



universität  
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# DISSERTATION / DOCTORAL THESIS

Titel der Dissertation /Title of the Doctoral Thesis

„Joint effects of climate change and human agency  
on future plant distribution“

verfasst von / submitted by

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

Doctor of Philosophy (PhD)

Wien, 2019 / Vienna 2019

Studienkennzahl lt. Studienblatt /  
degree programme code as it appears on the student  
record sheet:

A 794 685 437

Dissertationsgebiet lt. Studienblatt /  
field of study as it appears on the student record sheet:

Biologie

Betreut von / Supervisor:

Mag. Dr. Franz Essl, Privatdoz.



## MILCZENIE ROŚLIN

Jednostronna znajomość między mną a wami  
rozwija się nie najgorzej.

Wiem co listek, co płatek, kłos, szyszka, łodyga,  
i co się z wami dzieje w kwietniu, a co w grudniu.

Chociaż moja ciekawość jest bez wzajemności,  
nad niektórymi schylam się specjalnie,  
a ku niektórym z was zadzieram głowę.

Macie u mnie imiona:  
klon, łopian, przyłuszczka,  
wrzos, jałowiec, jemięta, niezapominajka,  
a ja u was żadnego.

Podróż nasza jest wspólna.  
W czasie wspólnych podróży rozmawia się przecież,  
wymienia się uwagi choćby o pogodzie,  
albo o stacjach mijanych w rozpędzie.

Nie brakłoby tematów, bo łączy nas wiele.  
Ta sama gwiazda trzyma nas w zasięgu.  
Rzucamy cienie na tych samych prawach.  
Próbujemy coś wiedzieć, każde na swój sposób,  
a to, czego nie wiemy, to też podobieństwo.

Objaśnię jak potrafię, tylko zapytajcie:  
co to takiego oglądać oczami,  
po co serce mi bije  
i czemu moje ciało nie zakorzenione.

Ale jak odpowiadać na niestawiane pytania,  
jeśli w dodatku jest się kimś  
tak bardzo dla was nikim.

Porośla, zagajniki, łąki i szuwary –  
wszystko, co do was mówię, to monolog,  
i nie wy go słuchacie.

Rozmowa z wami konieczna jest i niemożliwa.  
Pilna w życiu pospiesznym  
i odłożona na nigdy.

-----  
*Wisława Szymborska*

## THE SILENCE OF PLANTS

Our one-sided acquaintance  
grows quite nicely.

I know what a leaf, petal, ear, cone, stalk is,  
what April and December do to you.

Although my curiosity is not reciprocal,  
I specially stoop over some of you,  
and crane my neck for others.

I've got a list of names for you:  
maple, burdock, hepatica,  
mistletoe, heath, juniper, forget-me-not,  
but you have none for me.

We're travelling together.  
But fellow passengers usually chat,  
exchange remarks at least about the weather,  
or about the stations rushing past.

We wouldn't lack for topics: we've got a lot in common.  
The same star keeps us in its reach.  
We cast shadows based on the same laws.  
We try to understand things, each in our own way,  
and what we don't know brings us closer too.

I'll explain as best as I can, just ask me:  
what seeing with two eyes is like,  
what my heart beats for,  
and why my body isn't rooted down.

But how to answer unasked questions,  
while being furthermore a being so totally  
a nobody to you.

Undergrowth, coppices, meadows, rushes –  
everything I tell you is a monologue,  
and it's not you who listens.

Talking with you is essential and impossible.  
Urgent in this hurried life  
and postponed to never.

-----

*Wisława Szymborska*  
*(translated by Clare Cavanagh*  
*and Stanisław Barańczak)*

# Acknowledgements

First of all, I thank my supervisor Franz Essl for his continued (and always quick!) support!

Many thanks to my wonderful colleagues at the Division of Conservation Biology, Vegetation and Landscape Ecology at the University of Vienna – for the absolutely great, amicable working atmosphere.

Special thanks go to Michael Kuttner, Stefan Kapeller and Florian Danzinger for being such great officemates; to Andreas Gattringer for all his help and support; and most of all to Johannes Wessely for being the best R mentor I could wish for and for all the fun we had.

I want to thank my parents and my grandparents – also for their support but first and foremost for all those summers by the Baltic Sea which have shaped profoundly who I became.

To my friends, for so many different things – to the other four ‘Spice Girls’ (Lena, Julia, Karin, Sylvia) for being what I call my ‘Viennese family’; to Julia – for our damn good talks and for so many beautiful holidays within the last years; to Sylvia for being my sauna buddy; and to Lena for being my sports buddy; to Johanna for our ‘primordial soup’ weekends; to Schlencho, Lena, Esa and Ina for sharing a huge passion with me (books); and to Stichi and Naida for sharing another (hospice work); to Letti for being like an older brother to me; to Marie – for our nourishing (in a double sense) cake/tea/cooking sessions; to Judl – because it just doesn’t feel like we are separated by many, many kilometres; to Lili – for sharing the weirdest beginning of a friendship (we met at a funeral) and for all the comfort thereafter; and, of course, to Luki – for all the closeness that is so dear to me – you are deeply missed.

To Konsti and Jonas for making me feel welcome.

And, last but not least, to Stefan, my husband, my human home – simply for being the most generous, loveable and loving person. It’s cheesy but it’s true!

# Table of Contents

<b>Abstract</b> .....	<b>8</b>
<b>Preamble</b> .....	<b>9</b>
Setting the Scene: The Anthropocene.....	9
Climate change effects on biodiversity.....	9
Effects of (two aspects of) human agency on biodiversity.....	10
Land use.....	10
Exchange of non-native species.....	10
Combined effects of climate change and human agency.....	11
Modelling species distributions.....	12
<b>Thesis overview</b> .....	<b>13</b>
Part 1: Naturalization and hybridization risk from garden plants under climate change.....	14
Chapter 1: Naturalization risk from garden plants under climate change.....	14
Chapter 2: Hybridization risk from garden plants under climate change.....	15
Part 2: Climate change and land-use change effects on future plant distribution.....	15
Chapter 3: Better integration of land use into models of biodiversity.....	16
Chapter 4: Climate change and land-use change impacts on regional plant diversity.....	16
<b>Concluding Discussion</b> .....	<b>17</b>
Climate change effects on species distribution.....	17
Effects of human agency on species distribution.....	18
Gain or loss? A matter of origin and scale.....	19
Conclusions.....	20
<b>References</b> .....	<b>21</b>
<b>Chapter 1: Climate change will increase the naturalization risk from garden plants in Europe</b> .....	<b>27</b>
Abstract.....	28
Introduction.....	29
Methods.....	29
Results.....	31
Discussion.....	32
Supporting Information.....	39

<b>Chapter 2: Will climate change increase hybridization risk between potential plant invaders and their congeners in Europe? .....</b>	<b>67</b>
Abstract .....	68
Introduction.....	69
Methods.....	70
Results .....	71
Discussion .....	72
Conclusion.....	75
Supporting Information .....	78
<b>Chapter 3: Towards better integration of land use into models of species distribution and diversity .....</b>	<b>91</b>
Introduction.....	93
Three facets of land use to inform biodiversity models .....	94
Issues of scale: Interacting dimensions again .....	98
Do we have the data to move forward?.....	101
Conclusions.....	103
Supporting Information .....	113
<b>Chapter 4: A socio-ecological model for predicting impacts of land-use and climate change on regional plant diversity .....</b>	<b>123</b>
Abstract .....	124
Introduction.....	125
Methods.....	127
Results .....	133
Discussion .....	136
Supporting Information .....	153
<b>Abstract in German.....</b>	<b>181</b>
<b>Publication Record .....</b>	<b>182</b>

## **Abstract**

Climate change, land-use change and the exchange of non-native species threaten biodiversity in multiple, often interacting ways. These joint effects represent one of the largest uncertainties in projections of future biodiversity change. In my doctoral thesis, I investigate the potential responses of plant distribution patterns to combinations of these three components of 21<sup>st</sup> century global change at different spatio-temporal scales applying a species distribution modelling approach. First, I focus on the effects of climate change on the naturalization and hybridization potential of a pool of ornamental alien species in Europe for the second half of the century, taking into account current land-use patterns. Second, I examine the combined effects of climate change and land-use change on future plant distribution. Therefore, I begin with outlining the challenges in integrating land use into models of species distribution and diversity. Then I investigate the combined effects of these two drivers on the regional species pool of an area located in Central Austria for the mid of the century.

I found that hotspots of naturalization risk from ornamental alien species will increase considerably under climate change. Thus, the risk of negative impacts from invasion by these plants will also grow in the future. However, hybridization risk is predicted to remain constant.

Concerning land use, important steps towards a better, more systematic integration of this driver into predictive biodiversity models include an appropriate representation of the complexity of land use – biodiversity relationships and an improvement in data availability. For my study region in Central Europe and the time horizon considered, my model suggests a strong effect of future climate on regional plant range sizes, in contrast to the relatively small effects of land use. Nevertheless, including land use scenarios into biodiversity forecasts is important, as the relative effects of climate and land use change may vary considerably across regions.

My results demonstrate the importance of including several global change components in predictive species modelling. In fact, only by treating changes in species distributions as multi-causal processes will predictions approximate reality and become useful for guiding management and conservation efforts.

## Preamble

### **Setting the scene: The Anthropocene**

Driven by the large impact of human activities, the world is undergoing rapid changes. Mankind has even opened a new epoch in Earth's history – the Anthropocene (Crutzen & Stoemer, 2000; Crutzen, 2002), based on unprecedentedly fast socio-economic changes such as human population growth, economic growth, technical progress as well as changes in lifestyle and diets (Steffen *et al.*, 2015). These developments have massively accelerated, especially since the mid-20<sup>th</sup> century ("Great Acceleration", Steffen *et al.*, 2015) and they increasingly impact negatively on ecosystems and their biodiversity (Rockström *et al.*, 2009; Butchart *et al.*, 2010; Devictor *et al.*, 2012). In fact, we are experiencing a major biodiversity crisis and now face the risk of a sixth – human-mediated – mass extinction (Barnosky *et al.*, 2011; Ceballos *et al.*, 2015). Among the man-made threats to biodiversity land-use change, climate change and the exchange of non-native species are among the most prevalent ones (Sala *et al.*, 2000; Secretariat of the Convention on Biological Diversity, 2006; Maxwell *et al.*, 2016) and they are predicted to become even more pronounced in the future.

### **Climate change effects on biodiversity**

Global mean temperature has increased by c. 0.8°C since the beginning of the 20<sup>th</sup> century, accompanied by rising sea levels, altered seasonality and changes in extreme events (Diffenbaugh & Field, 2013) and these trends are expected to continue in the future. Long-term emission scenarios are designed to provide a range of plausible emission trajectories for the decades to come (Moss *et al.*, 2010; van Vuuren *et al.*, 2010). The IPCC process, for example, has resulted in four generations of emission scenarios, the Representative Concentration Pathways (RCPs) being the most recent one (Moss *et al.*, 2010). Even the weakest of these scenarios (RCP2.6) predicts global mean temperatures to further increase to 1.5°C (IPCC, 2013). In fact, the latest carbon dioxide emissions continue to track the high end of these emission scenarios (RCP8.5), making it even less likely that global warming will stay below 2°C as compared to the pre-industrial standard (Peters *et al.*, 2012).

The distributions of both individual species and species richness is known to strongly relate to climate (von Humboldt & Bonpland, 1807), leading to a sensitivity of plants, animals, and ecosystems to climate and climate-related processes (Ackerly *et al.*, 2010; Sunday *et al.*, 2011; Sunday *et al.*, 2012). Climate change therefore has already led to numerous shifts in species distributions and abundances (Parmesan & Yohe, 2003; Root

*et al.*, 2003) and to physiological and phenological responses of species (Hughes, 2000; Bellard *et al.*, 2012). It is expected that impacts of climate change on biodiversity will further rise in the future as the magnitude of climate change increases (Thuiller *et al.*, 2005).

### **Effects of (two aspects of) human agency on biodiversity**

#### **- Land use**

Land use has played a crucial role in the development of human societies for more than 10,000 years. However, in recent decades land use has globally entered a period of profound transformation (Erb *et al.*, 2016) that is historically unique in terms of velocity and transformative dimension (Klein Goldewijk *et al.*, 2011; Ellis *et al.*, 2013).

Human land uses act similarly as other ecological disturbance regimes (*sensu* Pickett & White, 1985) and may cause population declines and even species extinctions (Pimm & Raven, 2000; Sala *et al.*, 2000). The consequences of land use on the environment are manifold (wide disturbance gradient), including alteration of biophysical and biogeochemical properties (Erb *et al.*, 2017) as well as impacts on biota via altered or new pressures. Land-use practices range from subtle modifications of ecosystem properties (often denoted as *land modification*) to large-scale transformations (e.g. large-scale *land-cover conversion* such as tropical deforestation, Erb *et al.*, 2017). Changes in land use also modify the spatial arrangement of habitats and thus may affect permeability and connectivity of remaining habitats (Oliver & Morecroft, 2014). These changes have become widespread and meanwhile affect approximately three-quarters of the earth's ice-free land mass (Erb *et al.*, 2007; Ellis *et al.*, 2013). Most likely the extent and intensity of land use will rise in the decades to come (Foley *et al.*, 2011; Tilman *et al.*, 2011; Erb *et al.*, 2016).

#### **- Exchange of non-native species**

While humans have transported and traded plant and animal species for millennia, there were two notable peak stages in the past: the first at the end of the Middle Ages and the second at the beginning of the Industrial Revolution (Hulme, 2009). Yet, due to globalization, recent decades show the highest number of exchanges in alien plant and animal species (Perrings *et al.*, 2005; Hulme, 2009; Hulme, 2011). In fact, as a result of human activity, 3.9 % of all vascular plant species (i.e. approx. the size of the native European flora) have become naturalized somewhere on the globe (van Kleunen *et al.*, 2015).

Alien species are taxa that are introduced outside their natural range either intentionally

or unintentionally by human agency (IUCN, 2000) and can become invasive. Biological invasions can be conceptualized as a series of consecutive stages – from transport out of the native range to introduction of the alien species into a new region, its naturalization or establishment of self-sustaining populations, and its spread across the introduced range (Blackburn *et al.*, 2011). According to this concept, invasive species therefore are species that have rapidly spread into multiple sites across a large area. Specific barriers to survival, establishment and spread have to be overcome by an alien species to pass on to the next stage. However, the first introduction of a species to a new territory and the start of its rapid regional population growth, i.e. its transformation to a problematic invader, are often separated by considerable time lags (Essl *et al.*, 2011). As a consequence, the currently accumulated regional pools of non-native organisms might contain a number of species which have not even managed to naturalize yet but may become problematic invaders years or even decades into the future.

The intense human-mediated exchange of species leads to the homogenization of species assemblages (Winter *et al.*, 2009; Capinha *et al.*, 2015). Furthermore, the biological invasions that have resulted from the reshuffling of floras and faunas are considered a major ecological problem (Lambertini *et al.*, 2011; Maxwell *et al.*, 2016). Their impacts include, for example, decreases in local native plant species diversity and abundance or changes to basic ecosystem functions such as nutrient cycling (Vilà *et al.*, 2011). Furthermore, biological invasions have already generated substantial economic costs (Kettunen *et al.*, 2009; Perrings, 2011) and are also widely expected to become an even greater problem in the future (Walther *et al.*, 2009; Bradley *et al.*, 2012; Seebens *et al.*, 2017).

### **Combined effects of climate change and human agency**

One of the most pressing questions in ecology and nature conservation is how the simultaneous exposure of ecosystems to multiple global change components will impact future species distributions and biodiversity (Sirami *et al.*, 2017). Effects of these components may be additive or interactive. For example, climate change may influence the rate and extent of biological invasions as well as the spread and eventual distribution of non-native species. In fact, global warming has already enabled many alien species to expand or shift their ranges into new regions (Parmesan & Yohe, 2003; Walther *et al.*, 2009; Chen *et al.*, 2011). Nevertheless, it is still common practice to analyse and forecast the effects of climate change and the exchange of non-native species on ecosystems and biodiversity separately (Walther *et al.*, 2009; O'Donnell *et al.*, 2012). Similarly, climate change may force land owners to re-consider their land use decisions. This will probably involve changes to land management practices, geographic shifts in

land use patterns and the choice of new crop varieties (e.g. see Intergovernmental Panel on Climate Change, 2005). Such changes in land-use practices may have additional effects on local and regional species composition and abundance. Yet, the combined effects of climate change and land use change on biodiversity are notoriously understudied (de Chazal & Rounsevell, 2009; Titeux *et al.*, 2016).

In summary, the ecological consequences of multiple, simultaneously acting global change components on ecosystems, their species composition and species richness as well as their functions are still poorly understood. Strengthening research on such additive or interactive impacts should hence become a priority. In my thesis, I will particularly focus on how climate change will interact with and accelerate threats from exchange of non-native species and land use-change (Brook *et al.*, 2008).

### **Modelling species distributions**

Within the recent decades, the ability to model and predict species distributions has improved due to major methodical and technological advances, especially the increase in computing power. As a result, interest in species distribution models has grown dramatically during the first decades of the 21<sup>st</sup> century (Guisan *et al.*, 2017). In fact, SDMs have become popular in different fields of ecological research like biogeography and macroecology (Guisan & Rahbek, 2011), conservation biology (Guisan *et al.*, 2013), and global change biology (Dirnböck *et al.*, 2003; Thuiller *et al.*, 2005; Engler *et al.*, 2011) during the last 20 years.

Species distribution modelling (Guisan & Thuiller, 2005) is a statistical modelling technique that relates data on the incidence (or abundance) of species to a suite of, mostly abiotic, site conditions by means of a variety of different algorithms (e.g. Thuiller *et al.*, 2009). The calibrated statistical functions are then applied for spatial exploration, i.e. to predict the occurrence probability (or abundance) of species at sites which have not been surveyed yet, but where information on site conditions is available.

Species distribution models are based on the concept of ecological niches (Wiens *et al.*, 2009), for which the foundations were laid by Grinnell in 1917 (Wiens *et al.*, 2009; Guisan *et al.*, 2017). The concept was further developed by many (see Chase & Leibold, 2003), but it was Hutchinson (1957), who distinguished fundamental and realized niches. While the fundamental niche represents the envelope of environmental conditions within which a species can maintain a viable population in the absence of biotic interactions, the realized niche represents a subset of the fundamental niche constrained by biotic interactions and dispersal (Guisan *et al.*, 2017). As SDMs correlate species occurrences at a certain point with the environmental conditions at this point, the model results hence

describe the realized niche of the species. However, species interactions are only considered non-explicitly in SDMs, making it impossible to segregate them from the effects of environmental variables (Thuiller *et al.*, 2008). Furthermore, they neglect demographic and dispersal processes that are crucial to range shifts (Thuiller *et al.*, 2008; Wiens *et al.*, 2009; Dullinger *et al.*, 2012). However, SDMs also have several advantages: they are based on well-known and tested statistical methods which are implemented in standard statistical software (e.g. Thuiller *et al.*, 2009), and parametrization data are rather easily available both from steadily growing databases on species occurrences and increasingly detailed maps of environmental variables including climatic, topographical, land cover and soil parameters. SDMs hence still represent valuable tools to assess the effects of environmental changes on species pools (Dirnböck *et al.*, 2011; Guisan & Rahbek, 2011; Thuiller *et al.*, 2011; Araújo & Peterson, 2012), i.e. on the number and identity of species that may potentially thrive in a certain area under altered environmental conditions, particularly if applied at an appropriate spatial scale (Randin *et al.*, 2009).

## **Thesis overview**

In my doctoral thesis, I investigate the potential responses of plant distribution patterns to three components of 21<sup>st</sup> century global change at different spatio-temporal scales. The three global change components under study are climate change and two aspects of direct human agency, namely land use and the exchange of non-native species.

My doctoral thesis is comprised of two major parts: in the first part (Chapter 1-2), I focused on the effects of climate change on the spread and hybridization potential of a pool of alien plant species in Europe for the second half of the century. This species set comprises ornamental plants currently cultivated in Europe and naturalized somewhere outside of Europe, and thus, one of the most important source pools for potential future invaders. In Chapter 1, species distribution models were used to assess changes in the invasion risk from garden plants in Europe under a changing climate. In Chapter 2, we evaluated whether hybridization of a subset of these garden plants with native (or other already naturalized alien) species may increase under climate change, again applying a species distribution modelling approach.

