., 2018).

6.4.2. Rewilding anthropogenic systems

Evaluating the quality of the remaining (semi-)natural areas facing global changes has been widely discussed and is one of the main topics of this thesis. However, instead of relying on what is left of the natural areas to conserve species, other approaches advocate for increasing the quality of the anthropogenic matrix through lowering our impacts on biodiversity as well as re-naturing and rewilding our urban spaces. Indeed, increased natural surfaces together with a more sustainable management of semi-natural lands enable more species to inhabit these areas ensuring more ecological functions and ecosystem services (Balvanera et al., 2016; Felipe-Lucia & Comin, 2015; Maestre et al., 2012; Schwarz et al., 2017; Tilman & Downing, 1994; Tilman et al., 1996; Walker, 1992). Furthermore, the renaturation of the anthropogenic matrix would help species migrating through the urban environment to follow their optimal climatic conditions, ultimately participating in mitigating the effects of global changes on species. Indeed, the quality of natural areas outside protected lands is essential for the conservation of plant species (Espeland & Kettenring, 2018; Heywood, 2019).

The concept of rewilding has many definitions and incorporates a wide variety of transdisciplinary concepts related to the restoration of self-regulating ecosystems, and to the transformation of the relationships between humans and nature for an improved conservation of biodiversity (Carver *et al.*, 2021; Jørgensen, 2015; Lorimer *et al.*, 2015; Pereira & Navarro, 2015; Prior & Ward, 2016; Soulé & Terborgh, 1999). Rewilding recognizes that ecosystems are intrinsically dynamic and that focusing on the restoration of ecological functions, processes and interactions is fundamental to mitigate the anthropogenic effects of climate change and biodiversity loss (Carver *et al.*, 2021). Alongside ecological restoration objectives, rewilding also emphasizes the importance of people's perceptions and experiences of wilderness which are essential topics to understand and consider in a successful rewilding initiative (Perino *et al.*, 2019; Prior & Brady, 2017). A study done in Switzerland by Bauer *et al.*, (2009) has shown antithetical results regarding the willingness toward rewilding the Swiss landscape for local inhabitants, showing the multiple perceptions of Nature according to people's location, age or social status. While most of the studies are based on rewilding landscape, the applications of this concept to cities is quite new and is less widely discussed (Owens & Wolch, 2019). Rewilding might be seen as a potential adaptation tool in the context of global changes (Carroll & Noss, 2021) but, as mentioned in the previous section of this discussion, the degree to which we should intervene in natural processes is highly debated (Corlett, 2016b). Although rewilding brings a lot of exciting new questions about what we want the natural world to be, as a human being, and new paradigms for conservation biology, many of its assumptions are still debated (Corlett, 2016c).

It has been shown that rewilding urban spaces offers benefits to human health, biodiversity and food security as well as climate change mitigation (Evans, 2021). Some authors even proposed the hypothesis that a greater exposure to biodiverse habitats in the urban environment would contribute to the amelioration of the microbiome of the human body (Mills *et al.*, 2017). It would also help to recreate links between people and their environment, which could favour the recognition of wilderness as a cultural service. Indeed, if people have more frequent interactions with less intensively managed (semi-)natural habitats, they might value these ecosystems more, which in turns would greatly help the local biodiversity inducing a positive feedback loop. Therefore, we urgently need to reduce our detrimental impacts on nature and favour a massive rewilding of the anthropogenic land-use classes, even the core of the urban environment, in order to allow the access to wilderness to urban residents (Butt *et al.*, 2018; Kowarik, 2013, 2018; Müller *et al.*, 2018; Torres *et al.*, 2018). These ideas also relate to the debate of conservationists between land sparing and land sharing, especially for agricultural lands, demonstrating the limits of land sparing (Fischer *et al.*, 2011, 2013; Kremen, 2015; Loconto *et al.*, 2020) and ultimately raising questions about food security and food sovereignty (Perfecto *et al.*, 2009). Bringing back wilderness in cities and profoundly changing the agricultural systems would bring many benefits to humanity and biodiversity. The possibility to implement such wide scale changes are in the hands of decision-makers.

6.4.3. Outlooks for global biodiversity conservation

There are two extreme ways of seeing biodiversity conservation, one that lets the natural systems and functions build adaptive-capacities with low human interventions, and the second advocating for a massive human intervention to manage biodiversity, as developed in the previous section (Prober *et al.*, 2019). The less-interventionist approaches are criticized by the other side who argues that climate change velocity would not account for the adaptive-capacity of ecosystems, the ability of species to migrate or for the capacity of our societies to take rapid decisions, thus justifying a massive global intervention to keep the natural world in the same state that it is today by using assisted migration or genetic engineering of species (Burrows *et al.*, 2014; Dumroese *et al.*, 2015; Millar & Stephenson, 2015). However, these methods are still poorly supported in the scientific community and most examples only consider climatic predictors to predict future species distributions, or only focus on one specific habitat, such as forests. Although most of the examples might be hidden in the grey literature, there is also a limited amount of evidence demonstrating the effectiveness of interventionist approaches (Prober *et al.*, 2019). This suggests that they may be counter-productive and represent a misuse of economic resources that could have been directed towards to other conservation actions. This binarity demonstrates antagonistic views regarding the way of seeing nature and the trust accorded to the development of future technologies and innovation, supposedly that are able to repair the damage that has been done to the biosphere and climatic systems. The proposed solutions are mostly divergent and we might, ultimately, have to choose between one or the other. However, it appears highly unrealistic to maintain the natural world as it is today given the rate at which the ecosystems and the climate are changing (Gardner & Bullock, 2021; Stein *et al.*, 2013). Accepting the fact that the distribution of species will be altered, while enabling natural processes and species migration by lowering anthropogenic impacts and rewilding ecosystems would represent an interesting option for future conservation practices.