In the second part of my doctoral thesis (Chapter 3-4), I examined the combined effects of climate change and land-use change on future plant distribution. For this purpose, I first addressed the challenges in integrating land use into models of species distribution and diversity (Chapter 3). In Chapter 4, I then investigated the combined effects of both

drivers – climate and land-use change – on the regional species pool of an area located in Central Austria for the mid of the century. Again, species distribution models were the method of choice.

In the following, I give a short summary of these two parts of my thesis and conclude with a discussion.

## **Part 1: Naturalization and hybridization risk from garden plants under climate change**

Alien species become introduced from one location to another by different introduction pathways (Hulme *et al.*, 2008). The human mediation of biological invasions is still an underestimated phenomenon (Kowarik, 2003): while in the analysis of introduction pathways focus has often been put on accidental introductions (as, e.g., in ballast water), many currently invasive species were introduced intentionally, for instance, as ornamentals (Hulme *et al.*, 2008; Hulme, 2009). In fact, ornamental horticulture has even been identified as the number one pathway for plant invasions worldwide (Mack & Erneberg, 2002; Dehnen-Schmutz *et al.*, 2007; Hulme *et al.*, 2008; Chrobock *et al.*, 2011; Hulme, 2011). Ornamental plants are probably particularly successful as invaders as they possess several traits and characteristics which are both sought for in cultivation and promote invasive spread, like rapid growth, early and high reproduction, climatic hardiness and disease resistance (Perrings *et al.*, 2005; Pemberton & Liu, 2009; Chrobock *et al.*, 2011; van Kleunen *et al.*, 2018). The high incidence of classical 'invasive' traits among them makes them a huge pool of potential future invaders. Species which have already managed to become naturalized or invasive somewhere in the world have a documented higher probability of successful escape from cultivation in other regions, too (Williamson 1999). Here, I use this criterion for defining a subset of the European garden flora that I consider particularly likely to represent the pool from which future potential invaders could emerge. This pool contains all those ornamentals which are currently cultivated in Europe and which have already naturalized as aliens somewhere outside of the continent, but not in Europe itself.

### **- Chapter 1: Naturalization risk from garden plants under climate change**

In my first study, I identified this subset by combining the list of non-native European garden plants (Cullen *et al.*, 2011) with the list of non-European plants that have already naturalized elsewhere in the world, but not in Europe (taken from GloNAF; van Kleunen *et al.*, 2015). Changes in the invasion risk of this species pool were assessed by modelling their current and future climatic niches. Future climate was characterized by

three climate change scenarios from the RCP family (RCP2.6, RCP4.5, RCP8.5). Moreover, I incorporated propagule pressure from gardens and urban areas into my assessment, as propagule pressure is one of the best predictors for invasion success (Lockwood *et al.*, 2005). Therefore, I produced a weighted land-cover map, which accounted for the proportional area available for gardening. Together with hotspots of potential future naturalization (i.e. areas predicting the highest number of species) these weighted maps were then combined into 'hotspots of naturalization risk' from this species pool under future climates.

- Chapter 2: Hybridization risk from garden plants under climate change

Interspecific hybrids are known to be potentially successful invaders (Hovick & Whitney, 2014). Species transport around the world increasingly lifts existing barriers to geographic and genetic isolation between introduced and resident species (Thomas, 2013a). The risk of hybridization between these species pools will depend on the introduced species' ability to naturalize. Thus, newly established garden plants have the potential to hybridize with resident congeneric species. Hence, in Chapter 2, we assessed the hybridization risk between alien garden plants and native (or already naturalized alien) species and its change under future climate change. For this purpose, species distribution maps of both, future potential ornamental invaders already introduced to Europe and their native congeneric species have been used. The risk of hybridization was quantified as spatial overlap between the suitable areas of these two species sets, again for current climate and for three future climate change scenarios. The set of potentially invasive garden plants was therefore restricted to congeners from genera for which hybridization has already been documented in literature.

## **Part 2: Climate change and land-use change effects on future plant distribution**

While scenarios of future land use have become increasingly available in the last decade (Busch, 2006; Rounsevell *et al.*, 2006; Verburg *et al.*, 2006; Verburg *et al.*, 2011), they often are either not easily accessible (especially in comparison to climate change scenarios) or unsuitable for biodiversity assessments, due to their low spatial or thematic resolution (Martin *et al.*, 2013; Verburg *et al.*, 2013; Titeux *et al.*, 2016). As a corollary, relatively few studies have accounted for the cumulative impacts of both, climate change and land use/cover change, on biodiversity. Three recent reviews (de Chazal & Rounsevell, 2009; Titeux *et al.*, 2016; Sirami *et al.*, 2017), for instance, concluded that land use/cover change are insufficiently represented in biodiversity scenarios. In fact,

only a small number of empirical studies include the effects of land use/cover change in contrast to the large number of studies on climate change. Further, the imbalance towards climate change projections has increased over time (Titeux *et al.*, 2016). Possible reasons for this imbalance include the complex nature of land use – biodiversity relations (which is in contrast to the strive towards simple predictor variables), and the apparent lack of appropriate data.

Lacking representation of land use/cover changes in biodiversity projections has been claimed to result in inappropriate or even misleading conclusions, often over- or underestimating future threats to biodiversity (de Chazal & Rounsevell, 2009). Here, I outline challenges in integrating land use into models of species distribution and diversity and then investigate the combined effects of both climate change and land use change on the regional species pool of an area located in Central Austria for the mid of the century.

- *Chapter 3: Better integration of land use into models of biodiversity*

In this review, I discussed important issues towards a better integration of land use into predictive models of biodiversity. Therefore, I introduced conceptual distinctions of land-use facets and dimensions from land-use science and emphasized that biodiversity models should routinely use sets of variables that represent all these dimensions and facets. Then, using the ‘land-use intensity’ facet as an example, I reviewed the literature to evaluate the representation of these different dimensions in biodiversity research.

- *Chapter 4: Climate change and land-use change impacts on regional plant diversity*

Within my fourth study, I focused on a regional species pool of a Central European mountainous region. I assessed the changes in range sizes of this species pool under different scenarios of future climate and future land-use. More specifically, future climate was again characterized by three climate change scenarios from the RCP family (i.e. RCP2.6, RCP4.5, RCP8.5) and land-use change was characterized by a business-as-usual scenario (BAU) and two scenarios from the Shared Socio-Economic Pathways (SSP) family (i.e. SSP1 and SSP5). Changes in land use were modelled by means of an Agent Based Modelling (ABM) approach, which offers a way of establishing land use scenarios with a high spatial and thematic resolution (Matthews *et al.*, 2007; Valbuena *et al.*, 2010). Moreover, I demonstrated how the ABM was coupled with a SDM, a combination that represents a potentially powerful ‘innovative model architecture’ (Verburg *et al.*, 2016).

## Concluding Discussion

In my doctoral thesis, I investigated the effects of three global change components on the future distribution of different plant species pools at different spatio-temporal scales. For this purpose, I applied a species distribution modelling approach. I found both similarities in the components' effects across the various study settings as well as specific peculiarities and interactions in dependence of the study context.

### Climate change effects on species distributions

In Chapter 1, I have shown that a sizable fraction of the studied ornamental species (> 20 %) would already find suitable conditions in parts of Europe (> 5 %) under current climate. Potential range sizes of European garden plants are predicted to increase, on average, under climate change. This enlargement is greater the more pronounced the climate scenario. However, there are also species predicted to lose climatically suitable area. The gap between those species likely to gain and those likely to lose climatically suitable area becomes the more pronounced the more severe the climatic scenario. Hotspots of naturalization risk defined by climatic suitability alone are projected to increase by up to 102 % (i.e. more than double) under climate change depending on the scenario. Furthermore, a north- and eastward shift of potential naturalization hotspots is predicted.

By contrast, in Chapter 2 we have shown that future climate change is predicted to decrease the mean geographic overlap of climatic ranges between European garden plants and their resident congeners. Reasons for this probably lie in the diverging trends of climatically suitable areas for the future: projections suggest that suitable ranges of garden plants will increase, on average, while those of their congeneric species will remain constant or decrease. Nevertheless, some of the potentially hybridizing species that we modelled showed a significantly rising range overlap (Klonner *et al.*, 2017). The coupled model in Chapter 4 suggests a strong effect of future climate on native plant range sizes in the Central Austrian study region: more than two thirds of the modelled species are predicted to lose climatically suitable areas, while about a quarter of the species are predicted to gain climatically suitable area. Again, the stronger the climate scenario, the more extreme 'losers' (those losing 80 – 100 % of their current range area) and extreme 'winners' (those gaining > 200 % of their current range).

Taken together, my results show strong effects of climate change on future species distributions. The direction of the alteration depends on the considered species pool: while non-native garden species are predicted to gain climatically suitable area under

climate change (see Chapter 1 and Chapter 2), their native congeners as well as native species from Central Austria will lose climatically suitable area under a warming climate, on average (see Chapter 2 and Chapter 4). Thus, my results are in line with other studies that have either reviewed the consequences of climate warming on alien species' ranges (e.g. Walther *et al.*, 2009) or modelled its consequences on species distributions in mountainous environments (e.g. Dirnböck *et al.* 2003, Randin *et al.* 2009, Engler *et al.* 2011, Hämmerle *et al.* 2018).

### **Effects of human agency on species distributions**

In Chapter 1, CORINE land cover classes were weighted by their estimated amount of potential area for ornamental plant cultivation. Therefore, highest weights were assigned to classes including private and public gardens like green urban areas, for example. This proxy of propagule pressure was then combined with species' climatic projections to produce maps of naturalization risk. I have found that hotspots of naturalization risk defined by a combination of climatic suitability and appropriate land cover (potential planting area) show similar trends as the results based on climatic suitability only: areas of high invasion risk tend to increase and to shift north- and eastwards under climate change. However, the combined maps predict the hotspots to occur mainly in areas with a high population density (Dullinger *et al.*, 2017). In contrast to Chapter 4, where three scenarios of future land use have been applied to assess the future distribution of a regional species pool, here, the weighted land cover maps remain constant in the future. Therefore, further analysis of how naturalization risk may change when land use change is taken into account, is needed, especially as urban areas are predicted to expand significantly in the future (United Nations, 2018).

In Chapter 3, I have outlined important steps towards a better, more systematic integration of land use into predictive biodiversity models. These include an appropriate representation of the complexity of land use – biodiversity relationships. In this context, I have discussed data availability and scaling issues. I have discussed possible solutions for a better integration of land use in models of biodiversity suggesting, for example, the development of coupled models for predicting the effects of human agency on biological populations.

In Chapter 4, I have followed the suggestion in Chapter 3 and modelled the combined effects of climate change and land-use change by applying a coupled ABM-SDM model. By implementing an ABM, thematically and spatially fine-grained land-use maps were obtained. By combining these maps with a SDM, I have shown that both climate and land use determine the current realized niches of the plants under study, with land use having

a stronger effect than any single climatic variable. In contrast, the species' future distributions are predicted to be more influenced by climate than by land use. This can be explained through the modest changes predicted by the applied land-use scenarios. Reasons for these modest changes probably lie in the long-lived tradition of land use in Central Europe: the region under study has already undergone many centuries of continued agricultural use and at least half a century of recent intensification, and consequently, the option space for further intensification is limited. Alterations to expect will rather result from the abandonment or reforestation of economically marginal parts of the land (Giupponi *et al.*, 2006; Henle *et al.*, 2008). However, generalizations from these results can, of course, only be drawn with care. Different parts of the world are in different land-use transition stages, depending on their history, social and economic conditions, and ecological context (Foley *et al.*, 2005). Thus, a similar approach should be applied to other regions of the world where the magnitude of future land-use change is expected to be higher than in Europe (Sala *et al.*, 2000; Jetz *et al.*, 2005). For the alien ornamental species in Chapter 1 and 2, human agency plays a different role, as in this case the option space has not been exhausted. In fact, there is no saturation in the exchange and accumulation of alien species worldwide due to continuing globalization and increasing international traffic and trade and it is thus very likely that more species will be introduced and will naturalize in the future (Seebens *et al.*, 2017). Especially, as naturalisation is known to be higher in deliberately introduced plants as compared to accidental introductions (Kowarik, 2003) and cultivation is known to be an important vector for the dispersal of a species following the initial introduction (Mack, 2000). Furthermore, the predicted expansion of climatically suitable areas under a changing climate in Chapter 1 is particularly troublesome in the case of ornamental plants because many of them are already cultivated far beyond their known natural range limits (Van der Veken *et al.*, 2008). Hence, ornamental plant cultivation may cause benefits for migration through lifted dispersal limitation and thus allow the naturalization of garden plants to keep track with climate change (Corlett & Westcott, 2013). Thus, with continuing globalization, increasing international traffic, rising income levels in different parts of the world and the associated trade and cultivation of ornamental plants, it is very likely that more and more plant species will be introduced outside their natural ranges and naturalize (van Kleunen *et al.*, 2015; Seebens *et al.*, 2017).

### **Gain or loss? A matter of origin and scale**

My results are in line with studies stressing that global decreases in species diversity are commonly contrasted by increases in regional diversity (Sax & Gaines, 2003; Thomas, 2013b; Thomas, 2013a; Vellend *et al.*, 2013; Vellend *et al.*, 2017). In Europe,

introductions of non-native species already increased overall plant species richness by 20-25 % (Winter *et al.*, 2009). This increase in numbers of alien species does not show any sign of saturation (Seebens *et al.*, 2017), especially as shifting geographic ranges resulting from climate change may also bring new species to particular regions (Parmesan & Yohe, 2003; Walther *et al.*, 2009) as also demonstrated in the first two chapters of my thesis. By contrast, the distribution of native species has already decreased, mainly due to changes in land use (Sax & Gaines, 2003; Vellend *et al.*, 2017), but also in response to recent warming (Parmesan & Yohe, 2003; Lenoir & Svenning, 2015). However, as the losses of native species can be offset by the establishment of alien species, species richness might even increase, at least at the regional scale (Ellis *et al.*, 2012) (Sax & Gaines, 2003). At global scales, by contrast, these processes will most likely cause a net decrease in species and lead to biotic homogenization (McKinney & Lockwood, 1999; Baiser *et al.*, 2012; Vellend *et al.*, 2017).

## **Conclusions**

Throughout my PhD thesis I tried to model the combined effects of climate change and aspects of human agency on future plant distribution. My results demonstrate the importance of including several global change components in predictive species modelling.

In fact, only by treating changes in species distributions as multi-causal processes will predictions for approximate reality and become useful for guiding management and conservation efforts. Modelling several components of global change is more challenging and time-consuming than modelling single components in isolation, but to effectively mitigate biodiversity loss, multiple threatening processes need to be managed simultaneously over longer terms. Management and conservation actions which tackle individual threats risk ending in failure, due to uncontrolled interacting and / or cascading effects (Brook *et al.*, 2008). I hence consider the studies conducted within my PhD thesis as a contribution towards a more appropriate, multi-dimensional assessment of global change threats to biodiversity.

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# Chapter 1

## Climate change will increase the naturalization risk from garden plants in Europe

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### Publication Reference

Dullinger, I., Wessely, J., Bossdorf, O., Dawson, W., Essl, F., Gatringer, A., Klöner, G., Kreft, H., Kuttner, M., Moser, D., Pergl, J., Pyšek, P., Thuiller, W., van Kleunen, M., Weigelt, P., Winter, M., Dullinger, S. (2017): Climate change will increase the naturalization risk from garden plants in Europe. *Global Ecology and Biogeography*, 26, 43-53.

### Status

Published

### Contribution

I computed the SDMs, analysed the data and led the writing of the manuscript.

RESEARCH  
PAPER

# Climate change will increase the naturalization risk from garden plants in Europe

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## ABSTRACT

**Aim** Plant invasions often follow initial introduction with a considerable delay. The current non-native flora of a region may hence contain species that are not yet naturalized but may become so in the future, especially if climate change lifts limitations on species spread. In Europe, non-native garden plants represent a huge pool of potential future invaders. Here, we evaluate the naturalization risk from this species pool and how it may change under a warmer climate.

**Location** Europe.

**Methods** We selected all species naturalized anywhere in the world but not yet in Europe from the set of non-native European garden plants. For this subset of 783 species, we used species distribution models to assess their potential European ranges under different scenarios of climate change. Moreover, we defined geographical hotspots of naturalization risk from those species by combining projections of climatic suitability with maps of the area available for ornamental plant cultivation.

**Results** Under current climate, 165 species would already find suitable conditions in > 5% of Europe. Although climate change substantially increases the potential range of many species, there are also some that are predicted to lose climatically suitable area under a changing climate, particularly species native to boreal and Mediterranean biomes. Overall, hotspots of naturalization risk defined by climatic suitability alone, or by a combination of climatic suitability and appropriate land cover, are projected to increase by up to 102% or 64%, respectively.

**Main conclusions** Our results suggest that the risk of naturalization of European garden plants will increase with warming climate, and thus it is very likely that the risk of negative impacts from invasion by these plants will also grow. It is therefore crucial to increase awareness of the possibility of biological invasions among horticulturalists, particularly in the face of a warming climate.

## Keywords

Alien species, horticulture, hotspot analysis, invasion debt, ornamental plants, species distribution model.

## INTRODUCTION

Biological invasions can be conceptualized as a series of consecutive stages – from transport out of the native range to introduction into a new territory, naturalization or establishment of self-sustaining populations, and spread across the introduced range (e.g. Blackburn *et al.*, 2011). The term ‘invasive’ or ‘invader’ is thereby commonly reserved for species that have rapidly spread into multiple sites across a large area. To pass on to the next stage a species has to overcome specific barriers to its survival, establishment and spread. Whether and how fast a species manages to pass these barriers depends on a number of interacting factors that can be grouped into those relating to anthropogenic propagule pressure, physical conditions of the recipient area and biotic traits of the invader itself as well as of the invaded communities (Catford *et al.*, 2009). As a result of these consecutive filters, the number of species at each stage diminishes (Williamson & Fitter, 1996), and, even for eventually successful invaders, extensive time lags may separate first introduction, naturalization and subsequent spread (Essl *et al.*, 2011).

As climatic suitability of the new territory is particularly crucial for naturalization and spread (Catford *et al.*, 2009), expected climate change may importantly modify the number and identity of already introduced species able to pass to these subsequent invasion stages. Indeed, many examples have already been documented of alien species that have naturalized and/or started to spread in a region because recent warming trends have lifted former climatic limitations (Walther *et al.*, 2009). Predicting which species from a given pool of non-natives might actually benefit from upcoming climate warming, and where these species might become naturalized or invasive in the future, would provide a valuable basis for proactive management (Bradley *et al.*, 2012). So far, however, research efforts have concentrated on potential range expansions of species that have already become harmful (e.g. O’Donnell *et al.*, 2012; Bellard *et al.*, 2013) or at least naturalized (Duursma *et al.*, 2013) in the recipient area. These pre-selections exclude potentially large numbers of species introduced but not yet naturalized or invasive, which make up the pending invasion debt of a region (Essl *et al.*, 2011).

Alien species are introduced to recipient areas via different pathways (Hulme *et al.*, 2008). For vascular plants, intentional introduction for ornamental use has been identified as the major pathway world-wide (Hulme *et al.*, 2008). In Europe, for example, more than 16,000 species from more than 200 families are currently in cultivation for ornamental purposes (Cullen *et al.*, 2011). Public and domestic gardens thus contain the greatest pool of non-native plants on the continent (Niinemets & Peñuelas, 2008). The chance that in a warming Europe future invaders will primarily emerge from this pool is further increased by the fact that garden plants are often cultivated beyond the climatic limits of their natural populations and hence may get ‘a head start on climate change’ (Van der Veken *et al.*, 2008). In addition,

horticulture often selects for traits that also promote naturalization and spread, such as rapid growth, early and prolific reproduction and disease resistance (Mack, 2000; Pemberton & Liu, 2009; Chrobock *et al.*, 2011).

It remains hard to predict which particular species from the pool of introduced garden plants will actually manage to naturalize or even become invasive. What we do know, however, is: (1) species that have already managed to become naturalized somewhere in the world are more likely to escape from cultivation in other regions too (Williamson, 1999); and (2) that climate matching between native and introduced range is one of the few factors that consistently predicts invasion success across taxonomic groups and regions (Thuiller *et al.*, 2005; Hayes & Barry, 2008). Using these two ‘filters’ should hence help to at least select a subset of species with a higher risk of future naturalization and spread.

Here, we follow this rationale and explore whether the naturalization risk from currently cultivated garden plants will increase under a warmer climate in Europe. In essence, we first define the pool of non-native garden plants that have already naturalized as aliens somewhere outside of the continent, but not in Europe itself. Second, we parameterize species distribution models and use them to assess to what extent these species would already find suitable conditions for naturalization under the current climate and whether potential alien ranges would increase, on average, under three scenarios of climate warming. Third, we combine predictions for individual species into a ‘hotspot analysis’ (O’Donnell *et al.*, 2012; Bellard *et al.*, 2013) to identify areas with the highest numbers of potential future invaders under both current and future climatic conditions. Finally, we overlay these climatic hotspot maps with a weighted land-cover map accounting for the amount of potential ornamental planting area of each land-cover class (EEA, 2000) as an indicator of generic propagule pressure from gardening and urban landscaping.

## METHODS

### Data

#### *Species selection and data*

We selected from the European Garden Flora (EGF; Cullen *et al.*, 2011) all vascular plant species not native to Europe. (The EGF is the most comprehensive encyclopaedia of ornamental plants in Europe.) From this pool of species, we selected those which have successfully naturalized somewhere outside Europe but not yet anywhere in Europe, based on the Global Naturalized Alien Flora (GloNAF; van Kleunen *et al.*, 2015), a newly established global alien plant species distribution database which contains lists of naturalized alien plants in more than 850 regions covering 83% of the world’s terrestrial area. Cultivated taxa flagged as varieties or subspecies in the EGF were excluded to avoid overestimation when modelling the niches of the respective species. Moreover, we did not consider any taxa marked in the EGF as hybrids.

For this species subset, we then collated distribution data from the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>) using the *rgbif* library in R (Chamberlain *et al.*, 2015). All species were cross-checked for synonyms using The Plant List (<http://www.theplantlist.org>). Duplicates (i.e. multiple occurrences within 10' × 10' grid cells) and obviously erroneous records, i.e. those on an ocean surface, were removed. After these cleaning steps, we retained 783 species with more than 50 occurrences irrespective of whether these stem from the species' native or non-native ranges (Gallien *et al.*, 2010; see Appendix S1 in Supporting Information).

#### Climate data

To characterize present-day climate, we used climatic data (averaged for the baseline period 1950–2000) from the WorldClim database (Hijmans *et al.*, 2005, [www.worldclim.org](http://www.worldclim.org)) at a 10' resolution. From the 19 bioclimatic variables provided by WorldClim, we selected six which, in combination, represent a range of regional temperature and precipitation conditions together with an estimate of seasonal variability, and which are known to influence species distributions (Root *et al.*, 2003): (1) temperature seasonality, (2) maximum temperature of the warmest month, (3) minimum temperature of the coldest month, (4) precipitation seasonality, (5) precipitation of the wettest quarter and (6) precipitation of the driest quarter. Correlations (Pearson's *r*) among these variables were < 0.75 throughout and the impact of multicollinearity on model projections should hence be negligible (Dormann *et al.*, 2013).

Future climate was characterized by three different IPCC5 scenarios from the new Representative Concentration Pathways family: RCP2.6 ('mild' scenario), RCP4.5 ('intermediate' scenario) and RCP8.5 ('severe' scenario). Based on climatic models available at the Cordex portal (<http://www.euro-cordex.net>), we calculated mean predicted values of the six selected bioclimatic variables for the years 2050–2100 under these three scenarios (for detailed model selection and down-scaling procedure see Appendix S2).

#### Land-cover data

For the calculation of land-cover weighted risk maps, we used CORINE land-cover (CLC) data at a resolution of 100 m (EEA, 2000). The CLC land-cover classes were weighted by the estimated proportional area available for ornamental plant cultivation according to the descriptions in EEA (2000; cf. Chytrý *et al.*, 2009, for a similar approach). To safeguard against rating errors, we used three different weighting schemes, i.e. three different estimates of this proportional area per land-cover class (see Appendix S3 for details). In all three schemes, the highest weights were given to classes including private and public garden spaces (e.g. green urban areas). Within each scheme, we subsequently calculated the area-weighted means of these proportions for each 10' × 10' raster cell.

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## Species distribution models

### Model parameterization and evaluation

We modelled the global realized climatic niche of each species by combining available occurrence data with current climatic data within the *biomod2* platform (Thuiller *et al.*, 2009) in R (R Development Core Team, 2014). The four modelling algorithms used were: generalized linear model (GLM), general additive model (GAM), boosted regression tree (BRT) and random forest (RF). Since those algorithms require presence and absence data, but GBIF provides just 'presence-only' information, we generated 'pseudo-absences' following the recommendations of Barbet-Massin *et al.* (2012): for the regression technique models (GLM and GAM), we used 10,000 randomly distributed absences, and for machine-learning technique models (BRT and RF), we used a number of pseudo-absences equal to the number of occurrences found in GBIF and selected outside a radius of 200 km around these occurrences. For the latter approach, pseudo-absence generation, and hence model calibration, was repeated ten times per species to ensure that selected pseudo-absences did not bias the final predictions. For all models, the weighted sum of presences equalled the weighted sum of pseudo-absences. The predictive performance of the models was evaluated by means of the true skill statistic (TSS; Allouche *et al.*, 2006) based on a repeated (three times) split-sampling approach in which models were calibrated with 80% of the data and evaluated over the remaining 20%.

### Model projections

Calibrated models were used to project the climatically suitable area for each species in Europe under current and possible future climatic conditions by means of an ensemble forecast approach (Araújo & New, 2007). As pseudo-absence generation differed between the two groups of models, we generated two separate ensemble predictions for each species, one from a combination of GLM and GAM, and one from a combination of BRT and RF models. In other words, the model projections from the repeated split-sampling approach (and from the repeated pseudo-absence selection in the case of BRT and RF) were aggregated to a weighted mean of projections. The contribution of each model to the ensemble forecast was weighted according to its TSS score. Models with a TSS score < 0.5 were excluded from building projections (see Appendix S4 for full information on model performance). The two probabilistic ensemble forecasts were translated into two binary maps using the value that maximizes the TSS score as the threshold for distinguishing presence and absence predictions. The two binary maps were then combined to a final consensus map where a 10' cell was defined to be suitable for a species (under a particular climate scenario) only if both binary ensemble layers predicted its presence. The latter decision rule makes the projections conservative, i.e. the extent of climatically suitable habitat is likely to be under- rather than overestimated.

To assess whether potential alien ranges of the 783 species will, on average, increase, decrease or remain constant in Europe under future climates, we compared SDM projections under current and future climates in terms of the number of cells predicted to be suitable for these species. As the distribution of these numbers was highly skewed, with an excess of zeros, we used a permutation test to evaluate the significance of differences: for each species, we randomly reshuffled the number of cells predicted to occur under current conditions and the future scenario, respectively, and calculated the difference (cells in the future scenario minus cells under current conditions). This calculation was done 1000 times, resulting in a vector of 1000 mean differences among the 783 species, which is normally distributed and centred around zero. Finally, we assessed if the actually observed difference was within or outside the central 95 or 99.9% of the simulated differences.

To analyse whether possible increases or decreases of alien ranges under climate change might depend on a species' biogeographical origin, we assigned the native regions of our study species to the nine climatically defined zoniobiomes distinguished by Walter & Breckle (1991). Native regions were available for 704 of the 783 species in the GRIN database (<http://www.ars-grin.gov/>). Where native regions were assigned to more than one zoniobiome, species were assigned to all of these zoniobiomes. Finally, we re-did the same permutation tests as described above for the subset of species of each zoniobiome separately.

### Hotspot analysis and risk maps

For each climatic scenario, final binary consensus maps of all 783 species were stacked. From this overlay, we calculated for each 10' grid cell (*c.* 220 km<sup>2</sup> at latitude 50° N) the number of species that would find suitable climatic conditions there. We defined potential naturalization hotspots as the 10% of cells that provide a suitable climate to the highest numbers of species. To depict potential contraction or expansion of hotspots, we mapped the relative change in the areal extent of hotspots in comparison with the current climatic situation by applying the top 10% cut-off value (i.e. the number of species that separates the top 10% of the grid cells from the rest) determined under current conditions to the future climatic scenarios, too.

The hotspot maps represent the number of species that are predicted to be able to naturalize in particular regions (10' grid cells) based on their climatic requirements alone. Actual naturalization risk, however, also depends on the spatially variable amount of potential ornamental planting area. To create risk maps, we hence combined the stacked binary projections of the 783 species with each of the three weighted CORINE land-cover maps by multiplying the number of potential invaders by the area available for ornamental plant cultivation. We again defined hotspots of naturalization risk as the 10% of cells with the highest such multiplied values. The three resulting risk maps, one per weighting scheme of land-cover classes, were similar, but differed in some details (*cf.* Appendix S5).

46

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We hence created a final consensus map where hotspots of naturalization risk were defined as those cells flagged as such by at least two of the three alternative risk maps.

## RESULTS

### Model projections and hotspot analysis

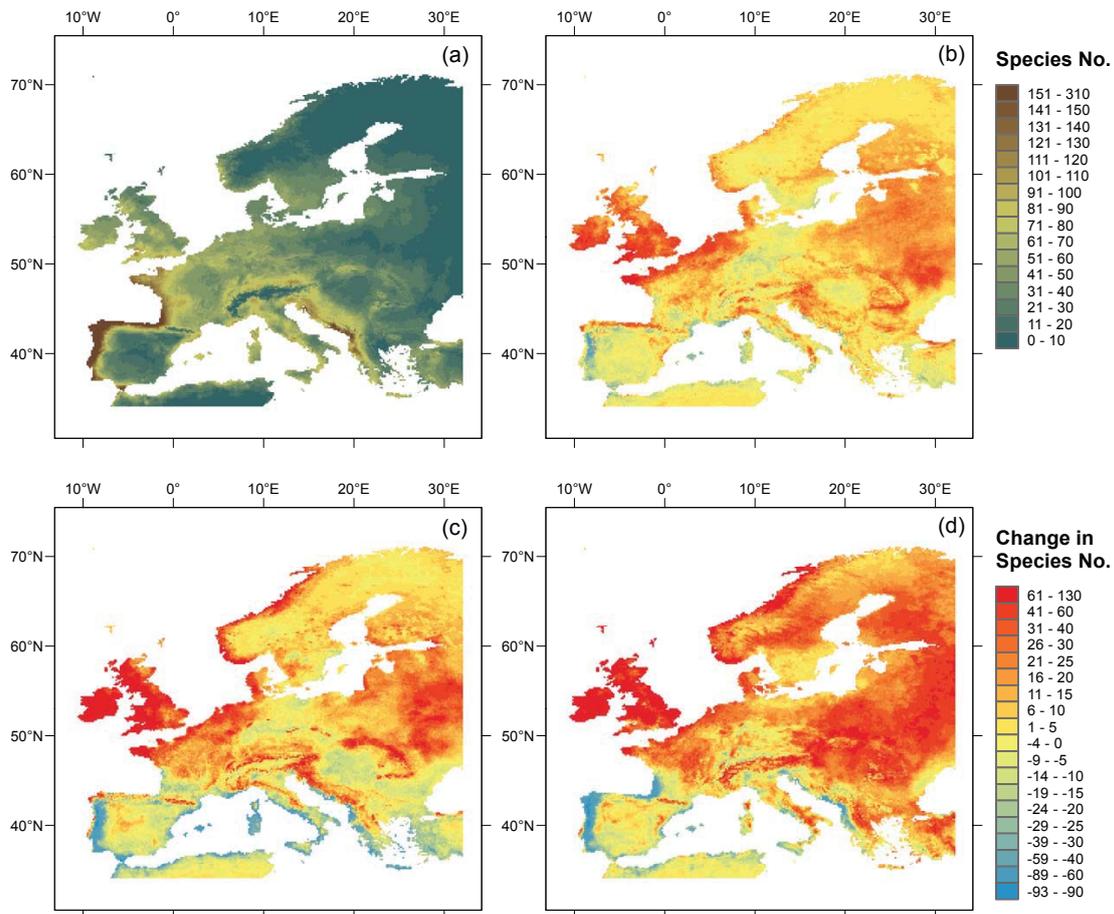
For 455 (*c.* 58%) of the 783 species included in our analysis, there is already a certain amount of suitable habitat (> 100 cells) in Europe under current climatic conditions. The number of suitable grid cells varies considerably among species (minimum 0, maximum 18,059, i.e. *c.* 58% of Europe), but is already > 1600 cells (*c.* 5% of Europe) for 21% of the species (165 species). Per raster cell, the number of species predicted to encounter suitable climatic conditions ranges between 0 and 305 (Fig. 1a). Northern and eastern Europe currently appear least suitable and western and southern Europe most suitable for our study species.

Under a warmer climate, both the mean potential range size per study species (Fig. 2a–c) and the number of species finding particularly large climatically suitable ranges in Europe (Fig. 2d) increase. Enlargement of mean potential range sizes is greater the more pronounced the climate-change scenario (Fig. 3). However, not all the analysed species are predicted to profit from warmer climates. The modelled species pool is separated into those likely to gain and those which will lose climatically suitable area in a warmer Europe. The gap between these two groups becomes, again, the more pronounced the more severe the climatic scenario (Fig. 2a–c).

Separating species according to their biogeographical origin demonstrates that those native to nemoral and laurophyllous zoniobiomes profit most, especially under the most severe scenario, while those native to boreal and Mediterranean zoniobiomes benefit least or even decrease in mean range size under the most severe climate scenario (Fig. 3). However, at least some species from any zoniobiome show particularly strong reduction or enlargement of potential range size under each climate scenario, with pronounced losers being particularly frequent among boreal, nemoral and Mediterranean species (Fig. 2, Appendix S6).

Similar to species, geographical regions are also separated into those gaining and losing potential invaders with a warming climate (Fig. 1b–d). Gains are particularly pronounced in the north-western and eastern parts of Europe while the southern Atlantic and most of the Mediterranean coast are predicted to be suitable for a lower number of ornamentals under future climates.

Under current climatic conditions 10% of Europe is climatically suitable for at least 70 from our pool of 783 species. These climatic hotspots are clustered along the Atlantic coast of Portugal, Spain, France and the southern British Isles as well as along the Mediterranean coast of the Balkan Peninsula and in southern central Europe (Fig. 4a). Under future climates, the hotspot area is predicted to grow, i.e. the area that provides climatically suitable habitat to  $\geq 70$  species will become larger by 62% under RCP2.6, by 75% under RCP4.5



**Figure 1** Projected climatic suitability for 783 ornamental species currently not naturalized in but somewhere outside of Europe in  $10' \times 10'$  grid cells. The figure shows the total numbers of species that are projected to encounter climatically suitable conditions per grid cell under current climate (a), and changes to these numbers under three different climate change scenarios (b–d).

and by 102% under RCP8.5 (i.e. more than doubling) (Fig. 4b–d).

Although part of the southern Atlantic and the Balkan coasts will lose potential invaders under climate warming (Fig. 1), they nevertheless remain among those areas climatically suitable to a particularly high proportion of the analysed ornamental plants. The increasing extent of climatic hotspot area is mainly driven by a gradual expansion to the north including most of the British Isles, parts of north-western continental Europe, southern Norway and the western Pannonian region (Fig. 4b–d). However, most of northern and eastern Europe still does not qualify as a climatic hotspot, even under the most severe climatic scenario, although the number of potential invaders increases considerably there (Fig. 1b–d).

### Risk maps

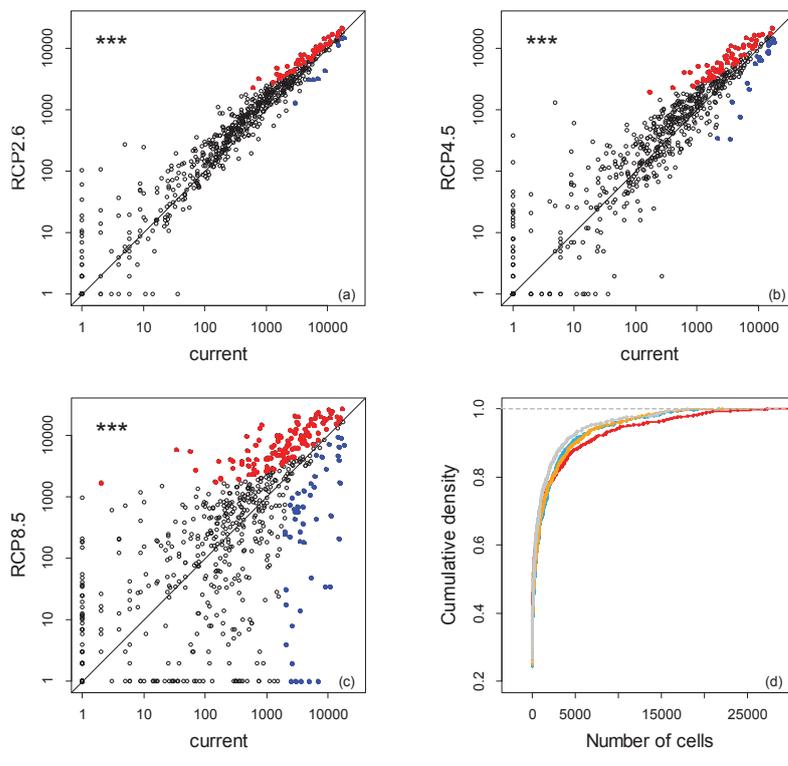
Similar to the extent of climatic hotspots, the area of high naturalization risk is predicted to grow under climate

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warming by 28% under RCP2.6, by 30% under RCP4.5 and by 68% under RCP8.5 (Fig. 4f–h). Weighting by land-cover, however, results in some important changes to the purely climatic hotspot patterns (Fig. 4e–h). High-risk areas tend to extend further eastwards into densely populated areas of central and eastern Europe under all climate scenarios. By contrast, most of the Balkan coastal regions as well as parts of the Spanish coast are climatic hotspots under all scenarios but do not qualify as high-risk areas. Finally, parts of north-western Europe (e.g. Ireland, Scotland) and the southern Scandinavian coast become climatic hotspots when climate warms, but still do not appear to be areas with high naturalization risk.

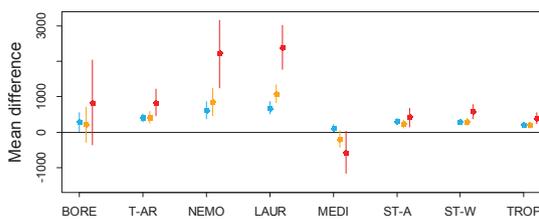
### DISCUSSION

Our results demonstrate that there is a sizeable pool of species which: (1) are planted in European gardens, at least locally, and hence already exert a certain amount of



**Figure 2** (a)–(c) Comparison of the number of cells climatically suitable for the 783 ornamental species under current climatic conditions and three different climate change scenarios (RCP2.6, RCP4.5, RCP8.5). Asterisks symbolize significant differences in the mean number of cells ( $P < 0.001$ ). Blue and red points symbolize species that loose or gain  $> 1600$  cells (c. 5% of the study area) in comparison with current climate conditions, respectively. (d) Cumulative density of the number of cells occupied by the species, i.e. the probability that a randomly selected species has a climatically suitable range  $< x$  under current climatic conditions (grey), and under the three climatic scenarios (RCP2.6, light blue; RCP4.5, orange; RCP 8.6, red). In (a)–(c) axes are log-scaled.