The close collaboration between academic researchers, conservation practitioners, on-the-ground naturalists, stakeholders and decision makers is key to ensuring effective conservation practices in the face of global changes (Guisan *et al.*, 2013; McSHEA, 2014; Sofaer *et al.*, 2019; Villero *et al.*, 2017; Zimmermann & Bugmann, 2008). A closer collaboration between countries is also essential at the global scale for a common framework to be created made up of different conservation approaches according to the context, and facilitating increased mutual financial support (Obura *et al.*, 2021). At the local scale, it is important to mention that people could also play a major role in conserving natural spaces and species (Chan *et al.*, 2016). The release and wide availability of the knowledge regarding the expected effects of global changes on species or biodiversity distributions would be highly beneficial for successful conservation planning. Raising awareness by communicating widely about these issues to the general public, or mobilizing people through citizen science initiatives are key features to reach ambitious conservation objectives (Iwamura *et al.*, 2018). Furthermore, this would help recreate a bond between people and their natural environment and territory.

It is difficult to solve the complex equation for conserving biodiversity, mitigating climate change effects on our societies, helping emerging countries to develop, keeping a sufficiently good level of life, having access to sufficient quantities and qualities of food, keeping the global economy on track and avoiding societal collapse (IPBES, 2019)(Fig. 5). In order to do that, we need to change the business-as-usual model we were following during the last century to adopt a more sober way of life of the occidental world, reducing our consumption of goods and energy, profoundly transforming our intensive agricultural systems and giving higher value to wilderness (Kareiva & Marvier, 2012). We need dramatic efforts and rapid changes, to implement transdisciplinary cross-cutting solutions involving all actors to bend the curve of biodiversity decline and require the adoption of precise global targets, inspired from the international climatic targets limiting global warming by a maximum of +2°C at the end of the century (Mace *et al.*, 2018). Until we collectively accept and implement such profound changes, there is no doubt biodiversity collapse will continue and probably even accelerate, due to changing climatic conditions.

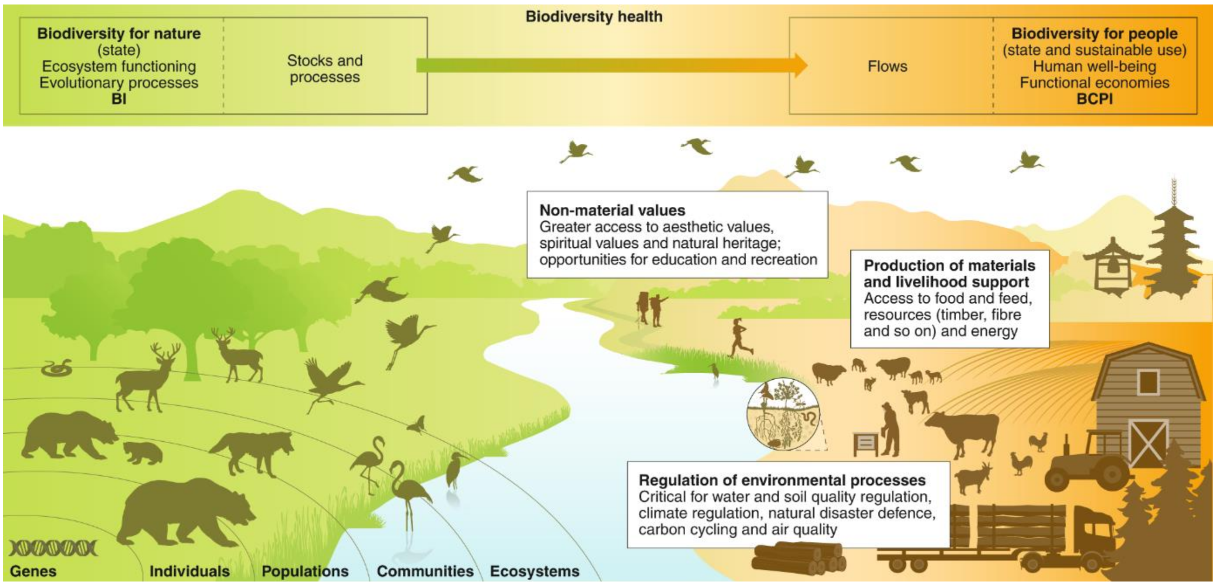

Figure 5. Representation of the "Biodiversity Health" by Soto-Navarro et al., (2021) representing the value of biodiversity for itself and its contributions to human well-being.

6.5. Conclusions and perspectives

6.5.1. Main contributions

The main results of this PhD are to be used by local authorities as inputs for local conservation actions as well as to better understand current and future distributions of species and biodiversity in the Grand Genève region, highlighting important trends regarding species vulnerability. The deliverables represent: 1) a reflexion on how to identify a GI in the territory; 2) the current distribution of 1692 species of plants and a few hundred animals which were not presented in this thesis; 3) a set of highly performant predictors with topographic, edaphic, climatic and biotic explanatory variables identified for the study area; 4) the projected distributions of 1692 species of plants for six different global circulation models, two scenarios of greenhouse gas emissions and one scenario of LULC change for 2050; 5) an assessment of the relevance of conservation areas for current and future conditions; 6) several aspects of the distribution of plant diversity such as the hotspots of specific richness and priority areas considering vulnerable species; 7) 30% of the most interesting areas for plant diversity distribution to be integrated in GI assessment, and finally; 8) a new vulnerability index to assess global changes for 1692 plant species that can be used as a complement to red list statuses.

This PhD has produced contributions to SDM methodology. It has shown that habitat predictors increased SDM performances and that peak performances were reached for a moderately complex set of habitats while overly complex or simplified sets of habitats lowered performances on average. This result has already been shown in other contexts, but rarely at such fine resolution and local scale. Remote sensing images were shown to be inadequate in replacing habitat predictors, at least when used raw, which was surprising because most of the literature deals with successful uses of such predictors, although they were rarely (if ever) explicitly compared to habitat ones in SDM. Finally, two methodologies were used and compared to forecast species distributions by 2050 using the combination of two different models of climatic and edaphic/topographic/biotic predictors considering LULC future changes, which have rarely been done in the literature. The implications for integrating biotic, topographic and edaphic predictors in future habitat suitability maps has been discussed.

Interesting contributions of this PhD were also linked to biological conservation. Indeed, a review of GI assessments, the proposition of a three-pillars approach and the identification of five levels to support a more qualitative GI implementation contribute in biodiversity conservation, nature's contributions to people and landscape's connectivity. The comparison of models' performances according to the ecological group of species showed that some groups were inherently more challenging to model due to their habitat preferences. A new method was designed to evaluate the vulnerability of plants to global changes in the study area. Results showed no difference according to the red list status of species but a clear trend regarding the vulnerability of native species. Several aspects of plant diversity were mapped for current and future scenarios with the aim of helping conservationists anticipate the evolution of diverse areas. Finally, highly interesting areas for plant diversity conservation were identified that can be integrated in the GI implementation and/or to expand current conservation areas. GI ability to conserve long-term biodiversity in changing conditions was assessed and compared to current conservation areas.

In summary, one of the major outputs of this PhD is the detailed description of the territory by the use of very fine scale predictors, habitat suitability maps for current and future climatic and biotic conditions, and the various aspects of plant diversity distributions derived from these, the combination of which is extremely rare when assessed all at the same location. In other words, this PhD participated in improving the knowledge of the environmental conditions in Grand Genève and their potential evolution in the near future which, I hope, might be of a great use for local decision makers and conservationists.

6.5.2. Perspectives and ameliorations

The future distributions of species were modelled with an adapted LULC map derived from CORINE Land Use because the existing local and highly precise LULC map could not be projected into the future because some habitats were missing for the calibration phase of LULC prediction. Thus, it would be highly interesting to modify the old LULC map in order to integrate missing habitats (wetlands) in order to be able to fit the LULC change models with the current LULC map of the Grand Genève in order to use more precise information in the models.

Further studies could be done regarding the effect of global changes on the ecological groups because interesting differences were found when looking at the vulnerability index of these groups. The vulnerability index would also benefit from a better display in order to have a quick access to the six indicators that have been calculated for each species, as done in Maggini *et al.*, (2014).

Further research should be done on the use of remotely sensed information as predictors because they might represent a very interesting option if habitat distribution data is missing. However, they have to be modified and not used raw to better match habitats distributions. It would be interesting to further study how their modification impacts models' performances and which adaptation produces the most interesting outputs in different contexts.

As developed in the Chapter 5, it would be interesting to map priority areas with varying weight for vulnerable species or to weights more endangered or rare species as modelled by Provost A. in his master thesis (Provost, 2021). Furthermore, it would be interesting to model the future distributions of such rare species using ensemble modelling to complement the ones already assessed and compare the associated distribution of hotspots and priority areas. Other aspects of biodiversity distribution would be interesting to map in the study area, such as the beta-diversity and other diversity indexes.

Finally, in order to fully describe the natural environment of the territory, it would be highly beneficial to run the same models but with data on animals. It is complicated task because it would necessitate a restart from the beginning of this project with the selection of interesting predictors that might be different for animal species. Indeed, while plants are motionless, animals have several movement patterns and might better rely on other variables than plants to survive, eat, and reproduce. It would probably require creating new predictors, such as access to water, the distance to urban environments or forests, light intensity, etc.

It might also be interesting to share the results from this PhD with a wider audience, for example creating an online database where the distribution maps of plants would be available at different time-steps and scenarios, as well as their vulnerability index and values for all the indicators measured. The same could be done for the distribution of hotspots and priority areas in order to better involve people in biodiversity conservation and share the knowledge about the distribution of plant diversity.

6.5.3. Concluding words

This project has been possible thanks to an efficient monitoring of the flora of Grand Genève as well as the availability of many data allowing models to fully describe the territory of the study area and its characteristics. Indeed, the numerous occurrences and associated information as well as the precise LULC map have all played a major role in the feasibility of such local scale, fine resolution assessment. Thus, the availability of such data and their sharing across institutions represents a great opportunity to better understand the evolution of biodiversity and should be further strengthened in the future. The close collaboration between conservationists, decision-makers, on-the-ground ecologists and the academic world is key to a successful conservation planning outlook, especially when dealing with complex questions such as the integration of potential impacts of global changes on species distributions. Furthermore, a wider collaboration between neighbouring countries is also essential in order to correctly respond to global issues that go beyond political borders. For example, allowing species migration and redefining the role and status of exotic species by increasing transboundary species monitoring and management, as well as a shared governance between them would be necessary (Scheffers & Pecl, 2019). Furthermore, using a common taxonomic reference would be beneficial because it is still missing today and species taxonomy has been a real struggle during this whole thesis.

The trends identified in this work are likely to intensify further after 2050 if no concrete, effective and urgent actions are taken globally to reduce our impacts on the natural and climatic systems. Land-sharing and rewilding are interesting options to mitigate the impenetrability of our cities, roads, crops and of all overly managed systems, to wild species. The communication of these issues to a general audience is also key in order to galvanize people to participate to conservation action plans and to increase their (re-)appropriation of the natural systems and the territory surrounding them. If we collectively want to limit global warming under +1.5°C by the end of the century, global greenhouse gas emissions have to peak at the latest in 2025 and only decrease over the next decades (IPCC, 2022b). We are currently far from being capable of reaching this objective, and even further away from being able to manage this decrease and thus need an urgent strengthening of our environmental policies and a clearer vision of a desirable future (IPCC, 2022b; Vittoz *et al.*, 2013). To conclude, it is our responsibility to reverse as much as being possible the current state of biodiversity and avoid a sixth mass extinction – or the first mass extermination of life on Earth created by a unique species as claimed by some activists – by deeply changing our ways of life and pressuring decision makers to do more, to do better and to do faster.