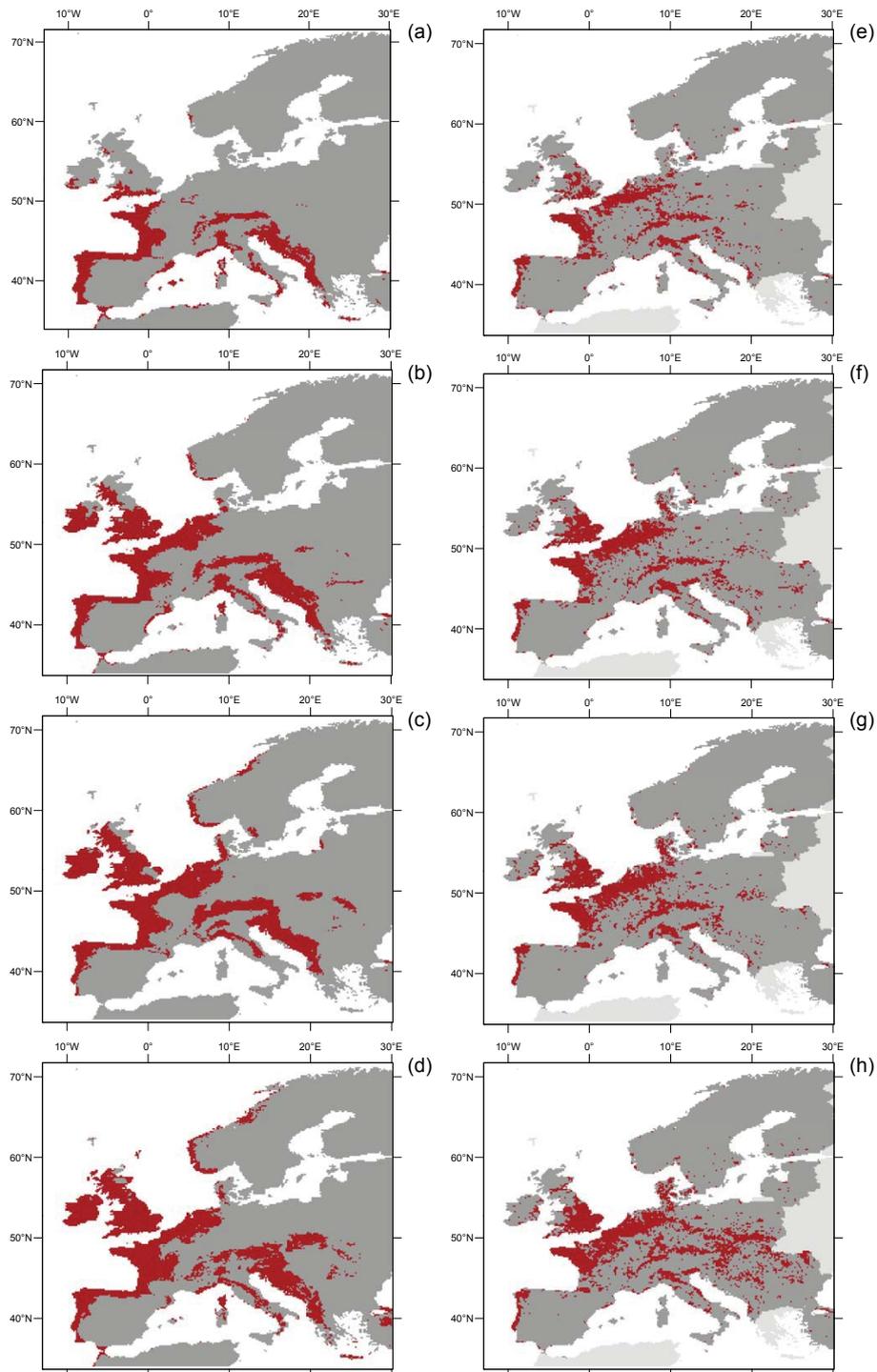
propagule pressure, (2) have proven their naturalization capacity in other parts of the world, and (3) find abundant suitable climatic space in Europe. The risk that at least some of these species will become naturalized in Europe in the future appears substantial, and it is likely that this risk will increase as climate change intensifies.



**Figure 3** Mean difference in the number of cells climatically suitable to the 783 ornamental species under current climatic conditions and three different climate change scenarios (RCP2.6, RCP4.5, RCP8.5), separated by species zonobiome of origin. Points symbolize observed mean differences and lines 0.95 confidence intervals as derived from permutation tests. Key: blue, RCP2.6; orange, RCP4.5; red, RCP8.5; BORE, boreal; T-AR, temperate-arid; NEMO, nemoral (= temperate); LAUR, laurophyllous; MEDI, Mediterranean; ST-A, subtropical-arid; ST-W, subtropical seasonally dry; TROP, tropical.

### Geographical distribution of current climatic hotspots

Climatically suitable areas for potential naturalization of garden plants are unequally distributed across Europe. Most parts of northern and eastern Europe are unsuitable for the vast majority of the analysed species under current climatic conditions, whereas hotspots are concentrated along the southern and western Atlantic shorelines and the eastern Adriatic coast. This geographical contrast suggests that not only temperature but a combination of temperature and precipitation regimes controls current patterns of climatic suitability for garden plants in Europe. The peculiarity of the Atlantic coastal areas, in particular, is a combination of relatively mild winters and humid summers keeping both frost and aridity stress low. These areas are hence likely to be within physiological tolerance limits of species from a wide array of different origins. By contrast, the Mediterranean region is warm enough in winter for nearly all selected species to be cultivated (Cullen *et al.*, 2011), but arid summers represent a climatic filter to naturalization. In line with this interpretation, the Balkan coastal area, which receives more precipitation than all other parts of the Mediterranean coast in Europe, is the only Mediterranean region that ranks among potential naturalization hotspots. In the eastern and northern parts of Europe, the climate is generally colder and/or more continental, with low winter temperatures, dry



**Figure 4** Geographical distribution of hotspots of potentially suitable climatic conditions for 783 ornamental species not yet naturalized in, but somewhere outside of Europe, under current climate (a) and three scenarios of climate warming: (b) mild scenario (RCP2.6), (c) intermediate scenario (RCP4.5) and (d) strong scenario (RCP8.5). (e)–(h) Maps of high naturalization risk calculated from combining climatic suitability under these four different assumptions of climatic conditions with the estimated area available for ornamental plant cultivation.

summers or a combination of both. These conditions are obviously hostile to the naturalization of most species from the current pool of European garden plants.

### Effects of climate change

Release from climatic restrictions has been identified as a major potential driver of rising invasion risk under climate warming (e.g. Walther *et al.*, 2009). Our results generally support this notion. The prevailing pattern detected is an increasing number of potential invaders, in particular of laurophyllous and nemoral origin, in more northern and eastern parts of Europe and a concurrent shift of potential naturalization hotspots. This predicted expansion of climatically suitable ranges is particularly worrisome in the case of ornamental plants because many of them are already cultivated far beyond conditions that would currently allow population establishment in the wild (Van der Veken *et al.*, 2008). The presence of species propagules in regions that become newly climatically suitable to them effectively lifts dispersal limitations, and may therefore allow the naturalization of garden plants to keep track with climate change more closely than is commonly assumed for native plants (e.g. Corlett & Westcott, 2013).

The mean increase of climatically suitable area, however, masks pronounced variation among species. For a sizeable minority of the study species, the potential range is predicted to shrink under climate change, and under the most pronounced scenario the number of species finding suitable climate in <1% of the European area (320 cells) is approximately the same as under current conditions (442 vs. 441 species). The reasons for climatic range loss are likely to differ among individual species, but the fact that 'losers' are particularly widespread among species of boreal and Mediterranean origin suggests that two factors may be of particular importance. First, species adapted to cool conditions might lose potential area because temperatures become too warm in most parts of Europe. Second, species that would currently find climatically suitable area in Mediterranean Europe may not be able to deal with the more arid conditions that are predicted for these regions (Mariotti *et al.*, 2008) while, simultaneously, winter temperature does not become warm enough to compensate for such loss by expansion to the more northern, temperate parts of Europe. In accordance with the latter assumption, the regions that are currently both warm and relatively moist but will become drier in the future, like the southern Atlantic coast and the Balkan coastal area, are (1) predicted to lose the highest numbers of potential invaders and (2) are geographically separated from the more northern areas that show highest increases in the number of potential invaders.

### Combining climatic suitability and potential ornamental planting area

Urban and suburban areas usually function as centres of introduction and cultivation for ornamentals, and the

proportion of introduced species usually decreases dramatically along an urban–rural gradient (Kowarik, 1995; Niinemets & Peñuelas, 2008). Combining projections of climatic suitability with the proportional area of the respective land-use types hence pinpoints some densely populated and economically prosperous regions in Europe as potential naturalization hotspots despite a sub-optimal climate, e.g. Great Britain under current climatic conditions. By contrast, relatively large areas appear less threatened although they would be climatically suited to many garden plants, at least under a warmer climate, like most of the coastal Balkan Peninsula, Ireland or some southern parts of coastal Scandinavia.

The risk maps presented here assume, however, that current land-cover patterns in Europe remain unchanged. Whether and how these patterns will change depends on future European socio-economic policies (Spangenberg *et al.*, 2012). Interestingly, a recent study projecting invasion levels in Europe as dependent on land-use change scenarios for the 21st century revealed patterns that partly resemble those found in our study, particularly with respect to rising naturalization risk in north-western and northern Europe (Chytrý *et al.*, 2012). Taken together, these parts of Europe will hence offer both climatically more suitable conditions and land-use patterns more susceptible to alien plant establishment in the future. By contrast, in the easternmost parts of the continent rising climatic suitability to potential invaders might be attenuated by abandonment and loss of former agricultural land in these economically marginal areas (Chytrý *et al.*, 2012; Spangenberg *et al.*, 2012).

### Caveats

The use of species distribution models to predict range shifts under changing climatic conditions has important limitations, mainly related to the disregard of biotic interactions (e.g. Wisz *et al.*, 2013), intraspecific variation in niche breadth (Valladares *et al.*, 2014), dispersal limitations (Svenning & Skov, 2007) and, particularly in an invasion context, possible niche shifts (Early & Sax, 2014). In the case of our study, biotic interactions may be of limited relevance because the spatial resolution of our predictions is far beyond the scale at which plants usually interact (Pearson & Dawson, 2003). Likewise, dispersal limitation is probably less relevant as we model potential ranges of species that are actively distributed by humans, and for which the frequency of long-distance dispersal events can be expected to rise sharply in the future with the growing importance of e-commerce in the ornamental plant trade (Lenda *et al.*, 2014; Humair *et al.*, 2015). However, not all the plants modelled here will be traded and cultivated with equal intensity, and even of those planted frequently, only a subset will escape into the wild (Dehnen-Schmutz *et al.*, 2007). We hence stress that the numbers of species predicted in our study should not be taken at face value but represent a measure of spatial and temporal variation of naturalization risk. On the other hand, we note that the pool of potential invaders among European garden plants

might be even larger than assumed here because species could become established or even invasive in Europe although they have not yet done so in other regions of the world. Finally, with respect to niche shifts, we took care to parameterize our models not only with data from the native ranges of the species but also from all those areas where they have already naturalized. While this strategy should characterize the climatic potential of species as accurately as possible, further changes to realized niches during their possible future establishment and invasion in Europe can of course not be completely excluded.

The reliability of species distribution models depends on the quality of the data used to fit them. GBIF combines the advantage of global coverage, and hence the possibility to fit niches of species comprehensively, with the disadvantage of the errors and biases implicit in such large databases (Meyer *et al.*, 2016). However, we do not think that these errors and biases affect our results qualitatively. First, we took care to handle taxonomic problems and spatial errors when extracting occurrence data. Second, the poor coverage of northern Asia, and Russia in particular, which is probably the most important geographical bias of GBIF in our context, has little impact on our results as the number of species native to Russia in our pool is low (38 species). In addition, the detected increase of the invasion level is especially pronounced for species from nemoral and laurophyllous zonobiomes, which are mostly situated in regions with especially high record densities. Third, although predictions for individual species might suffer from inaccuracies, the multispecies patterns predicted here are consistently interpretable in terms of geographical gradients of climatic harshness in Europe, and hence appear highly plausible.

### Conclusions

One of the greatest uncertainties in assessing the invasion risk of ornamental plants comes from the difficulty of estimating the potential impacts of climate change (Dehnen-Schmutz, 2011). Despite pronounced species-specific differences, our results suggest that climate warming leads to an increase in currently cultivated garden plants able to naturalize in Europe as well as the area across which they may spread. Which species will eventually become invasive or have a negative environmental and/or economic impact cannot be inferred from our models. However, a larger number of naturalized species probably also implies a greater risk of impact if the ratio of naturalized and harmful species remains about constant (Jeschke & Strayer, 2005). In addition, the growing importance of trade in ornamental plants via the internet (Humair *et al.*, 2015) increasingly removes any limitations on the availability of particular plants for the individual customer and hence largely eliminates the dispersal barriers that control range responses of non-cultivated species to climate warming (Svenning & Sandel, 2013). As a corollary, raising awareness of the invasion problem among individuals and institutions involved in gardening, urban landscaping and the

horticultural trade appears even more important in the face of a warming climate.

### ACKNOWLEDGEMENTS

This research was funded by the ERA-Net BiodivERsA, with the national funders FWF (Austrian Science Fund, I 1443-B25), DFG (German Research Foundation) and ANR (French National Research Agency, ANR-13-EBID-0004), part of the 2012-2013 BiodivERsA call for research proposals. M.v.K. and W.D. acknowledge funding by the Deutsche Forschungsgemeinschaft (KL 1866/6-1 and KL 1866/9-1). P.P. and J.P. were supported by the Czech Science Foundation (projects no. 14-36079G Centre of Excellence PLADIAS, and P504/11/1028), long-term research development project RVO 67985939 (The Czech Academy of Sciences) and by Praemium Academiae award from The Czech Academy of Sciences. H.K. acknowledges funding from the Deutsche Forschungsgemeinschaft in the course of the Excellence Initiative at the University of Göttingen, P.W. from the BEFmate project of the Ministry of Science and Culture of Lower Saxony and M.W. from the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118). We thank two anonymous referees and the editor, Linda Beaumont, for their helpful comments on the manuscript.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

**Appendix S1** Selected species and number of suitable cells under current and future climate.

**Appendix S2** Detailed model selection and downscaling procedure.

**Appendix S3** Selection and weighting of relevant CORINE land-cover classes for risk map assessment.

**Appendix S4** Information on model performance.

**Appendix S5** Naturalization risk maps calculated according to three different weighting schemes.

**Appendix S6** Species predicted gain or loss of area under climate change.

## BIOSKETCH

**Iwona Dullinger** is a doctoral student with research interests in global change biology, conservation biology and social ecology. Her research mainly focuses on modelling the impacts of climate and land-use change on species diversity.

Editor: Linda Beaumont

SUPPORTING INFORMATION

Climate change will increase the naturalization risk from garden plants in Europe

Iwona Dullinger, Johannes Wessely, Oliver Bossdorf, Wayne Dawson, Franz Essl, Andreas Gatttringer, Günther Klöner, Holger Kreft, Michael Kuttner, Dietmar Moser, Jan Pergl, Petr Pyšek, Wilfried Thuiller, Mark van Kleunen, Patrick Weigelt, Marten Winter, Stefan Dullinger

Appendix S1. Selected species and number of suitable cells under current and future climate.

Selected species (nomenclature as in The Plant List (<http://www.theplantlist.org/>)) and number of suitable cells under current climate and future climate (RCP2.6, RCP4.5, RCP8.5), total number of cells: 31.139.

species	current	RCP2.6	RCP4.5	RCP8.5	species	current	RCP2.6	RCP4.5	RCP8.5
Abelmoschus manihot	49	50	118	0	Anacardium occidentale	0	0	0	0
Abelmoschus moschatus	0	0	0	0	Ananas comosus	5	0	0	42
Abrus precatorius	0	0	4	6	Angelonia angustifolia	0	0	0	0
Acacia pravissima	2819	4577	3918	6414	Anigozanthos flavidus	151	170	128	63
Acalypha hispida	10	0	0	5	Annona cherimola	150	151	59	50
Acalypha wilkesiana	74	99	91	230	Annona glabra	0	0	0	0
Acanthocereus tetragonus	0	0	0	0	Annona muricata	0	0	0	0
Acer buergerianum	9230	12049	13524	18645	Annona reticulata	0	0	0	1
Acer japonicum	5883	3147	5336	1471	Annona squamosa	1	0	0	16
Acer palmatum	10247	15433	17037	26982	Anoda cristata	7954	11054	10109	4548
Acer spicatum	613	397	642	2307	Anthurium pentaphyllum	0	0	0	0
Actinidia arguta	2248	2317	3320	7218	Anthurium schlechtendalii	0	0	0	0
Actinidia polygama	617	2321	4178	2852	Antigonon leptopus	109	78	105	247
Adansonia digitata	15	15	31	0	Apodytes dimidiata	256	313	186	158
Adenanthera pavonina	0	0	0	0	Archontophoenix cunninghamiana	94	188	134	486
Adenium obesum	0	0	0	0	Arctotis fastuosa	118	135	22	7
Aesculus glabra	4053	3624	3537	8724	Ardisia crenata	207	416	777	619
Agastache rugosa	14899	14556	15299	16282	Ardisia japonica	8	49	87	1187
Ageratina ligustrina	0	0	3	24	Aristolochia grandiflora	0	0	0	0
Ageratum conyzoides	126	147	148	269	Artemisia ludoviciana	2002	2337	2026	245
Albizia chinensis	125	193	143	259	Artocarpus altilis	0	0	0	0
Albizia lebbek	175	391	479	863	Artocarpus heterophyllus	133	323	254	690
Albizia saman	0	0	0	0	Arum palaestinum	24	16	5	1
Albuca bracteata	2107	996	568	1423	Arundina graminifolia	120	274	239	282
Albuca canadensis	117	87	15	1	Asimina triloba	2623	2589	3901	1
Aleurites moluccana	155	150	144	290	Asparagus africanus	358	434	195	5
Allamanda cathartica	0	0	0	0	Asparagus declinatus	147	171	78	225
Allium tuberosum	15835	16953	18100	19784	Asparagus falcatus	75	154	45	73
Allocauarina littoralis	389	917	724	684	Asparagus retrofractus	23	38	4	94
Allocauarina verticillata	1214	2591	2380	2524	Asparagus scandens	712	1344	812	1534
Alnus nepalensis	158	250	352	175	Asparagus virgatus	564	589	461	8
Alocasia macrorrhizos	45	92	132	279	Atriplex canescens	2612	2484	2595	7
Alstonia scholaris	0	0	12	15	Atriplex nummularia	2415	2583	1677	741
Alternanthera ficoidea	0	0	0	188	Averrhoa carambola	0	0	0	0
Ammobium alatum	5089	6134	5468	1079	Banisteriopsis caapi	0	0	0	0
Ampelopsis glandulosa	92	205	258	760	Banksia ericifolia	368	643	700	971

species	current	RCP2.6	RCP4.5	RCP8.5
Barleria cristata	437	617	644	136
Barringtonia asiatica	0	0	0	0
Bartlettina sordida	88	160	47	173
Basella alba	501	881	1222	1408
Bauhinia galpinii	225	242	180	33
Bauhinia purpurea	45	136	144	381
Bauhinia variegata	1361	1772	1567	1925
Begonia cucullata	330	339	305	1443
Begonia heracleifolia	0	0	0	0
Begonia humilis	0	0	0	0
Begonia nelumbiiifolia	0	0	0	0
Berberis glaucocarpa	1854	1781	1943	5800
Berberis repens	3618	2810	1371	0
Bertholletia excelsa	0	0	0	0
Betula platyphylla	5158	6116	6491	1678
Bignonia capreolata	33	194	267	5979
Billardiera heterophylla	1192	1534	1460	261
Bixa orellana	0	0	0	0
Bocconia frutescens	13	10	0	0
Boltonia asteroides	375	609	577	1669
Bomarea multiflora	237	498	66	187
Bombax ceiba	0	10	20	5
Bouteloua curtipendula	1266	2120	2238	2893
Brachychiton acerifolius	1153	2432	2632	4449
Brachychiton discolor	2289	3811	4059	4380
Brachychiton populneus	2283	3375	2933	1937
Brexia madagascariensis	0	0	0	0
Breynia disticha	0	1	0	8
Bromus briziformis	6877	3241	2186	0
Bromus danthoniae	1306	548	1035	0
Browallia americana	35	0	0	0
Brownea coccinea	0	0	0	0
Brownea grandiceps	0	0	0	0
Brugmansia sanguinea	3	36	0	205
Brunfelsia uniflora	238	368	398	731
Bucida buceras	0	0	0	0
Buddleja asiatica	836	1326	1510	2027
Buddleja indica	0	0	0	0
Buddleja saligna	403	588	190	20
Buddleja salviiifolia	309	638	251	0
Buddleja stachyoides	257	374	545	790
Bulbine semibarbata	3206	4754	4163	1153
Bursera simaruba	0	0	1	1
Caesalpinia coriaria	0	0	0	0
Caesalpinia pulcherrima	0	0	46	48
Caladium bicolor	0	1	0	11
Calceolaria chelidonioides	2572	2985	2318	2450
Calliandra haematocephala	3	18	32	125
Calliandra houstoniana	0	0	0	0
Calliandra surinamensis	0	0	0	0
Callicarpa dichotoma	284	492	1013	581
Callicarpa japonica	233	392	772	1503
Callisia repens	230	339	366	466
Callistemon speciosus	658	814	514	507
Callistemon viminalis	1182	1226	752	468
Calophyllum inophyllum	0	0	0	0