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APPENDICES

6.6. Appendix 3

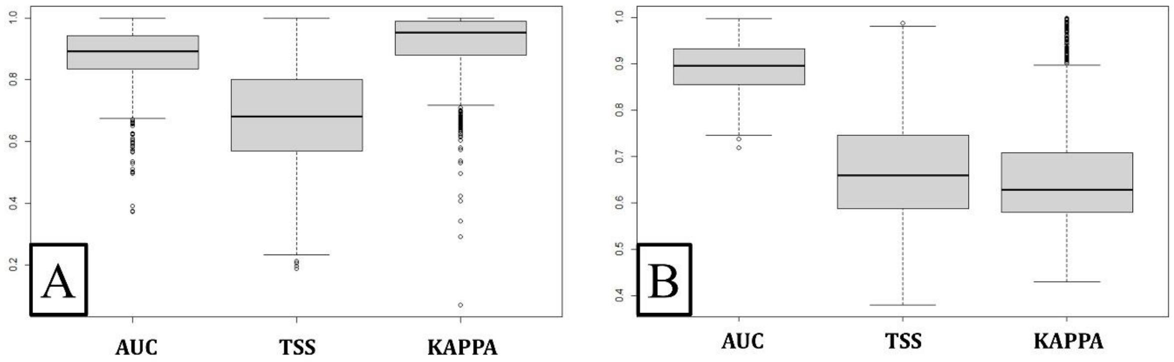

Figure 3A. Boxplot of evaluation metrics for A) biotopo models at local scale and B) climatic models at the European scale.

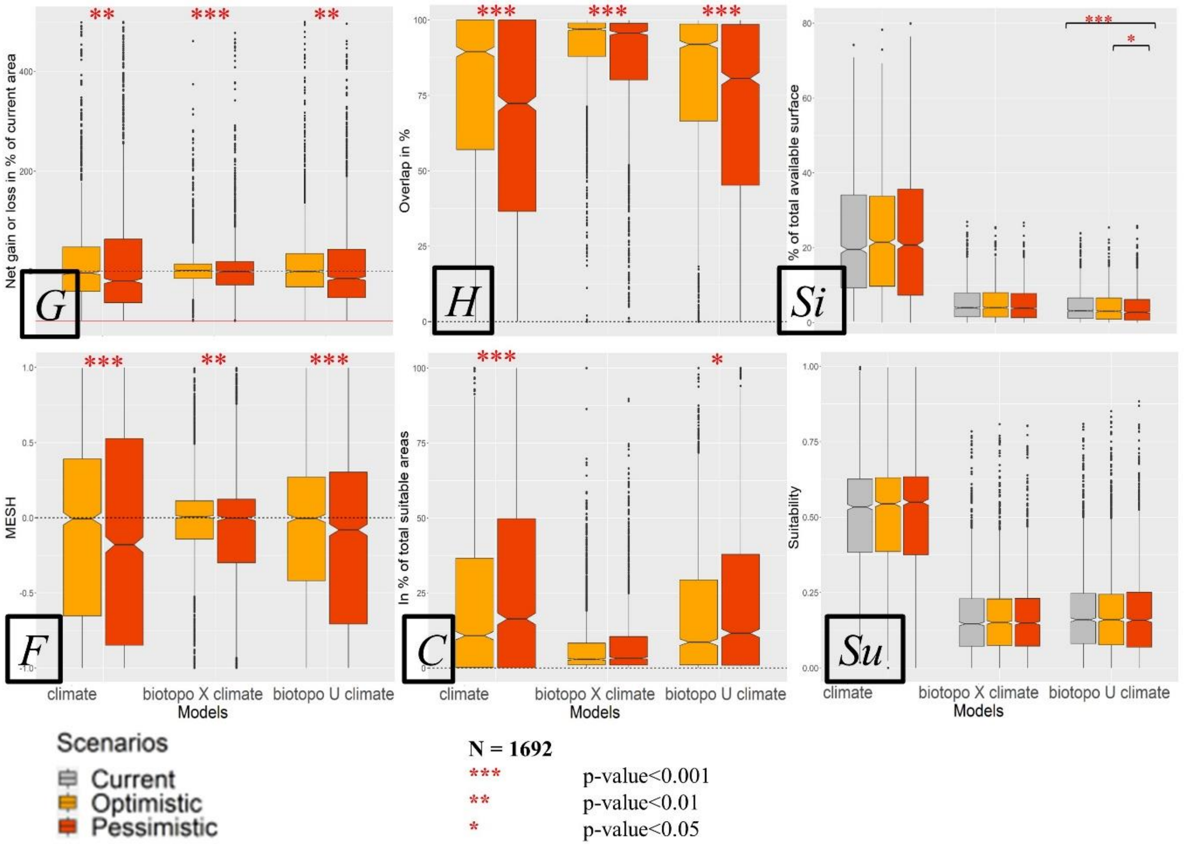

Figure 3B. Boxplots of all indicators' value for climatic, "biotopo x climate" and "biotopo U climate" predictions with the p-value score corresponding to a Wilcoxon mean test, according to the time-step considered. (G) Gain or loss of suitable surface in percentage of current suitable surface, the red line indicates -100% (loss all of its suitable surface), the dashed line indicates 0 (no change); (F) Mesh size rate corresponding (or habitat fragmentation), the dashed line indicates 0 (no change), below it the distributions are more fragmented in the future, above it they are more continuous than current; (H) Overlap between current and future suitable surfaces (habitat persistence), the dashed line represents 0 (no overlap) indicating that all suitable areas either shifted or disappeared; (C) Proportion of new suitable areas (colonisation potential), the dashed line indicates 0 (no new suitable areas in the future); (Si) Proportion of suitable surface occupied and (Su) average suitability of suitable areas.

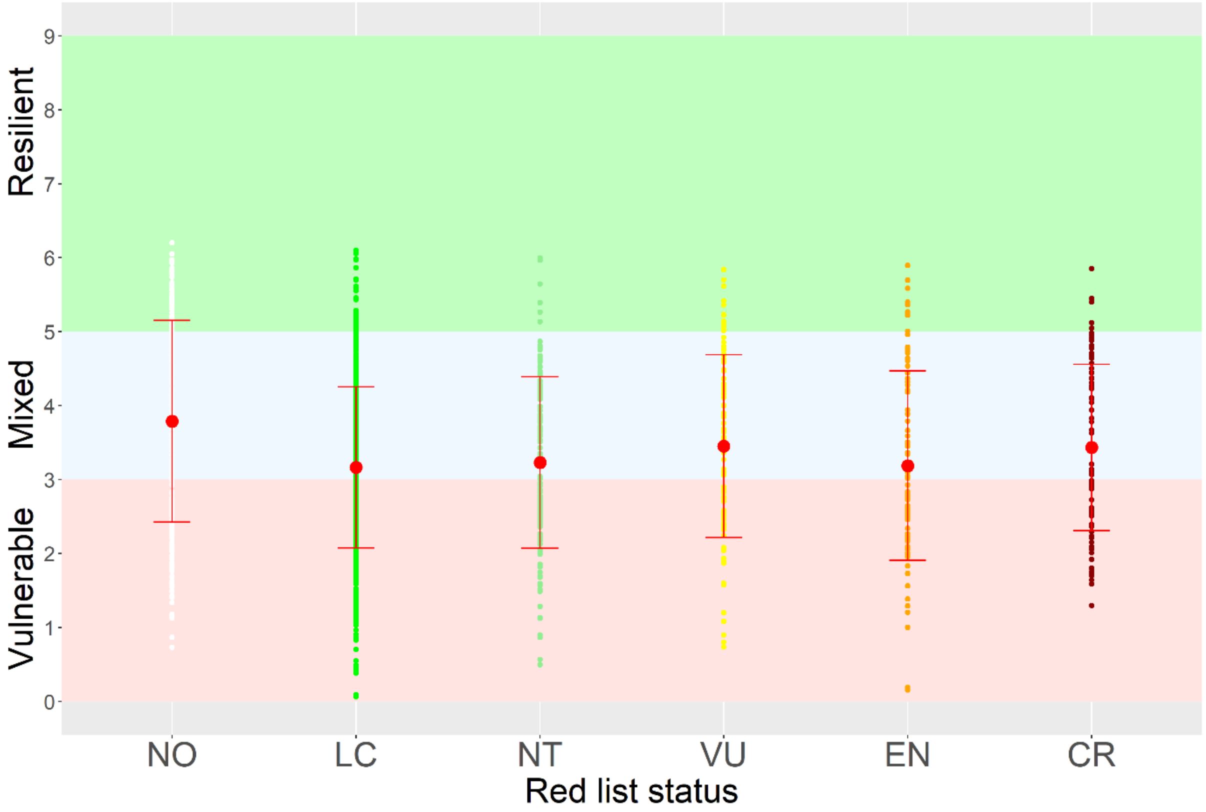

Figure 3C. Vulnerability of plant species to global changes according to their red list status for pessimistic scenarios. The upper green part of the figure represents values between five and nine which indicates that species located there are resilient to global changes, even benefiting from them. The central blue part represents values between three and five indicating mixed results with neutral, beneficial or detrimental impacts. The lower part in red indicates values between zero and three which signals that all measured indices are neutral or detrimental to species' distribution. Plants located in this range of the figure are vulnerable to global changes. A) Results for optimistic scenarios and B) for pessimistic scenarios.

Table 3A – Results of the suitable surface occupied (Si) according to the modelling method, the red list and native status. Curr = current; Opt = optimistic future scenario; Pess = pessimistic future scenario.

Available here: https://zenodo.org/record/6618908

Table 3B – Gain or loss of suitable surface (G) for all species according to the modelling method, the red list and native status, in km^2 and in percentage of current area. Opt = optimistic future scenario; Pess = pessimistic future scenario.

Available here: https://zenodo.org/record/6618908

Table 3C – Overlap between current and future suitable areas (Habitat persistence H) and proportion of new suitable area (Colonisation potential C) for all species according to the modelling method, the red list and native status. Opt = optimistic future scenario; Pess = pessimistic future scenario.

Available here: https://zenodo.org/record/6618908

Table 3D – Values of the six indicators and the vulnerability index. Opt = optimistic future scenario; Pess = pessimistic future scenario.