species	current	RCP2.6	RCP4.5	RCP8.5
Calotropis procera	9	246	609	832
Calystegia hederacea	62	120	154	2
Camellia japonica	1914	2790	2971	4352
Camellia sinensis	456	767	1195	1791
Campanula punctata	1268	2895	3221	2597
Cananga odorata	0	0	0	0
Canavalia cathartica	223	390	253	769
Canavalia ensiformis	170	175	150	468
Canna glauca	78	58	57	12
Cardiocrinum cordatum	25	52	40	0
Carica papaya	7	2	26	27
Carissa macrocarpa	1096	1304	1536	1994
Carpinus caroliniana	1229	2034	2059	5229
Carya illinoensis	3738	6716	8203	7597
Cascabela thevetia	4	4	4	2
Cassia fistula	0	0	0	0
Cassia grandis	0	0	0	0
Castanea mollissima	1897	2725	3524	3126
Castanospermum australe	60	144	133	248
Casuarina cunninghamiana	2074	2719	2421	2164
Casuarina glauca	117	330	303	654
Cedrela odorata	23	13	10	28
Ceiba pentandra	0	0	0	0
Celastrus scandens	661	1424	1164	6957
Centrosema virginianum	267	841	981	3956
Ceratopetalum gummiferum	69	217	142	0
Ceratopetalum triloba	176	166	120	60
Cercestis mirabilis	0	0	0	0
Cercidiphyllum japonicum	13777	14119	13621	20671
Cestrum aurantiacum	1406	1917	1633	1880
Cestrum fasciculatum	578	916	815	132
Cestrum nocturnum	134	233	234	657
Chamaedorea elegans	0	34	13	1
Chamaelucium uncinatum	353	459	292	767
Cheilocostus speciosus	0	0	0	0
Chenopodium quinoa	5673	5588	4848	7331
Chrysobalanus icaco	0	0	0	0
Chrysophyllum cainito	0	0	0	0
Chrysophyllum oliviforme	0	0	0	0
Chrysothemis pulchella	0	0	0	0
Cinnamomum camphora	3224	6532	9533	20213
Cissus alata	0	0	0	0
Cissus antarctica	211	472	489	540
Cissus quadrangularis	0	0	0	1
Cissus rotundifolia	26	18	9	33
Cissus verticillata	0	0	0	11
Citharexylum spinosum	0	0	0	0
Citrus aurantiifolia	0	0	0	0
Citrus maxima	553	924	1365	1368
Clarkia amoena	10995	11548	6560	502
Clarkia pulchella	14766	13809	9218	4038
Clematis paniculata	589	663	699	2447
Clematis tangutica	6472	6728	2791	433
Clematis terniflora	2993	3817	4528	12846
Cleome gynandra	867	723	510	593
Clerodendrum bungei	1109	1306	1365	77

species	current	RCP2.6	RCP4.5	RCP8.5
Clerodendrum chinense	24	100	155	236
Clerodendrum splendens	0	0	0	0
Clerodendrum trichotomum	1872	2104	2926	5104
Cleyera japonica	71	170	573	1025
Clidemia hirta	0	0	0	0
Clitoria ternatea	0	0	0	19
Clusia rosea	0	0	0	0
Cobaea scandens	895	1316	774	796
Coccinia grandis	0	0	0	0
Coccoloba uvifera	0	0	0	1
Cochlospermum vitifolium	0	0	0	0
Cocos nucifera	0	0	0	0
Codiaeum variegatum	0	0	0	0
Coffea liberica	0	0	0	0
Cola acuminata	0	0	0	0
Combretum grandiflorum	0	0	0	0
Combretum indicum	0	0	0	0
Commelina benghalensis	924	957	606	686
Commelina coelestis	26	29	107	102
Conicosia pugioniformis	200	525	94	13
Coprosma robusta	103	278	335	213
Corchorus olitorius	523	860	1358	48
Cordyline fruticosa	0	0	0	11
Cortaderia jubata	2630	3624	2687	3213
Corylus heterophylla	361	547	709	358
Corymbia citriodora	978	1310	1115	2091
Cosmos sulphureus	340	786	790	52
Cotoneaster glaucophyllus	4511	4857	4226	3659
Couroupita guianensis	0	0	0	0
Crassula ericoides	28	121	53	0
Crataegus pubescens	0	8	2	10
Crescentia cujete	0	0	0	0
Crinum asiaticum	396	1019	1151	3489
Crinum zeylanicum	0	0	0	0
Crotalaria capensis	239	302	179	3
Crotalaria juncea	272	399	414	832
Crotalaria micans	275	495	457	693
Crotalaria retusa	0	0	0	0
Cucumis anguria	246	232	208	137
Cucumis dipsaceus	69	69	46	81
Cucumis metuliferus	169	218	131	33
Cucurbita argyrosperma	16	15	0	0
Cucurbita ficifolia	6296	8862	7351	7402
Cucurbita moschata	3914	4257	3412	695
Cuphea hyssopifolia	117	156	142	448
Curcuma longa	24	19	65	248
Cymbopogon nardus	636	1027	849	463
Cynoglossum amabile	14342	16365	12337	13374
Cynoglossum zeylanicum	3356	3819	3675	4026
Cyperus albobstriatus	937	1864	1420	20
Cytisus proliferus	5877	6617	5373	6264
Dahlia imperialis	0	4	0	0
Dahlia pinnata	14781	18785	15559	18081
Datura ceratocaula	44	23	1	182
Debregeasia longifolia	124	287	371	463
Delonix regia	0	0	7	6

species	current	RCP2.6	RCP4.5	RCP8.5
Desmodium elegans	894	1148	1111	1
Deutzia crenata	4055	4519	5678	187
Deutzia gracilis	3269	2718	4135	569
Dianella ensifolia	429	811	937	1059
Dieffenbachia seguine	0	0	0	0
Dimorphotheca cuneata	0	0	0	0
Dimorphotheca pluvialis	7421	9466	6722	6399
Dimorphotheca sinuata	3556	3421	3405	13
Dioscorea bulbifera	36	59	114	107
Dioscorea mexicana	0	0	0	0
Dioscorea polystachya	493	1036	1426	4064
Diospyros virginiana	252	1043	1446	4067
Diplocyclos palmatus	218	236	241	146
Dodonaea viscosa	3476	4875	4281	4275
Dolichandra unguis-cati	348	374	330	469
Dombeya burgessiae	137	120	78	34
Dombeya tiliacea	0	0	15	0
Dorotheanthus bellidiformis	5	19	3	3
Dorstenia contrajerva	0	0	0	0
Dracaena fragrans	3	3	0	6
Dracaena reflexa	0	0	0	0
Drosera aliciae	1911	2879	3067	4193
Drosera binata	2555	3724	3761	4535
Drosera capillaris	16	53	115	189
Echeveria secunda	0	0	0	0
Echinochloa polystachya	100	146	92	46
Echinodorus cordifolius	166	1115	1967	3801
Echinodorus subalatus	0	0	0	0
Ehretia acuminata	1243	2769	3075	2931
Eichhornia azurea	0	0	0	0
Elaeis guineensis	0	0	0	0
Embothrium coccineum	1920	2165	1384	603
Emilia sonchifolia	57	84	116	212
Empetrum rubrum	438	366	116	618
Entada phaseoloides	0	0	7	24
Epacris impressa	1195	1978	1342	676
Epipremnum pinnatum	1	0	0	5
Eragrostis trichodes	152	287	519	28
Erica glandulosa	34	76	31	0
Eriochloa villosa	201	228	329	727
Erythrina crista-galli	998	1480	1588	3186
Erythrina herbacea	1	107	42	1744
Etilingera elatior	0	6	7	151
Eucalyptus cinerea	1792	2585	2708	3272
Eucalyptus cladocalyx	1596	1407	656	733
Eucalyptus cornuta	290	295	145	0
Eucalyptus dalrympleana	767	1329	1538	886
Eucalyptus goniocalyx	1021	1722	1169	93
Eucalyptus leucoxydon	1015	1473	975	985
Eucalyptus nitens	915	1514	1767	731
Eucalyptus ovata	1973	2577	1942	454
Eucalyptus rubida	485	475	267	0
Eugenia uniflora	209	228	219	506
Eulophia alta	0	0	0	0
Euonymus alatus	2569	2286	3995	967
Euonymus hamiltonianus	5227	7152	6647	47

species	current	RCP2.6	RCP4.5	RCP8.5
Euphorbia balsamifera	0	1	0	0
Euphorbia leucocephala	0	0	0	0
Euphorbia mauritanica	109	145	32	18
Euphorbia tithymalooides	22	15	25	135
Euryops abrotanifolius	201	465	165	403
Euryops chrysanthemoides	21	12	0	0
Ficus auriculata	58	60	90	3
Ficus benjamina	74	84	91	110
Ficus drupacea	0	0	0	55
Ficus elastica	2331	2760	2490	3563
Ficus erecta	100	309	285	700
Ficus lutea	0	0	0	0
Ficus palmata	2756	2948	3191	636
Ficus racemosa	0	0	21	0
Ficus virens	77	59	65	75
Firmiana simplex	2121	2779	2815	6734
Fragaria chiloensis	6812	8394	6067	8576
Frangula purshiana	568	200	232	8
Fraxinus nigra	68	229	257	2809
Fraxinus uhdei	0	0	1	40
Freesia laxa	666	915	1097	791
Fuchsia paniculata	0	3	0	6
Galphimia glauca	8	8	64	122
Galphimia gracilis	0	0	2	0
Garcinia livingstonei	43	34	31	0
Gardenia jasminoides	521	1005	1301	2326
Geitonoplesium cymosum	395	716	767	197
Geranium incanum	739	1106	510	0
Geranium thunbergii	3044	5675	7898	16788
Gerbera jamesonii	487	501	722	616
Gibasis pellucida	64	215	161	440
Gilia tricolor	1641	799	398	141
Gladiolus papilio	351	508	430	0
Gladiolus tristis	866	1415	956	386
Gladiolus undulatus	1173	1931	1726	1456
Glandularia peruviana	704	972	1115	2591
Glandularia tenera	4094	5932	5934	7734
Gloriosa superba	103	93	57	10
Gloxinia perennis	0	0	0	0
Gloxinia sylvatica	0	0	0	0
Gmelina arborea	0	0	0	0
Gomphrena globosa	1229	1903	2107	1738
Grevillea banksii	271	461	302	158
Grevillea juniperina	1002	1822	1282	796
Grevillea rosmarinifolia	1505	2094	892	110
Hakea eriantha	330	509	441	292
Hakea laurina	397	478	233	520
Haloragis erecta	1010	1380	1148	2517
Hamelia patens	7	6	5	15
Hardenbergia comptoniana	123	178	133	159
Harpephyllum caffrum	148	138	74	61
Harrisia pomanensis	354	333	259	451
Hebenstretia dentata	402	756	508	9
Hedychium coronarium	429	831	775	881
Heimia salicifolia	156	391	348	760
Helanthium bolivianum	0	0	0	0

species	current	RCP2.6	RCP4.5	RCP8.5
Helanthium tenellum	37	123	258	41
Helenium bigelovii	747	339	272	0
Helianthus angustifolius	775	1332	1716	13329
Helianthus debilis	11600	17402	17524	25377
Helianthus giganteus	13563	13499	14464	15880
Helianthus salicifolius	13	0	6	0
Herbertia lahue	462	1795	1830	9794
Hesperantha coccinea	2844	2721	2309	436
Hesperantha falcata	149	271	83	79
Heterocentron subtriplinervium	0	1	0	0
Heterotis rotundifolia	0	0	0	0
Hevea brasiliensis	0	0	0	0
Hibiscus acetosella	0	0	0	0
Hibiscus diversifolius	225	340	242	540
Hibiscus mutabilis	245	381	729	1148
Hibiscus sabdariffa	0	0	0	0
Hibiscus schizopetalus	0	0	0	34
Hibiscus tiliaceus	0	0	0	24
Hippeastrum puniceum	0	0	0	0
Hippobroma longiflora	0	0	0	0
Hiptage benghalensis	0	15	28	0
Holmskioldia sanguinea	126	245	288	7
Homalanthus populifolius	982	2284	2824	4206
Homalocladium platycladum	15	15	50	199
Houstonia caerulea	402	392	413	549
Houttuynia cordata	6902	9648	11545	23910
Hovea pungens	195	121	24	5
Hovenia dulcis	749	1098	1397	592
Hoya australis	74	90	98	157
Hoya carnosa	4376	5303	6490	11799
Hura crepitans	0	0	0	0
Hydrangea paniculata	4176	4430	5366	7561
Hydrocleys nymphoides	197	543	607	261
Hydrocotyle americana	517	385	201	6
Hydrolea spinosa	1	9	20	2
Hylotelephium erythrostictum	4818	4137	3512	3447
Hymenocallis littoralis	0	0	0	0
Hypericum gramineum	2433	3239	2987	2408
Hypericum hypericoides	606	1503	1828	3485
Hypericum patulum	8804	10298	12032	17196
Hypoestes aristata	249	318	315	1
Hypoestes phyllostachya	22	17	25	7
Idesia polycarpa	718	946	1468	1893
Ilex crenata	1437	2333	3049	4906
Ilex paraguariensis	190	197	165	168
Ilex rotunda	95	121	398	841
Indigofera tinctoria	779	788	1059	180
Inga edulis	5	9	7	20
Ipomoea alba	76	70	83	209
Ipomoea cairica	1228	1566	1214	2923
Ipomoea carnea	137	118	103	211
Ipomoea pes-caprae	2	4	0	624
Ipomoea tricolor	678	638	709	192
Iris domestica	3131	4694	5976	6297
Iris japonica	4156	8009	10357	12968

species	current	RCP2.6	RCP4.5	RCP8.5
Iris sanguinea	2164	2475	347	1863
Isotoma fluviatilis	1005	1663	1280	2500
Ixia polystachya	383	813	590	697
Ixora coccinea	0	0	0	0
Jasminum dichotomum	0	0	0	0
Jasminum fluminense	163	145	80	62
Jasminum grandiflorum	3033	3543	3613	3804
Jasminum multiflorum	0	0	0	0
Jasminum polyanthum	2026	3078	3005	4055
Jasminum simplicifolium	346	764	633	2002
Justicia betonica	186	211	169	192
Justicia brandegeana	353	329	212	178
Justicia spicigera	0	0	0	0
Kalanchoe crenata	37	34	25	1
Kalopanax septemlobus	517	397	601	826
Kennedia rubicunda	266	514	479	532
Kigelia africana	102	81	67	51
Kolkwitzia amabilis	14668	16051	13306	212
Kummerowia stipulacea	176	901	728	2011
Kummerowia striata	679	1768	1792	4134
Kunzea ambigua	1018	2112	1841	2542
Kunzea ericoides	1008	1158	831	182
Lablab purpureus	1007	1639	1266	1617
Laelia rubescens	0	0	0	0
Lagerstroemia speciosa	0	0	0	0
Lampranthus spectabilis	1945	3370	3215	3874
Lawsonia inermis	0	0	0	2
Leonotis leonurus	736	1032	565	635
Leonotis ocyimifolia	284	567	212	6
Leonurus japonicus	954	1496	1591	1359
Leonurus sibiricus	510	672	723	1552
Leptospermum polygalifolium	425	761	723	914
Lespedeza bicolor	985	1764	2251	2655
Lespedeza cyrtobotrya	8	23	42	0
Lespedeza thunbergii	1721	1901	2572	333
Leucophyllum frutescens	72	359	471	680
Ligustrum obtusifolium	1638	2872	3215	10229
Ligustrum tschonoskii	198	297	615	830
Lilium formosanum	1528	2761	4176	8288
Limnobiium laevigatum	399	465	503	250
Limnocharis flava	0	0	0	211
Linaria maroccana	17489	18747	14919	16882
Linum grandiflorum	15546	15368	12440	1749
Liriope muscari	1019	2473	5180	4086
Liriope spicata	282	556	1033	2983
Livistona australis	152	244	241	458
Lobelia cardinalis	1675	3783	3770	9602
Lobelia inflata	3485	2077	2782	191
Lonicera sempervirens	1562	2310	3011	23
Lophostemon confertus	321	548	759	1462
Ludwigia alternifolia	0	104	391	995
Ludwigia octovalvis	114	145	121	1128
Ludwigia peruviana	492	822	743	1432
Luffa cylindrica	0	0	0	2
Luma apiculata	2599	3218	2874	3333
Lupinus mexicanus	0	0	0	0

species	current	RCP2.6	RCP4.5	RCP8.5
Lycianthes rantonnetii	3831	5168	5101	8628
Lycoris radiata	175	389	369	2043
Lysimachia japonica	213	199	459	113
Maackia amurensis	2886	4501	6737	11332
Magnolia grandiflora	16776	21678	22127	27286
Magnolia kobus	5249	6592	4472	16495
Magnolia obovata	834	2064	2539	15253
Malephora crocea	1061	1337	459	71
Mallotus philippensis	226	358	539	689
Malpighia emarginata	0	0	0	1
Malpighia glabra	0	0	0	0
Malpighia mexicana	0	0	0	0
Malus prunifolia	8835	4370	5756	34
Malva assurgentiflora	92	186	61	0
Malvaviscus arboreus	0	0	0	0
Mammea americana	0	0	0	0
Mandevilla laxa	209	283	427	89
Mangifera indica	93	89	83	118
Manilkara zapota	0	0	0	0
Maranta arundinacea	0	0	0	0
Margyricarpus pinnatus	2210	2873	2256	2458
Martynia annua	0	9	1	0
Maurandya antirrhiniflora	2865	3151	3632	583
Mazus pumilus	1908	3469	4573	5641
Melaleuca hypericifolia	558	1152	948	1179
Melastoma malabathricum	191	247	340	334
Melianthus major	759	1505	818	399
Melinis repens	1616	1670	1091	1090
Melothria pendula	19	76	302	1491
Miconia calvescens	1	1	10	6
Micranthemum umbrosum	142	375	617	1806
Mimosa pigra	0	0	0	1
Mimusops elengi	0	0	0	0
Molineria capitulata	32	40	194	392
Momordica balsamina	3521	3939	3323	3736
Momordica charantia	10	15	25	55
Momordica cochinchinensis	9	43	59	156
Monarda fistulosa	9327	9366	9320	12951
Monarda punctata	752	3234	4081	8728
Monochoria vaginalis	108	155	192	245
Moraea flaccida	1054	2016	1859	2728
Moraea fugax	537	621	231	9
Moraea miniata	409	868	421	344
Moraea polystachya	64	76	15	2
Moraea setifolia	1036	1839	1135	113
Morinda citrifolia	0	0	0	0
Moringa oleifera	5	1	9	29
Mucuna pruriens	5	3	4	1
Muehlenbeckia axillaris	498	799	1000	1355
Mukia maderaspatana	165	195	215	458
Musa acuminata	6840	8413	8120	11095
Myrica rubra	255	410	771	1167
Myrmecophila tibicinis	0	0	0	0
Nandina domestica	6306	10941	15084	23006
Nepeta racemosa	14417	14927	11644	4787
Neptunia oleracea	0	0	0	0