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6.7. Appendix 4

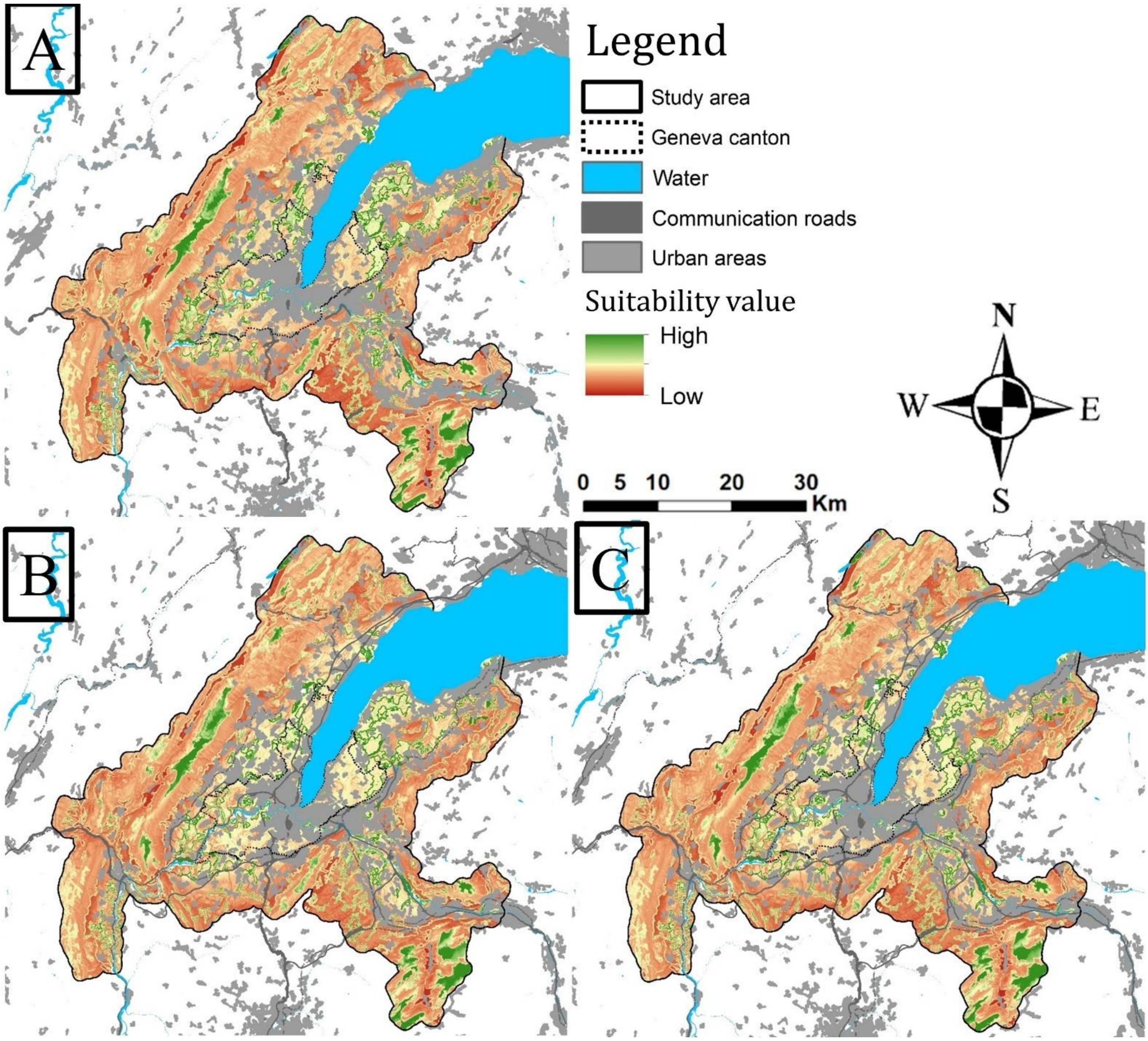

Figure 4A. Specific richness maps showing the distribution of the global suitability in the territory for the three time-steps: A) current, B) future optimistic and C) future pessimistic. We can see that the areas with the highest suitability value mostly remain the same across the time-steps.

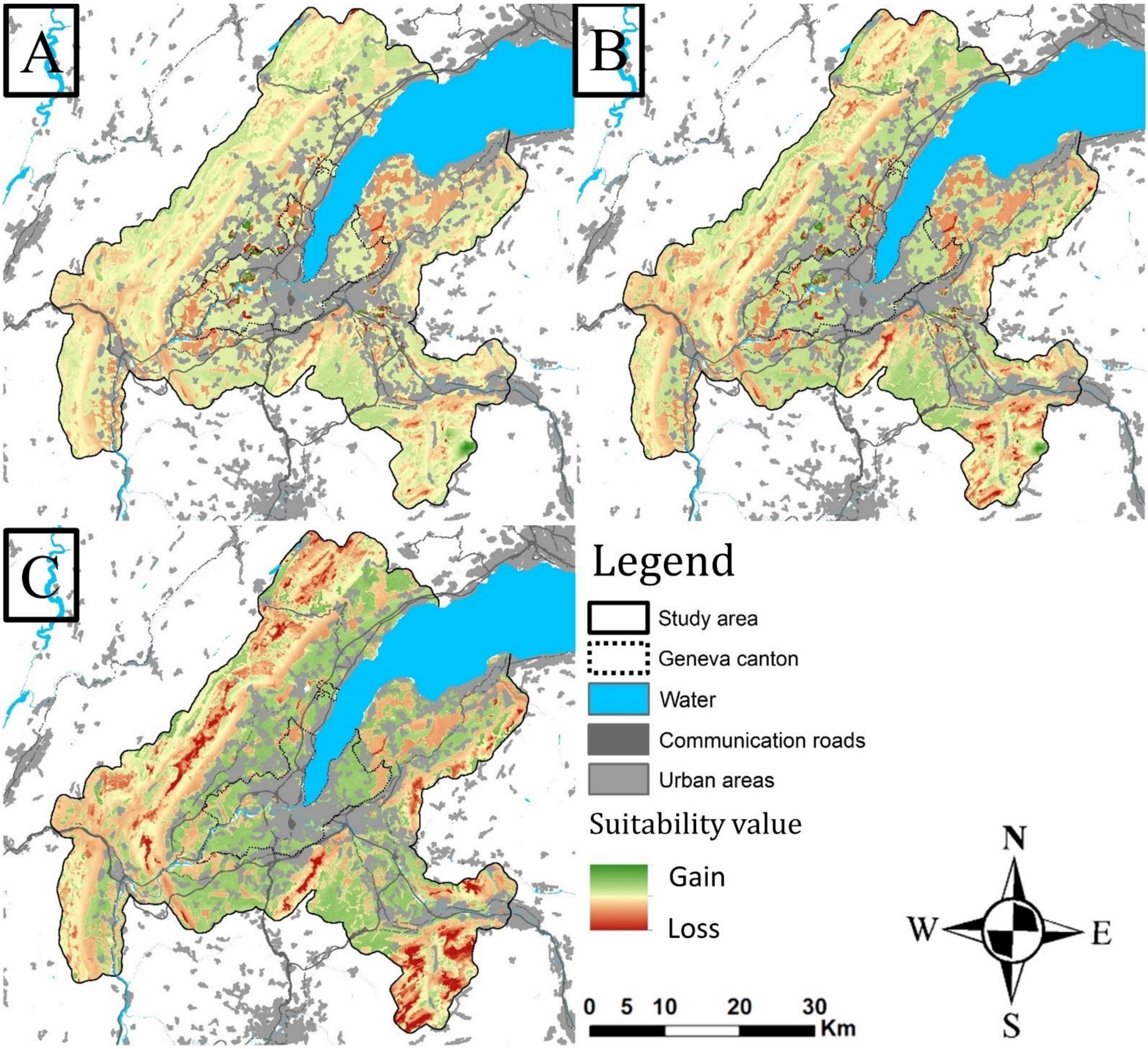

Figure 4B. Suitability change of specific richness map between current and optimistic future (A), current and pessimistic future (B) and the two future scenarios (C).

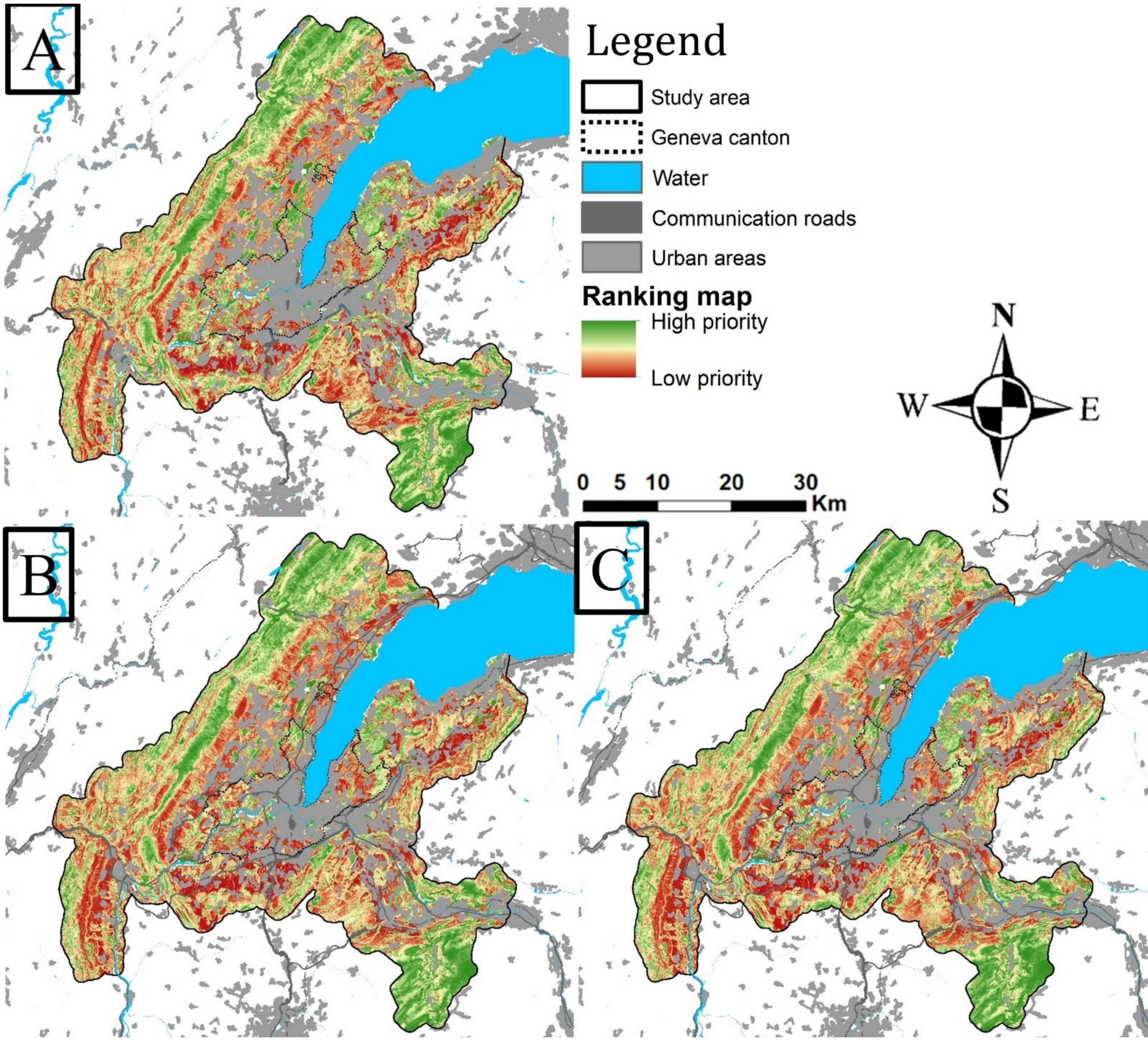

Figure 4C. Prioritization maps showing pixels' ranking according to their conservation priority for the three time-steps: A) current, B) future optimistic and C) future pessimistic. We can see that the areas with the highest priority mostly remain the same across the time-steps.