species	current	RCP2.6	RCP4.5	RCP8.5
Neptunia plena	0	0	0	0
Nertera granadensis	1564	1757	1332	1529
Nicotiana acuminata	2053	1377	771	3
Nicotiana longiflora	4951	6196	6191	10607
Nicotiana sylvestris	10675	12394	10947	19704
Nothoscordum bivalve	399	1678	2331	3805
Nymphaea nouchali	298	407	265	46
Nymphaea odorata	5889	6963	8164	19385
Ochroma pyramidale	0	0	0	0
Ocimum americanum	710	530	313	273
Ocimum gratissimum	228	228	180	252
Ocimum kilimandscharicum	24	70	76	177
Ocimum tenuiflorum	0	0	0	184
Odontonema tubaeforme	0	2	2	9
Oeceoclades maculata	32	26	44	34
Oenothera drummondii	2140	2442	3226	5382
Oenothera perennis	4209	3138	4757	3303
Opuntia aurantiaca	197	890	596	8
Opuntia basilaris	2517	2157	2246	0
Opuntia humifusa	1454	4830	5307	10246
Opuntia leucotricha	9	17	6	0
Opuntia polyacantha	659	773	806	210
Ornithogalum thyrsoides	497	777	290	1117
Orthrosanthus chimboracensis	147	403	216	142
Osmanthus heterophyllus	1364	2171	3077	5391
Osteospermum ecklonis	6422	9774	6946	4810
Oxalis depressa	1497	1418	854	0
Oxalis spiralis	589	1166	751	930
Oxalis tuberosa	0	18	0	0
Pachira aquatica	0	0	0	0
Paeonia lactiflora	16535	14703	12871	9111
Pandanus tectorius	30	31	46	52
Pandorea jasminoides	1069	2061	1770	1238
Pandorea pandorana	1707	3606	3366	3493
Papaver aculeatum	2046	3201	2337	31
Papaver nudicaule	14792	11554	8645	6561
Papaver orientale	14116	13017	8794	9356
Parmentiera aculeata	0	0	0	0
Parochetus communis	224	293	205	882
Passiflora amethystina	88	257	73	25
Passiflora coccinea	0	0	0	0
Passiflora foetida	77	55	70	88
Passiflora laurifolia	0	0	0	0
Passiflora ligularis	1	13	0	13
Passiflora mixta	268	438	1	38
Passiflora quadrangularis	0	0	0	0
Passiflora vitifolia	0	0	0	0
Pavonia hastata	1481	3838	4135	9911
Pelargonium alchemilloides	293	416	182	4
Pelargonium grossularioides	1126	1818	1355	0
Pennisetum alopecuroides	7703	11494	14083	20239
Pennisetum orientale	1817	2036	2288	1079
Penstemon gentianoides	0	0	0	0
Pentas lanceolata	215	158	84	305
Peperomia obtusifolia	0	0	0	0

species	current	RCP2.6	RCP4.5	RCP8.5
Pereskia aculeata	282	463	500	373
Perovskia atriplicifolia	6015	7181	6328	2180
Persea americana	645	1210	602	1022
Petrea volubilis	5	4	6	14
Petunia axillaris	8043	10466	10462	16106
Petunia integrifolia	8579	9227	11054	8504
Philadelphus mexicanus	0	0	0	1
Philadelphus pubescens	4897	3118	767	0
Philodendron bipinnatifidum	46	42	34	49
Philodendron ornatum	0	0	0	0
Phlox drummondii	11022	13487	12196	23059
Phoenix reclinata	75	63	43	12
Photinia glabra	422	660	1211	131
Phyllanthus amarus	0	0	0	0
Phyllanthus emblica	5	7	5	0
Pimenta dioica	0	0	0	0
Pinellia ternata	2827	4258	7586	21018
Piper aduncum	1	22	0	26
Piscidia piscipula	25	10	16	35
Pistacia chinensis	3530	5573	7277	8769
Pithecellobium dulce	0	1	22	6
Pittosporum bicolor	412	650	622	0
Pittosporum eugenoides	1137	1457	1210	2327
Plantago rugelii	279	868	885	3894
Plectranthus amboinicus	15	13	11	39
Plectranthus ciliatus	358	657	523	27
Plectranthus scutellarioides	0	0	0	0
Plectranthus verticillatus	753	1289	872	702
Plumbago zeylanica	987	1084	1383	1331
Plumeria obtusa	0	0	0	0
Plumeria rubra	177	125	145	101
Polygala lancifolia	47	74	79	672
Polygala senega	203	112	83	1685
Pomaderris lanigera	1155	2197	2043	2198
Populus acuminata	0	0	0	0
Portulacaria afra	2323	2454	1862	226
Pouteria caimito	0	0	0	0
Pratia repens	65	129	26	0
Prosopis chilensis	254	326	274	325
Prosopis juliflora	358	492	817	43
Prunus munsoniana	4	272	1320	737
Prunus pumila	8	47	208	413
Prunus salicina	2812	3511	3985	4618
Psoralea pinnata	804	1682	1420	2053
Pueraria montana	1979	3185	4328	6183
Pyracantha fortuneana	3831	5059	5573	369
Pyracantha koidzumii	4697	7328	10126	14678
Pyrus calleryana	5777	7803	10607	15201
Pyrus pyrifolia	421	622	1031	419
Quassia amara	0	0	0	0
Quercus acutissima	758	1242	1693	1236
Rauvolfia tetraphylla	0	0	0	0
Rauvolfia vomitoria	0	0	0	0
Rhamnus japonica	124	123	275	36
Rhaphiolepis indica	2499	4002	5094	9111
Rheum rhabarbarum	18059	15050	12761	7148

species	current	RCP2.6	RCP4.5	RCP8.5
Rhipsalis baccifera	8	10	6	28
Rhodanthe chlorocephala	3188	3376	1749	693
Rhododendron japonicum	1341	1954	2752	6938
Romneya coulteri	1529	2330	2027	224
Romulea flava	1446	1315	619	28
Rosa banksiae	4247	5218	6035	3316
Rosa chinensis	1992	2690	2744	279
Rosenbergiodendron formosum	0	0	0	0
Rubus ellipticus	1783	2645	2687	3737
Rubus rosifolius	2155	3956	4626	7399
Rudbeckia triloba	401	518	909	66
Ruellia brevifolia	156	251	277	367
Ruellia tuberosa	0	0	0	0
Russelia equisetiformis	240	175	129	408
Russelia sarmentosa	0	0	0	0
Sageretia thea	2808	3105	3298	3699
Sagittaria graminea	2568	4206	4632	6095
Sagittaria montevidensis	2185	5228	5921	8388
Salix gracilistyla	37	93	79	118
Salix humboldtiana	301	808	655	663
Salix nigra	1598	3253	3479	4818
Salvia africana-lutea	16	45	11	41
Salvia leucantha	490	872	602	969
Salvia leucophylla	379	454	441	0
Salvia microphylla	4026	5181	4641	1268
Salvia plebeia	3588	8140	11179	10230
Salvia splendens	4958	4736	4162	9846
Sansevieria hyacinthoides	153	214	197	11
Santalum album	0	0	0	0
Sanvitalia procumbens	1998	1932	519	758
Sauropus androgynus	136	281	252	159
Scadoxus multiflorus	72	64	30	5
Scaevola taccada	0	0	0	0
Schefflera arboricola	101	122	279	796
Schisandra chinensis	8	63	60	0
Schotia brachypetala	211	254	156	45
Senecio radicans	320	225	112	0
Senecio tamoides	314	493	515	0
Senna artemisioides	882	953	651	333
Senna italica	779	598	342	2
Senna siamea	0	2	39	1
Sesbania grandiflora	0	0	0	12
Sesbania sesban	131	126	109	0
Sisyrinchium atlanticum	1198	1773	2496	6637
Sisyrinchium micranthum	2285	2997	2302	2822
Sisyrinchium mucronatum	56	25	182	5585
Solandra maxima	65	53	42	78
Solanum aviculare	3881	4621	3969	4578
Solanum betaceum	5182	6713	3958	3806
Solanum capsicoides	599	1449	1380	1372
Solanum chrysotrichum	115	296	134	16
Solanum lanceifolium	0	0	0	0
Solanum mammosum	0	0	0	0
Solanum quitoense	0	0	0	0
Solanum retroflexum	694	977	307	1
Solanum seafortianum	319	365	321	389

species	current	RCP2.6	RCP4.5	RCP8.5
Solanum sessiliflorum	0	0	0	0
Solanum wendlandii	23	26	23	49
Solidago altissima	3147	5933	6123	15496
Solidago ptarmicoides	478	1345	1347	5681
Sophora tetraptera	74	144	195	1385
Sorbus alnifolia	533	787	1151	1646
Sparaxis grandiflora	29	71	4	0
Spathiphyllum cannifolium	0	0	0	0
Spathodea campanulata	0	0	0	1
Spathoglottis plicata	0	0	0	0
Spiraea prunifolia	2430	4296	5856	12465
Spondias dulcis	0	0	0	3
Spondias mombin	0	0	0	0
Stachytarpheta jamaicensis	0	0	0	0
Stachytarpheta mutabilis	5	5	0	0
Stapelia grandiflora	14	4	0	0
Stenocarpus sinuatus	28	108	117	156
Sterculia apetala	0	0	0	0
Stigmaphyllon ellipticum	0	0	0	0
Stipa tenuissima	10092	11096	7167	7355
Streptosolen jamesonii	3	2	0	209
Strophanthus gratus	0	0	0	0
Strophanthus preussii	0	0	0	0
Styrax japonicus	196	227	522	1184
Syagrus romanzoffiana	333	515	547	1172
Symplocos paniculata	1410	1482	1741	735
Syngonium angustatum	0	0	0	0
Syngonium podophyllum	0	0	0	0
Syringa reticulata	2943	1310	2964	0
Syzygium paniculatum	247	500	397	80
Tabebuia aurea	0	0	5	0
Tabernaemontana divaricata	0	0	0	35
Tacca leontopetaloides	0	0	0	0
Tagetes lucida	0	0	17	36
Tagetes tenuifolia	3458	2954	333	278
Tamarindus indica	46	35	51	33
Tamarix aphylla	3964	4340	5017	4148
Tamarix chinensis	1915	1961	1839	1969
Tanacetum coccineum	10506	9597	6615	34
Tecoma stans	648	851	1033	1187
Tephrosia candida	18	22	25	161
Tephrosia grandiflora	373	746	732	919
Tephrosia purpurea	629	548	397	384
Tephrosia vogelii	0	1	0	0
Terminalia catappa	0	0	0	0
Thalia geniculata	0	0	0	0
Theobroma cacao	0	0	0	0
Thunbergia alata	802	1288	890	1342
Thunbergia erecta	0	0	0	10
Thunbergia fragrans	47	40	89	84
Tigridia pavonia	301	492	622	6
Tillandsia stricta	46	42	20	85
Tillandsia usneoides	1048	2127	2233	4416
Tithonia rotundifolia	4	5	27	0
Toona ciliata	409	664	710	1129

species	current	RCP2.6	RCP4.5	RCP8.5
Trachelospermum asiaticum	421	659	1189	324
Trachelospermum jasminoides	8607	14689	16794	19063
Tradescantia spathacea	0	0	0	0
Triadica sebifera	1602	3002	4247	5889
Trichocentrum carthagenense	0	0	0	0
Trichosanthes cucumerina	0	0	0	0
Trichosanthes kirilowii	42	133	202	742
Tripsacum dactyloides	496	1530	1715	3298
Tulbaghia violacea	1122	1637	1081	278
Ullucus tuberosus	0	0	0	2
Ulmus parvifolia	5744	9461	11623	14695
Ursinia anthemoides	25	56	28	22
Ursinia speciosa	799	1660	1067	281
Utricularia livida	234	299	246	202
Vallisneria americana	7188	8459	8675	8454
Vallisneria nana	1595	2408	2239	2664
Verbena stricta	0	60	139	0
Vernicia fordii	807	1325	1643	1805
Veronica americana	9270	9532	7573	2879
Viburnum dilatatum	468	586	702	49
Viburnum plicatum	2808	2842	3780	11772

species	current	RCP2.6	RCP4.5	RCP8.5
Viburnum sieboldii	613	907	1136	834
Vigna caracalla	154	189	135	373
Viola hederacea	568	916	1022	944
Viola sororia	5135	4613	4839	4741
Vitex negundo	1826	3637	4829	5597
Vitis coignetiae	4491	5960	6402	6946
Washingtonia robusta	2018	1748	1346	17
Weigela floribunda	358	161	81	0
Westringia fruticosa	1018	1828	2335	3195
Wisteria floribunda	4100	4672	6755	10119
Xanthosoma sagittifolium	11	7	3	35
Ximenia americana	111	96	74	2
Zapoteca portoricensis	2	0	0	0
Zelkova serrata	5209	6827	7879	18763
Zingiber officinale	0	0	4	2
Zingiber zerumbet	0	0	0	0
Zinnia angustifolia	3	0	0	12
Zinnia elegans	15472	19176	17972	15670
Zinnia peruviana	811	1046	996	212
Ziziphus mauritiana	30	49	111	0
Ziziphus spina-christi	81	54	64	0

**SUPPORTING INFORMATION**

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**Appendix S2.** Detailed model selection and downscaling procedure.

The three different scenarios (RCP2.6, RCP4.5 and RCP8.5) we used reflect different radiative forcing trajectories for the 21<sup>st</sup> century relative to pre-industrial conditions: The RCP2.6 scenario assumes that radiative forcing peaks at  $\sim 3 \text{ W m}^{-2}$  before 2100 and then declines and is therefore referred to as mild scenario. In the intermediate scenario, RCP4.5, radiative forcing amounts to  $\sim 4.5 \text{ W m}^{-2}$  at stabilization after 2100, while in the severe scenario, RCP8.5, radiative forcing continues to rise throughout the 21<sup>st</sup> century and reaches  $> 8.5 \text{ W m}^{-2}$  in 2100 (Moss *et al.*, 2010). From all available models at the Cordex data portal ([www.euro-cordex.net](http://www.euro-cordex.net)) future climate data (daily near surface temperature, monthly precipitation) were extracted. For each scenario, we then selected one model providing a relatively smooth time series of future climate parameters, namely: ICHEC-EC-EARTH\_r12i1p1\_SMHI-RCA4, CNRM-CERFACS-CNRM-CM5\_r1i1p1\_SMHI-RCA4, EUR-11\_ICHEC-EC-EARTH\_r3i1p1\_DMI-HIRHAM5, from now on referred to as RCP2.6, RCP4.5 and RCP8.5, respectively. Subsequent processing of these data included the following steps: (1) download of hindcast projections of the specific climate models, (2) deriving minimum, maximum and mean monthly temperatures from the daily values, (3) calculation of anomalies, i.e. temperature differences and precipitation quotients between future climate and their hindcast projections, (4) spatial interpolation of these anomalies to the 10' resolution surface using the natural neighbour method, and (5) addition or multiplication, respectively, of the interpolated temperature and precipitation anomalies to/with the 10' resolution current climate data from WorldClim. The resulting annual time series of future minimum, maximum and mean temperature and precipitation sums per month were averaged for the years 2050-2100 and the six bioclimatic variables selected for modelling were then recalculated from these average values. For further details on the downscaling methods see Dullinger *et al.* (2012).

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<b>122 road and rail networks</b>	<b>2</b>	<b>3</b>	<b>5</b>
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Motorways and railways, including associated installations (stations, platforms, embankments). Minimum width for inclusion: 100 m. Including linear greenery.

#### 1.4 Artificial non-agricultural vegetated areas

<b>141 Green urban areas</b>	<b>30</b>	<b>75</b>	<b>100</b>
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Areas with vegetation within urban fabric, includes parks and cemeteries with vegetation, and mansions and their grounds.

<b>142 Sport and leisure facilities</b>	<b>2</b>	<b>5</b>	<b>20</b>
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Camping grounds, sports grounds, leisure parks, golf courses, racecourses, etc. Includes formal parks not surrounded by urban areas and cemeteries with vegetation situated outside of settlements, zoological and botanical gardens located outside of settlements, places of worship: e.g., convents, monasteries.

## 2. Agricultural areas

### 2.1 Arable land

<b>211 Non-irrigated arable land</b>	<b>1</b>	<b>2</b>	<b>10</b>
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Cereals, legumes, fodder crops, root crops and fallow land. Includes flowers and fruit trees (nurseries cultivation) and vegetables, whether open field, under plastic or glass (includes market gardening). Includes aromatic, medicinal and culinary plants, nurseries cultivation/gardens, and market gardening.

### 2.2 Permanent crops

<b>222 Fruit trees and berry plantations</b>	<b>0</b>	<b>1</b>	<b>5</b>
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Parcels planted with fruit trees or shrubs: single or mixed fruit species, fruit trees associated with permanently grassed surfaces, includes chestnut and walnut groves and plantations of Rosaceae.

### 2.4 Heterogeneous agricultural areas

<b>242 Complex cultivation patterns</b>	<b>1</b>	<b>2</b>	<b>10</b>
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Juxtaposition of small parcels of diverse annual crops, pastures and/or permanent crops, including hobby city gardens.

<b>243 Land occupied by agriculture, with significant natural vegetation</b>	<b>1</b>	<b>2</b>	<b>5</b>
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Areas principally occupied by agriculture, interspersed with significant natural areas, includes sporadically occurring houses of rural settlements or farm buildings and their gardens.

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Appendix S4. Information on model performance.

The table lists for all species and each modelling technique the mean TSS over all replicates and the percentage of replicates with TSS < 0.5.

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
Abelmoschus moschatus	0.823	0	0.823	0	0.856	0	0.847	0
Abrus precatorius	0.823	0	0.829	0	0.876	0	0.863	0
Acacia pravissima	0.968	0	0.934	0	0.943	0	0.941	0
Acalypha hispida	0.736	0	0.708	0	0.804	0	0.802	0
Acalypha wilkesiana	0.759	0	0.689	0	0.809	0	0.794	0
Acanthocereus tetragonus	0.895	0	0.888	0	0.916	0	0.917	0
Acer buergerianum	0.827	0	0.783	0	0.891	0	0.864	3.3
Acer japonicum	0.871	0	0.937	0	0.922	0	0.902	0
Acer palmatum	0.884	0	0.881	0	0.921	0	0.909	0
Acer spicatum	0.925	0	0.938	0	0.962	0	0.959	0
Actinidia arguta	0.904	0	0.858	0	0.945	0	0.944	0
Actinidia polygama	0.96	0	0.907	0	0.947	0	0.948	0
Adansonia digitata	0.808	0	0.761	0	0.825	0	0.824	0
Adenanthera pavonina	0.813	0	0.758	0	0.876	0	0.868	0
Adenium obesum	0.841	0	0.805	0	0.844	0	0.846	0
Aesculus glabra	0.911	0	0.888	0	0.931	0	0.922	0
Agastache rugosa	0.864	0	0.803	0	0.862	0	0.848	0
Ageratina ligustrina	0.907	0	0.91	0	0.923	0	0.917	0
Ageratum conyzoides	0.759	0	0.761	0	0.874	0	0.852	0
Albizia chinensis	0.878	0	0.823	0	0.87	0	0.87	0
Albizia lebeck	0.723	0	0.75	0	0.793	0	0.787	0
Albizia saman	0.807	0	0.796	0	0.852	0	0.85	0
Albuca bracteata	0.749	0	0.898	0	0.906	0	0.922	0
Albuca canadensis	0.937	0	0.873	33.3	0.972	0	0.956	0
Aleurites moluccana	0.849	0	0.81	0	0.848	0	0.848	0
Allamanda cathartica	0.823	0	0.828	0	0.873	0	0.871	0
Allium tuberosum	0.765	0	0.707	0	0.807	0	0.795	0
Allocasuarina littoralis	0.967	0	0.979	0	0.98	0	0.973	0
Allocasuarina verticillata	0.964	0	0.969	0	0.974	0	0.97	0
Alnus nepalensis	0.94	0	0.929	0	0.952	0	0.946	0
Alocasia macrorrhizos	0.835	0	0.837	0	0.861	0	0.847	0
Alstonia scholaris	0.882	0	0.785	0	0.842	0	0.844	0
Alternanthera ficoidea	0.754	0	0.815	0	0.837	0	0.83	0
Ammobium alatum	0.845	0	0.831	0	0.944	0	0.94	0
Ampelopsis glandulosa	0.9	0	0.86	0	0.944	0	0.937	0
Anacardium occidentale	0.811	0	0.818	0	0.889	0	0.885	0
Ananas comosus	0.717	0	0.73	0	0.802	0	0.781	0
Angelonia angustifolia	0.839	0	0.774	0	0.882	0	0.885	0
Anigozanthos flavidus	0.807	0	0.907	0	0.955	0	0.942	0
Annona cherimola	0.786	0	0.834	0	0.866	0	0.852	0
Annona glabra	0.845	0	0.872	0	0.885	0	0.878	0
Annona muricata	0.823	0	0.827	0	0.861	0	0.855	0

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
<i>Annona reticulata</i>	0.812	0	0.826	0	0.879	0	0.873	0
<i>Annona squamosa</i>	0.807	0	0.799	0	0.822	0	0.813	0
<i>Anoda cristata</i>	0.677	0	0.75	0	0.845	0	0.794	0
<i>Anthurium pentaphyllum</i>	0.887	0	0.873	0	0.914	0	0.915	0
<i>Anthurium schlechtendalii</i>	0.885	0	0.924	0	0.924	0	0.923	0
<i>Antigonon leptopus</i>	0.733	0	0.75	0	0.816	0	0.799	0
<i>Apodytes dimidiata</i>	0.858	0	0.883	0	0.925	0	0.907	0
<i>Archontophoenix cunninghamiana</i>	0.94	0	0.912	0	0.967	0	0.963	0
<i>Arctotis fastuosa</i>	0.884	0	0.88	0	0.944	0	0.944	0
<i>Ardisia crenata</i>	0.882	0	0.873	0	0.897	0	0.894	0
<i>Ardisia japonica</i>	0.965	0	0.953	0	0.971	0	0.967	0
<i>Aristolochia grandiflora</i>	0.84	0	0.819	0	0.856	0	0.854	0
<i>Artemisia ludoviciana</i>	0.778	0	0.81	0	0.905	0	0.842	0
<i>Artocarpus altilis</i>	0.849	0	0.829	0	0.872	0	0.868	0
<i>Artocarpus heterophyllus</i>	0.767	0	0.784	0	0.854	0	0.836	0
<i>Arum palaestinum</i>	0.874	0	0.846	0	0.945	0	0.93	0
<i>Arundina graminifolia</i>	0.856	0	0.897	0	0.892	0	0.887	0
<i>Asimina triloba</i>	0.949	0	0.956	0	0.963	0	0.954	0
<i>Asparagus africanus</i>	0.816	0	0.817	0	0.862	0	0.848	0
<i>Asparagus declinatus</i>	0.937	0	0.89	0	0.937	0	0.92	0
<i>Asparagus falcatus</i>	0.826	0	0.846	0	0.872	0	0.854	0
<i>Asparagus retrofractus</i>	0.947	0	0.96	0	0.959	0	0.951	0
<i>Asparagus scandens</i>	0.977	0	0.9	0	0.964	0	0.958	0
<i>Asparagus virgatus</i>	0.917	0	0.913	33.3	0.954	0	0.936	0
<i>Atriplex canescens</i>	0.78	0	0.805	0	0.917	0	0.872	0
<i>Atriplex nummularia</i>	0.908	0	0.91	0	0.958	0	0.952	0
<i>Averrhoa carambola</i>	0.831	0	0.754	0	0.791	0	0.794	0
<i>Banisteriopsis caapi</i>	0.801	0	0.708	0	0.912	0	0.906	0
<i>Banksia ericifolia</i>	0.961	0	0.935	0	0.987	0	0.975	0
<i>Barleria cristata</i>	0.673	0	0.618	0	0.769	6.7	0.774	3.3
<i>Barringtonia asiatica</i>	0.914	0	0.824	0	0.918	0	0.909	0
<i>Bartlettina sordida</i>	0.791	0	0.753	0	0.857	0	0.842	0
<i>Basella alba</i>	0.72	0	0.766	0	0.809	0	0.805	0
<i>Bauhinia galpinii</i>	0.894	0	0.865	0	0.919	0	0.907	0
<i>Bauhinia purpurea</i>	0.741	0	0.678	0	0.815	0	0.81	0
<i>Bauhinia variegata</i>	0.748	0	0.763	0	0.77	0	0.773	0
<i>Begonia cucullata</i>	0.782	0	0.733	0	0.858	0	0.848	0
<i>Begonia heracleifolia</i>	0.883	0	0.844	0	0.927	0	0.911	0
<i>Begonia humilis</i>	0.847	0	0.873	0	0.902	0	0.895	0
<i>Begonia nelumbiifolia</i>	0.844	0	0.786	0	0.879	0	0.875	0
<i>Berberis glaucocarpa</i>	0.92	0	0.801	0	0.961	0	0.942	0
<i>Berberis repens</i>	0.916	0	0.922	0	0.947	0	0.943	0
<i>Bertholletia excelsa</i>	0.942	0	0.741	33.3	0.925	0	0.923	0
<i>Betula platyphylla</i>	NaN	100	0.851	0	0.881	0	0.873	0
<i>Bignonia capreolata</i>	0.939	0	0.917	0	0.95	0	0.945	0
<i>Billardiera heterophylla</i>	0.866	0	0.886	0	0.89	0	0.883	0
<i>Bixa orellana</i>	0.807	0	0.801	0	0.881	0	0.877	0
<i>Bocconia frutescens</i>	0.818	0	0.816	0	0.913	0	0.905	0
<i>Boltonia asteroides</i>	0.849	0	0.862	0	0.929	0	0.914	0
<i>Bomarea multiflora</i>	0.957	0	0.936	0	0.966	0	0.97	0
<i>Bombax ceiba</i>	0.854	0	0.889	0	0.909	0	0.892	0
<i>Bouteloua curtipendula</i>	0.753	0	0.792	0	0.904	0	0.847	0
<i>Brachychiton acerifolius</i>	0.95	0	0.946	0	0.932	0	0.929	0
<i>Brachychiton discolor</i>	0.771	0	0.871	0	0.872	0	0.871	0
<i>Brachychiton populneus</i>	0.965	0	0.963	0	0.975	0	0.97	0
<i>Brexia madagascariensis</i>	0.916	0	0.916	0	0.942	0	0.944	0
<i>Breynia disticha</i>	0.77	0	0.791	0	0.86	0	0.857	0
<i>Bromus briziformis</i>	0.954	0	0.936	0	0.925	0	0.917	0
<i>Bromus danthoniae</i>	0.845	0	0.91	0	0.885	0	0.876	0
<i>Browallia americana</i>	0.83	0	0.871	0	0.909	0	0.903	0
<i>Brownea coccinea</i>	0.933	0	0.898	0	0.933	0	0.915	0
<i>Brownea grandiceps</i>	0.88	0	0.821	0	0.944	0	0.936	0
<i>Brugmansia sanguinea</i>	0.884	0	0.846	0	0.963	0	0.95	0
<i>Brunfelsia uniflora</i>	0.721	0	0.791	0	0.847	0	0.822	0

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
Bucida buceras	0.875	0	0.885	0	0.928	0	0.922	0
Buddleja asiatica	0.823	0	0.817	0	0.842	0	0.836	0
Buddleja indica	0.968	0	0.945	0	0.972	0	0.96	0
Buddleja saligna	0.95	0	0.941	0	0.942	0	0.927	0
Buddleja salviifolia	0.937	0	0.939	0	0.952	0	0.937	0
Buddleja stachyoides	0.744	0	0.821	0	0.936	0	0.904	0
Bulbine semibarbata	0.921	0	0.924	0	0.961	0	0.953	0
Bursera simaruba	0.813	0	0.826	0	0.863	0	0.846	0
Caesalpinia coriaria	0.84	0	0.869	0	0.871	0	0.87	0
Caesalpinia pulcherrima	0.691	0	0.723	0	0.816	0	0.801	0
Caladium bicolor	0.776	0	0.822	0	0.872	0	0.867	0
Calceolaria chelidonioides	0.866	0	0.814	0	0.902	0	0.909	0
Calliandra haematocephala	0.798	0	0.78	0	0.82	0	0.798	0
Calliandra houstoniana	0.838	0	0.889	0	0.91	0	0.891	0
Calliandra surinamensis	0.842	0	0.808	0	0.9	0	0.903	0
Callicarpa dichotoma	0.902	0	0.828	0	0.955	0	0.93	0
Callicarpa japonica	0.959	0	0.939	0	0.96	0	0.956	0
Callisia repens	0.771	0	0.783	0	0.837	0	0.825	0
Callistemon speciosus	0.756	0	0.816	0	0.861	0	0.831	0
Callistemon viminalis	0.818	0	0.856	0	0.9	0	0.886	0
Calophyllum inophyllum	0.93	0	0.932	0	0.912	0	0.91	0
Calotropis procera	0.699	0	0.746	0	0.807	0	0.772	0
Calystegia hederacea	0.935	0	0.918	0	0.974	0	0.969	0
Camellia japonica	0.895	0	0.912	0	0.913	0	0.912	0
Camellia sinensis	0.916	0	0.856	0	0.922	0	0.914	0
Campanula punctata	0.901	0	0.898	0	0.946	0	0.94	0
Cananga odorata	0.875	0	0.863	0	0.864	0	0.857	0
Canavalia cathartica	0.805	0	0.76	0	0.837	0	0.823	0
Canavalia ensiformis	0.762	0	0.713	0	0.75	0	0.75	0
Canna glauca	0.706	0	0.697	0	0.813	0	0.802	0
Cardiocrinum cordatum	0.977	0	0.96	0	0.996	0	0.991	0
Carica papaya	0.758	0	0.768	0	0.832	0	0.821	0
Carissa macrocarpa	0.649	0	0.596	33.3	0.813	0	0.773	0
Carpinus caroliniana	0.843	0	0.87	0	0.932	0	0.916	0
Carya illinoensis	0.849	0	0.851	0	0.87	0	0.859	0
Cascabela thevetia	0.8	0	0.727	0	0.773	3.3	0.73	3.3
Cassia fistula	0.725	0	0.704	0	0.801	0	0.792	0
Cassia grandis	0.801	0	0.807	0	0.878	0	0.876	0
Castanea mollissima	0.885	0	0.835	0	0.923	0	0.906	0
Castanospermum australe	0.954	0	0.903	0	0.938	0	0.929	0
Casuarina cunninghamiana	0.853	0	0.854	0	0.922	0	0.897	0
Casuarina glauca	0.967	0	0.934	0	0.976	0	0.975	0
Cedrela odorata	0.8	0	0.8	0	0.881	0	0.869	0
Ceiba pentandra	0.782	0	0.792	0	0.857	0	0.854	0
Celastrus scandens	0.912	0	0.926	0	0.968	0	0.957	0
Centrosema virginianum	0.735	0	0.769	0	0.859	0	0.84	0
Ceratopetalum gummiferum	0.985	0	0.985	0	0.994	0	0.986	0
Ceratotheca triloba	NaN	100	0.933	0	0.976	0	0.957	0
Cercestis mirabilis	0.931	0	0.932	0	0.951	0	0.945	0
Cercidiphyllum japonicum	0.859	0	0.85	0	0.912	0	0.908	0
Cestrum aurantiacum	0.81	0	0.763	0	0.875	0	0.865	0
Cestrum fasciculatum	0.742	33.3	0.825	0	0.905	0	0.887	0
Cestrum nocturnum	0.819	0	0.821	0	0.863	0	0.844	0
Chamaedorea elegans	0.879	0	0.781	0	0.92	0	0.907	0
Chamelaucium uncinatum	0.808	0	0.917	0	0.953	0	0.931	0
Cheilocostus speciosus	0.837	0	0.845	0	0.877	0	0.879	0
Chenopodium quinoa	0.837	0	0.77	0	0.875	0	0.858	0
Chrysobalanus icaco	0.844	0	0.84	0	0.9	0	0.891	0
Chrysophyllum cainito	0.845	0	0.826	0	0.852	0	0.84	0
Chrysophyllum oliviforme	0.859	0	0.932	0	0.915	0	0.892	0
Chrysothemis pulchella	0.91	0	0.886	0	0.924	0	0.924	0
Cinnamomum camphora	0.871	0	0.862	0	0.905	0	0.902	0
Cissus alata	0.878	0	0.729	0	0.91	0	0.914	0
Cissus antarctica	0.995	0	0.985	0	0.994	0	0.991	0
Cissus quadrangularis	0.862	0	0.859	0	0.863	0	0.863	0

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
Cissus rotundifolia	0.884	0	0.868	0	0.886	0	0.884	0
Cissus verticillata	0.785	0	0.773	0	0.89	0	0.868	0
Citharexylum spinosum	0.863	0	0.817	0	0.898	0	0.89	0
Citrus aurantiifolia	0.793	0	0.772	0	0.817	0	0.812	0
Citrus maxima	0.717	0	0.727	0	0.811	0	0.797	0
Clarkia amoena	0.856	0	0.898	0	0.942	0	0.927	0
Clarkia pulchella	0.886	0	0.893	0	0.925	0	0.915	0
Clematis paniculata	0.966	0	0.945	0	0.973	0	0.964	0
Clematis tangutica	0.84	0	0.848	0	0.925	0	0.914	0
Clematis terniflora	0.832	0	0.898	0	0.928	0	0.915	0
Cleome gynandra	0.704	0	0.729	0	0.797	0	0.772	0
Clerodendrum bungei	0.918	0	0.837	0	0.833	0	0.813	0
Clerodendrum chinense	0.809	0	0.79	0	0.847	0	0.835	0
Clerodendrum splendens	0.897	0	0.887	0	0.917	0	0.911	0
Clerodendrum trichotomum	0.921	0	0.905	0	0.934	0	0.926	0
Cleyera japonica	0.952	0	0.952	0	0.957	0	0.948	0
Clidemia hirta	0.857	0	0.853	0	0.925	0	0.919	0
Clitoria ternatea	0.74	0	0.739	0	0.832	0	0.823	0
Clusia rosea	0.837	0	0.844	0	0.881	0	0.881	0
Cobaea scandens	0.875	0	0.792	0	0.917	0	0.912	0
Coccinia grandis	0.718	0	0.719	0	0.737	0	0.739	0
Coccoloba uvifera	0.835	0	0.879	0	0.857	0	0.856	0
Cochlospermum vitifolium	0.82	0	0.819	0	0.862	0	0.856	0
Cocos nucifera	0.817	0	0.806	0	0.814	0	0.819	0
Codiaeum variegatum	0.848	0	0.831	0	0.891	0	0.881	0
Coffea liberica	0.86	0	0.831	0	0.91	0	0.903	0
Cola acuminata	0.917	0	0.853	0	0.867	0	0.863	0
Combretum grandiflorum	0.952	0	0.915	0	0.909	0	0.9	0
Combretum indicum	0.757	0	0.747	0	0.785	0	0.782	0
Commelina benghalensis	0.669	0	0.712	0	0.806	0	0.768	0
Commelina coelestis	0.887	0	0.846	0	0.905	0	0.9	0
Conicosia pugioniformis	0.988	0	0.969	0	0.968	0	0.951	0
Coprosma robusta	0.981	0	0.941	0	0.993	0	0.987	0
Corchorus olitorius	0.741	0	0.746	0	0.798	0	0.78	0
Cordyline fruticosa	0.807	0	0.732	0	0.839	0	0.844	0
Cortaderia jubata	0.86	0	0.823	0	0.918	0	0.907	0
Corylus heterophylla	0.766	0	0.783	0	0.903	0	0.892	0
Corymbia citriodora	0.858	0	0.863	0	0.895	0	0.875	0
Cosmos sulphureus	0.683	0	0.701	0	0.791	0	0.771	0
Cotoneaster glaucophyllus	0.942	0	0.925	0	0.968	0	0.956	0
Couroupita guianensis	0.904	0	0.859	0	0.913	0	0.926	0
Crassula ericoides	0.968	0	0.886	0	0.961	0	0.95	0
Crataegus pubescens	0.935	0	0.919	0	0.944	0	0.937	0
Crescentia cujete	0.803	0	0.81	0	0.853	0	0.849	0
Crinum asiaticum	0.872	0	0.853	0	0.869	0	0.873	0
Crinum zeylanicum	0.864	0	0.837	0	0.853	0	0.856	0
Crotalaria capensis	0.944	0	0.921	0	0.952	0	0.942	0
Crotalaria juncea	0.738	0	0.754	0	0.803	0	0.786	0
Crotalaria micans	0.778	0	0.791	0	0.873	0	0.859	0
Crotalaria retusa	0.78	0	0.793	0	0.868	0	0.864	0
Cucumis anguria	0.775	0	0.793	0	0.823	0	0.811	0
Cucumis dipsaceus	0.706	0	0.664	0	0.82	0	0.833	0
Cucumis metuliferus	0.703	0	0.781	0	0.784	0	0.779	0
Cucurbita argyrosperma	0.795	0	0.811	0	0.839	0	0.829	0
Cucurbita ficifolia	0.778	0	0.777	0	0.802	0	0.793	0
Cucurbita moschata	0.648	0	0.677	0	0.766	0	0.733	0
Cuphea hyssopifolia	0.79	0	0.811	0	0.83	0	0.815	0
Curcuma longa	0.881	0	0.792	0	0.844	0	0.858	0
Cymbopogon nardus	0.892	0	0.883	0	0.906	0	0.9	0
Cynoglossum amabile	0.799	0	0.838	0	0.821	0	0.806	0
Cynoglossum zeylanicum	0.871	0	0.852	0	0.878	0	0.872	0
Cyperus albstriatus	0.921	0	0.913	0	0.946	0	0.933	0
Cytisus proliferus	0.901	0	0.909	0	0.942	0	0.935	0
Dahlia imperialis	0.912	0	0.917	0	0.923	0	0.92	0
Dahlia pinnata	0.814	0	0.858	0	0.886	0	0.874	0