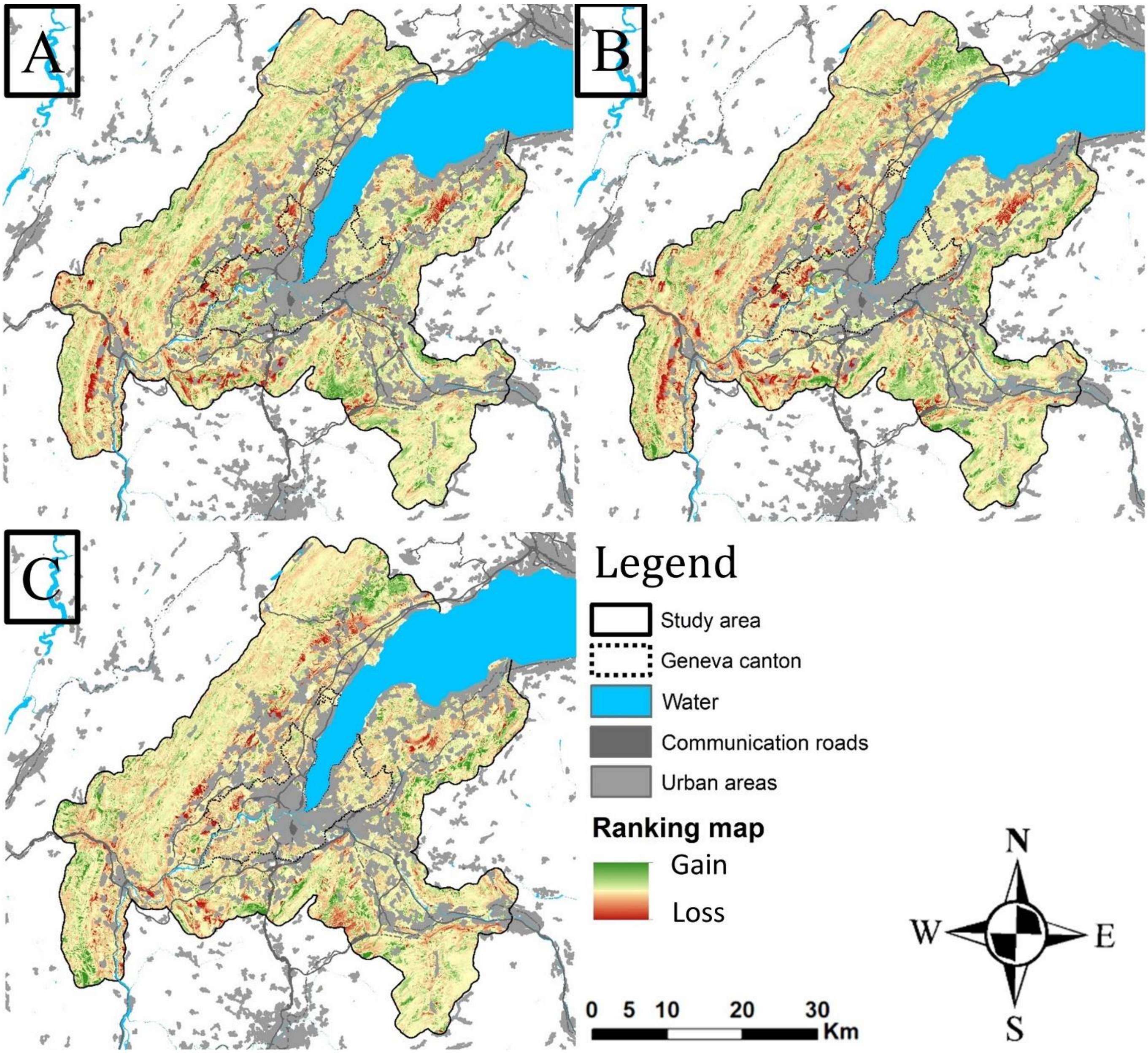

Figure 4D. Ranking change for the priority areas between current and optimistic future results (A), current and pessimistic future results (B) and the two future scenarios' results (C).

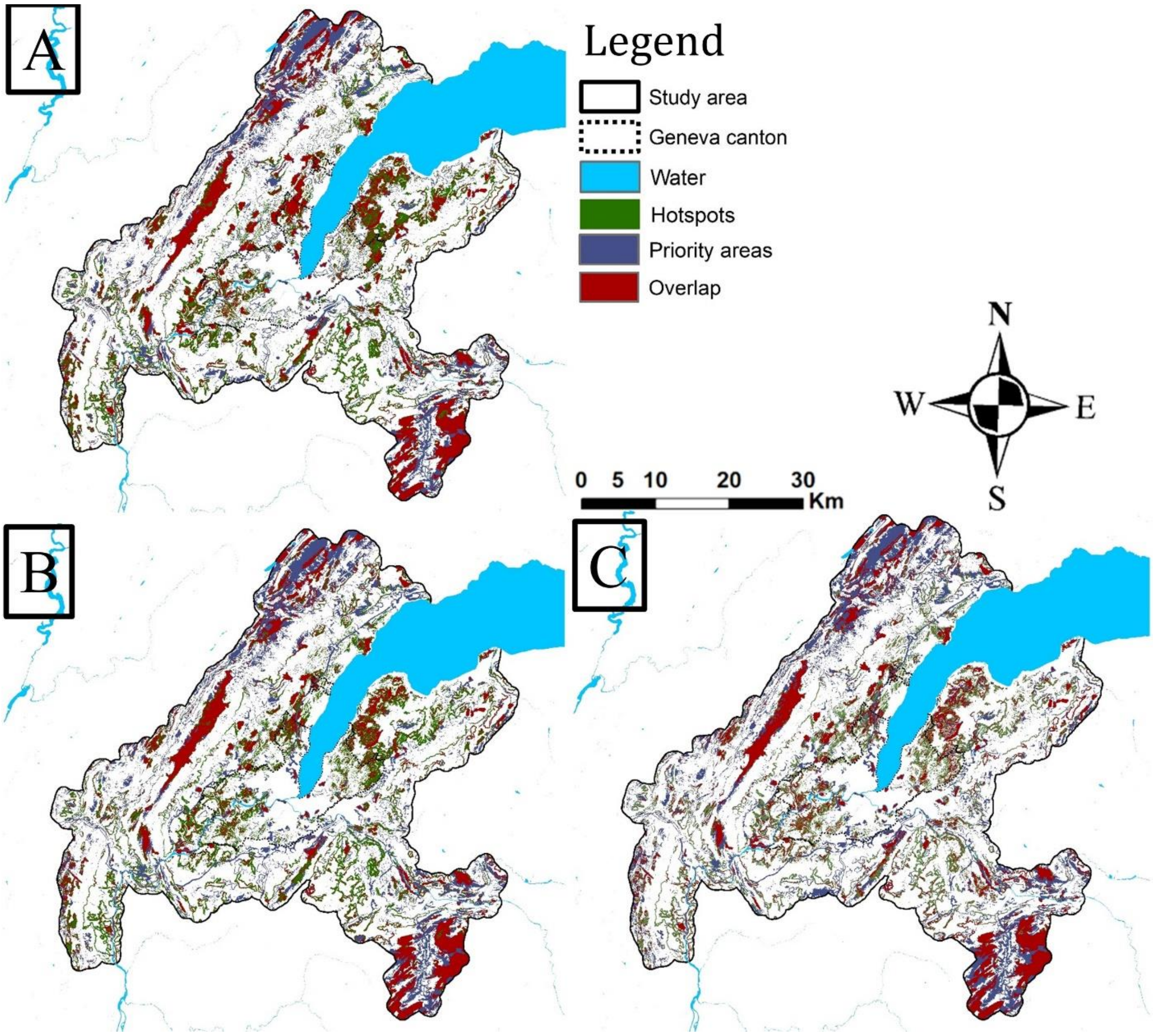

Figure 4E. Distribution of hotspots, priority areas and the overlap between them for current time (A), optimistic future scenarios (B), pessimistic future scenarios (C).

Table 4A – Proportion of species distribution integrated into conservation areas.

Available here: https://zenodo.org/record/6618908

Table 4B – Ability of the biodiversity pillar to include species' suitable surface

Available here: https://zenodo.org/record/6618908