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
<i>Datura ceratocaula</i>	0.925	0	0.88	0	0.896	0	0.894	0
<i>Debregeasia longifolia</i>	0.804	0	0.812	0	0.902	0	0.884	0
<i>Delonix regia</i>	0.752	0	0.72	0	0.787	0	0.777	0
<i>Desmodium elegans</i>	0.843	0	0.878	0	0.921	0	0.904	0
<i>Deutzia crenata</i>	0.94	0	0.96	0	0.962	0	0.956	0
<i>Deutzia gracilis</i>	0.913	0	0.859	0	0.942	0	0.928	0
<i>Dianella ensifolia</i>	0.881	0	0.865	0	0.881	0	0.871	0
<i>Dieffenbachia seguine</i>	0.827	0	0.809	0	0.919	0	0.91	0
<i>Dimorphotheca cuneata</i>	0.957	0	0.966	0	0.969	0	0.955	0
<i>Dimorphotheca pluvialis</i>	0.869	0	0.791	0	0.907	0	0.895	0
<i>Dimorphotheca sinuata</i>	0.855	0	0.882	0	0.904	0	0.891	0
<i>Dioscorea bulbifera</i>	0.776	0	0.819	0	0.867	0	0.853	0
<i>Dioscorea mexicana</i>	0.842	0	0.806	0	0.883	0	0.879	0
<i>Dioscorea polystachya</i>	0.926	0	0.749	0	0.91	0	0.918	0
<i>Diospyros virginiana</i>	0.915	0	0.928	0	0.945	0	0.931	0
<i>Diplocyclos palmatus</i>	0.833	0	0.799	0	0.865	0	0.849	0
<i>Dodonaea viscosa</i>	0.852	0	0.874	0	0.922	0	0.914	0
<i>Dolichandra unguis-cati</i>	0.729	0	0.756	0	0.857	0	0.838	0
<i>Dombeya burgessiae</i>	0.906	0	0.849	0	0.907	0	0.892	0
<i>Dombeya tiliacea</i>	0.829	0	0.795	0	0.967	0	0.95	0
<i>Dorotheanthus bellidiformis</i>	0.939	0	0.946	0	0.978	0	0.969	0
<i>Dorstenia contrajerva</i>	0.819	0	0.853	0	0.891	0	0.882	0
<i>Dracaena fragrans</i>	0.775	0	0.726	0	0.82	0	0.815	0
<i>Dracaena reflexa</i>	0.906	0	0.907	0	0.927	0	0.921	0
<i>Drosera aliciae</i>	0.906	0	0.879	0	0.928	0	0.916	0
<i>Drosera binata</i>	0.957	0	0.884	0	0.969	0	0.959	0
<i>Drosera capillaris</i>	0.908	0	0.906	0	0.914	0	0.902	0
<i>Echeveria secunda</i>	0.956	0	0.829	0	0.925	0	0.919	0
<i>Echinochloa polystachya</i>	0.778	0	0.81	0	0.88	0	0.852	0
<i>Echinodorus cordifolius</i>	0.842	0	0.862	0	0.895	0	0.886	0
<i>Echinodorus subalatus</i>	0.881	0	0.863	0	0.909	0	0.901	0
<i>Ehretia acuminata</i>	0.92	0	0.911	0	0.948	0	0.94	0
<i>Eichhornia azurea</i>	0.839	0	0.857	0	0.851	0	0.839	0
<i>Elaeis guineensis</i>	0.8	0	0.682	0	0.86	0	0.851	0
<i>Embothrium coccineum</i>	0.98	0	0.907	0	0.985	0	0.977	0
<i>Emilia sonchifolia</i>	0.771	0	0.79	0	0.867	0	0.854	0
<i>Empetrum rubrum</i>	0.572	33.3	0.859	0	0.962	0	0.956	0
<i>Entada phaseoloides</i>	0.905	0	0.855	0	0.936	0	0.948	36.7
<i>Epacris impressa</i>	0.981	0	0.981	0	0.989	0	0.975	0
<i>Epipremnum pinnatum</i>	0.758	0	0.804	0	0.821	0	0.82	0
<i>Eragrostis trichodes</i>	0.938	0	0.92	0	0.933	0	0.924	0
<i>Erica glandulosa</i>	0.992	0	0.949	0	0.964	0	0.962	0
<i>Eriochloa villosa</i>	0.888	0	0.867	0	0.923	0	0.902	0
<i>Erythrina crista-galli</i>	0.773	0	0.771	0	0.836	0	0.819	0
<i>Erythrina herbacea</i>	0.909	0	0.934	0	0.912	0	0.9	0
<i>Etlingera elatior</i>	0.832	0	0.782	0	0.84	0	0.828	0
<i>Eucalyptus cinerea</i>	0.976	0	0.902	0	0.902	0	0.9	0
<i>Eucalyptus cladocalyx</i>	0.946	0	0.928	0	0.93	0	0.924	0
<i>Eucalyptus comuta</i>	0.935	0	0.936	0	0.965	0	0.966	3.3
<i>Eucalyptus dalrympleana</i>	0.992	0	0.996	0	0.987	0	0.981	0
<i>Eucalyptus goniocalyx</i>	0.97	0	0.966	0	0.986	0	0.977	0
<i>Eucalyptus leucoxylon</i>	0.942	0	0.953	0	0.972	0	0.97	0
<i>Eucalyptus nitens</i>	0.931	0	0.879	0	0.953	0	0.978	90
<i>Eucalyptus ovata</i>	0.962	0	0.975	0	0.984	0	0.977	0
<i>Eucalyptus rubida</i>	0.984	0	0.989	0	0.984	0	0.979	0
<i>Eugenia uniflora</i>	0.746	0	0.793	0	0.863	0	0.852	0
<i>Eulophia alta</i>	0.854	0	0.835	0	0.888	0	0.877	0
<i>Euonymus alatus</i>	0.904	0	0.9	0	0.938	0	0.926	0
<i>Euonymus hamiltonianus</i>	0.752	0	0.849	0	0.865	0	0.846	0
<i>Euphorbia balsamifera</i>	0.904	0	0.844	0	0.905	0	0.898	0
<i>Euphorbia leucocephala</i>	0.73	0	0.776	0	0.843	0	0.85	0
<i>Euphorbia mauritanica</i>	0.949	0	0.936	0	0.967	0	0.95	0
<i>Euphorbia tithymaloides</i>	0.78	0	0.798	0	0.831	0	0.817	0
<i>Euryops abrotanifolius</i>	0.96	0	0.821	0	0.973	0	0.95	0
<i>Euryops chrysanthemoides</i>	0.866	0	0.817	0	0.97	0	0.973	0

species	model	GLM		GAM		RF		GBM	
		Mean TSS	% TSS < 0.5						
Ficus auriculata		0.863	0	0.715	0	0.9	0	0.885	0
Ficus benjamina		0.786	0	0.801	0	0.813	0	0.809	0
Ficus drupacea		0.911	0	0.819	0	0.872	0	0.859	0
Ficus elastica		0.535	66.7	0.597	0	0.717	6.7	0.714	6.7
Ficus erecta		0.944	0	0.939	0	0.968	0	0.96	0
Ficus lutea		0.835	0	0.813	0	0.863	0	0.862	0
Ficus palmata		0.664	0	0.834	0	0.843	0	0.823	0
Ficus racemosa		0.885	0	0.898	0	0.919	0	0.91	0
Ficus virens		0.851	0	0.86	0	0.921	0	0.885	0
Firmiana simplex		0.9	0	0.872	0	0.9	0	0.872	0
Fragaria chiloensis		0.859	0	0.878	0	0.911	0	0.903	0
Frangula purshiana		0.97	0	0.94	0	0.96	0	0.947	0
Fraxinus nigra		0.912	0	0.926	0	0.96	0	0.951	0
Fraxinus uhdei		0.879	0	0.863	0	0.879	0	0.866	0
Freesia laxa		0.89	0	0.913	0	0.938	0	0.92	0
Fuchsia paniculata		0.922	0	0.918	0	0.935	0	0.914	0
Galphimia glauca		0.888	0	0.878	0	0.891	0	0.886	0
Galphimia gracilis		0.771	0	0.696	0	0.843	0	0.817	0
Garcinia livingstonei		0.868	0	0.864	0	0.869	0	0.848	0
Gardenia jasminoides		0.838	0	0.86	0	0.84	0	0.828	0
Geitonoplesium cymosum		0.988	0	0.984	0	0.984	0	0.979	0
Geranium incanum		0.906	0	0.914	0	0.928	0	0.913	0
Geranium thunbergii		0.9	0	0.775	0	0.961	0	0.956	0
Gerbera jamesonii		0.805	0	0.795	0	0.87	3.3	0.851	3.3
Gibasis pellucida		0.838	0	0.798	0	0.865	0	0.851	0
Gilia tricolor		0.902	0	0.923	0	0.948	0	0.939	0
Gladiolus papilio		0.933	0	0.93	33.3	0.961	0	0.941	0
Gladiolus tristis		0.866	0	0.915	0	0.947	0	0.931	0
Gladiolus undulatus		0.922	0	0.925	0	0.955	0	0.942	0
Glandularia peruviana		0.926	0	0.918	0	0.943	0	0.929	0
Glandularia tenera		0.895	0	0.833	0	0.919	0	0.913	0
Gloriosa superba		0.781	0	0.805	0	0.876	0	0.869	0
Gloxinia perennis		0.855	0	0.786	0	0.905	0	0.907	0
Gloxinia sylvatica		0.764	0	0.811	0	0.917	0	0.903	0
Gmelina arborea		0.781	0	0.742	0	0.805	0	0.798	0
Gomphrena globosa		0.687	0	0.658	0	0.664	3.3	0.651	3.3
Grevillea banksii		0.706	33.3	0.861	0	0.869	0	0.859	0
Grevillea juniperina		0.949	0	0.935	0	0.978	0	0.972	0
Grevillea rosmarinifolia		0.926	0	0.919	0	0.98	0	0.969	0
Hakea eriantha		0.978	0	0.97	0	0.978	0	0.972	0
Hakea laurina		0.912	0	0.914	0	0.963	0	0.963	0
Haloragis erecta		0.987	0	0.939	0	0.953	0	0.945	0
Hamelia patens		0.781	0	0.81	0	0.892	0	0.872	0
Hardenbergia comptoniana		0.752	0	0.868	0	0.944	0	0.93	0
Harpephyllum caffrum		0.846	0	0.88	0	0.913	0	0.903	0
Harrisia pomanensis		0.784	0	0.923	0	0.945	0	0.894	0
Hebenstretia dentata		0.869	0	0.84	0	0.911	0	0.903	0
Hedychium coronarium		0.806	0	0.811	0	0.844	0	0.835	0
Heimia salicifolia		0.803	0	0.839	0	0.887	0	0.874	0
Helianthium bolivianum		0.801	0	0.803	0	0.86	0	0.857	0
Helianthium tenellum		0.691	0	0.721	0	0.815	0	0.79	0
Helenium bigelovii		0.939	0	0.944	0	0.956	0	0.953	0
Helianthus angustifolius		0.962	0	0.948	0	0.916	0	0.916	0
Helianthus debilis		0.735	0	0.72	0	0.817	0	0.807	0
Helianthus giganteus		0.878	0	0.817	0	0.886	0	0.875	0
Helianthus salicifolius		0.925	0	0.954	0	0.987	0	0.98	0
Herbertia lahue		0.915	0	0.918	0	0.927	0	0.903	0
Hesperantha coccinea		0.968	0	0.9	0	0.962	0	0.95	0
Hesperantha falcata		0.938	0	0.949	0	0.975	0	0.962	0
Heterocentron subtripinervium		0.917	0	0.865	0	0.942	0	0.909	0
Heterotis rotundifolia		0.855	0	0.846	0	0.875	0	0.871	0
Hevea brasiliensis		0.846	0	0.821	0	0.882	0	0.883	0
Hibiscus acetosella		0.803	0	0.699	0	0.851	0	0.851	0
Hibiscus diversifolius		0.828	0	0.82	0	0.871	0	0.869	0

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
Hibiscus mutabilis	0.792	0	0.721	0	0.833	0	0.828	0
Hibiscus sabdariffa	0.735	0	0.679	0	0.797	0	0.795	0
Hibiscus schizopetalus	0.753	0	0.704	0	0.774	3.3	0.769	0
Hibiscus tiliaceus	0.858	0	0.852	0	0.898	0	0.884	0
Hippeastrum puniceum	0.744	0	0.642	0	0.85	0	0.833	0
Hippobroma longiflora	0.842	0	0.822	0	0.881	0	0.877	0
Hiptage benghalensis	0.909	0	0.73	33.3	0.951	0	0.909	0
Holmskioldia sanguinea	0.689	0	0.761	0	0.811	3.3	0.797	0
Homalanthus populifolius	0.937	0	0.922	0	0.95	0	0.944	0
Homalocladium platycladum	0.783	0	0.703	0	0.842	0	0.818	0
Houstonia caerulea	0.979	0	0.955	0	0.986	0	0.972	0
Houttuynia cordata	0.849	0	0.833	0	0.894	0	0.885	0
Hovea pungens	0.976	0	0.959	0	0.986	0	0.979	0
Hovenia dulcis	0.829	0	0.841	0	0.923	0	0.896	0
Hoya australis	0.841	0	0.887	0	0.92	0	0.901	0
Hoya carnea	0.903	0	0.733	0	0.857	0	0.818	0
Hura crepitans	0.822	0	0.817	0	0.858	0	0.85	0
Hydrangea paniculata	0.937	0	0.915	0	0.927	0	0.919	0
Hydrocleys nymphoides	0.715	0	0.583	33.3	0.736	3.3	0.723	3.3
Hydrocotyle americana	0.93	0	0.963	0	0.955	0	0.946	0
Hydrolea spinosa	0.798	0	0.811	0	0.876	0	0.864	0
Hylotelephium erythrodictum	0.914	0	0.912	0	0.928	0	0.922	0
Hymenocallis littoralis	0.805	0	0.826	0	0.854	0	0.85	0
Hypericum gramineum	0.914	0	0.92	0	0.961	0	0.95	0
Hypericum hypericoides	0.912	0	0.924	0	0.95	0	0.944	0
Hypericum patulum	0.864	0	0.859	0	0.82	0	0.752	20
Hypoestes aristata	0.905	0	0.877	0	0.878	0	0.881	0
Hypoestes phyllostachya	0.829	0	0.864	0	0.857	0	0.837	0
Idesia polycarpa	0.966	0	0.836	0	0.923	0	0.923	0
Ilex crenata	0.938	0	0.895	0	0.928	0	0.915	0
Ilex paraguariensis	0.804	0	0.868	0	0.9	0	0.885	0
Ilex rotunda	0.931	0	0.878	0	0.948	0	0.94	0
Indigofera tinctoria	0.931	0	0.936	0	0.96	0	0.948	0
Inga edulis	0.853	0	0.849	0	0.892	0	0.886	0
Ipomoea alba	0.76	0	0.763	0	0.85	0	0.84	0
Ipomoea cairica	0.772	0	0.774	0	0.83	0	0.815	0
Ipomoea carnea	0.756	0	0.784	0	0.833	0	0.818	0
Ipomoea pes caprae	0.812	0	0.819	0	0.867	0	0.85	0
Ipomoea tricolor	0.67	0	0.635	0	0.795	0	0.807	0
Iris domestica	0.851	0	0.863	0	0.896	0	0.888	0
Iris japonica	0.923	0	0.921	0	0.965	0	0.954	0
Iris sanguinea	0.652	33.3	0.986	0	0.939	0	0.93	0
Isotoma fluviatilis	0.942	0	0.957	0	0.934	0	0.922	0
Ixia polystachya	0.939	0	0.963	0	0.973	0	0.964	0
Ixora coccinea	0.788	0	0.766	0	0.799	0	0.801	0
Jasminum dichotomum	0.877	0	0.852	0	0.876	0	0.887	0
Jasminum fluminense	0.808	0	0.811	0	0.864	0	0.858	0
Jasminum grandiflorum	0.631	0	0.57	33.3	0.72	3.3	0.697	3.3
Jasminum multiflorum	0.855	0	0.842	0	0.769	3.3	0.754	3.3
Jasminum polyanthum	0.804	0	0.843	0	0.927	0	0.918	0
Jasminum simplicifolium	0.94	0	0.852	0	0.939	0	0.931	0
Justicia betonica	0.838	0	0.821	0	0.88	0	0.874	0
Justicia brandegeana	0.683	0	0.907	0	0.8	0	0.772	0
Justicia spicigera	0.754	0	0.736	0	0.857	0	0.85	0
Kalanchoe crenata	0.884	0	0.749	33.3	0.841	0	0.841	0
Kalopanax septemlobus	0.9	0	0.87	0	0.941	0	0.936	0
Kennedia rubicunda	0.987	0	0.977	0	0.979	0	0.972	0
Kigelia africana	0.762	0	0.778	0	0.83	0	0.817	0
Kolkwitzia amabilis	0.913	0	0.881	0	0.921	0	0.919	0
Kummerowia stipulacea	0.917	0	0.901	0	0.964	0	0.96	0
Kummerowia striata	0.932	0	0.897	0	0.954	0	0.947	0
Kunzea ambigua	0.949	0	0.929	0	0.973	0	0.97	0
Kunzea ericoides	0.98	0	0.978	0	0.983	0	0.981	0

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
Lablab purpureus	0.752	0	0.762	0	0.804	0	0.799	0
Laelia rubescens	0.863	0	0.927	0	0.881	0	0.856	0
Lagerstroemia speciosa	0.836	0	0.763	0	0.873	0	0.853	0
Lampranthus spectabilis	0.787	0	0.751	0	0.91	0	0.887	0
Lawsonia inermis	0.762	0	0.755	0	0.817	0	0.817	0
Leonotis leonurus	NaN	100	0.944	0	0.931	0	0.915	13.3
Leonotis ocyimifolia	0.921	0	0.916	0	0.916	0	0.909	0
Leonurus japonicus	0.731	0	0.7	0	0.823	0	0.802	0
Leonurus sibiricus	0.682	0	0.705	0	0.829	0	0.809	0
Leptospermum polygalifolium	0.978	0	0.989	0	0.987	0	0.982	0
Lespedeza bicolor	0.867	0	0.814	0	0.928	0	0.911	0
Lespedeza cyrtobotrya	0.982	0	0.969	0	0.986	0	0.982	0
Lespedeza thunbergii	0.881	0	0.897	0	0.939	0	0.918	0
Leucophyllum frutescens	0.755	0	0.94	0	0.956	0	0.935	0
Ligustrum obtusifolium	0.883	0	0.889	0	0.944	0	0.935	0
Ligustrum tschonoskii	0.959	0	0.923	0	0.968	0	0.963	0
Lilium formosanum	0.95	0	0.937	0	0.946	0	0.942	0
Limnobiium laevigatum	0.691	0	0.795	0	0.8	0	0.788	0
Limnocharis flava	0.753	0	0.807	0	0.84	0	0.833	0
Linaria maroccana	0.814	0	0.832	0	0.865	0	0.837	0
Linum grandiflorum	0.891	0	0.894	0	0.923	0	0.911	0
Liriope muscari	0.884	0	0.815	0	0.911	0	0.898	0
Liriope spicata	0.877	0	0.863	0	0.915	0	0.917	0
Livistona australis	0.938	0	0.932	0	0.961	0	0.958	0
Lobelia cardinalis	0.727	0	0.786	0	0.876	0	0.812	0
Lobelia inflata	0.928	0	0.93	0	0.959	0	0.952	0
Lonicera sempervirens	0.96	0	0.937	0	0.957	0	0.935	0
Lophostemon confertus	0.953	0	0.936	0	0.963	0	0.957	0
Ludwigia alternifolia	0.962	0	0.958	0	0.979	0	0.977	0
Ludwigia octovalvis	0.724	0	0.76	0	0.865	0	0.836	0
Ludwigia peruviana	0.776	0	0.79	0	0.848	0	0.837	0
Luffa cylindrica	0.697	0	0.669	0	0.794	0	0.794	0
Luma apiculata	0.841	0	0.842	0	0.91	0	0.902	0
Lupinus mexicanus	0.95	0	0.891	0	0.947	0	0.94	0
Lycianthes rantonnetii	0.638	0	0.66	33.3	0.73	0	0.708	3.3
Lycoris radiata	0.917	0	0.891	0	0.993	0	0.963	0
Lysimachia japonica	0.945	0	0.974	0	0.958	0	0.946	0
Maackia amurensis	0.968	0	0.926	0	0.923	0	0.918	0
Magnolia grandiflora	0.744	0	0.722	0	0.789	0	0.777	0
Magnolia kobus	0.586	33.3	0.681	0	0.881	0	0.869	0
Magnolia obovata	0.866	0	0.833	0	0.93	0	0.924	0
Malephora crocea	0.924	0	0.946	0	0.964	0	0.958	0
Mallotus philippensis	0.783	0	0.799	0	0.868	0	0.847	0
Malpighia emarginata	0.8	0	0.776	0	0.846	0	0.833	0
Malpighia glabra	0.779	0	0.805	0	0.867	0	0.851	0
Malpighia mexicana	0.874	0	0.841	0	0.945	0	0.933	0
Malus prunifolia	0.876	0	0.879	0	0.9	0	0.889	0
Malva assurgentiflora	0.954	0	0.917	0	0.957	0	0.942	0
Malvaviscus arboreus	0.788	0	0.809	0	0.886	0	0.85	0
Mammea americana	0.852	0	0.825	0	0.813	0	0.802	0
Mandevilla laxa	0.823	0	0.832	0	0.933	0	0.924	0
Mangifera indica	0.743	0	0.769	0	0.825	0	0.807	0
Manilkara zapota	0.815	0	0.839	0	0.867	0	0.863	0
Maranta arundinacea	0.838	0	0.856	0	0.868	0	0.868	0
Margyricarpus pinnatus	0.877	0	0.81	0	0.917	0	0.909	0
Martynia annua	0.789	0	0.804	0	0.844	0	0.841	0
Maurandya antirrhiniflora	0.827	0	0.849	0	0.899	0	0.889	0
Mazus pumilus	0.847	0	0.863	0	0.903	0	0.902	0
Melaleuca hypericifolia	0.976	0	0.906	0	0.978	0	0.969	0
Melastoma malabathricum	0.799	0	0.858	0	0.901	0	0.874	0
Melianthus major	0.915	0	0.81	0	0.93	0	0.927	0
Melinis repens	0.679	0	0.708	0	0.86	0	0.812	0
Melothria pendula	0.729	0	0.773	0	0.86	0	0.831	0
Miconia calvescens	0.849	0	0.856	0	0.888	0	0.883	0

species	model		GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5								
Micranthemum umbrosum	0.731	0	0.764	0	0.846	0	0.82	0		
Mimosa pigra	0.762	0	0.773	0	0.875	0	0.861	0		
Mimusops elengi	0.888	0	0.867	0	0.904	0	0.891	60		
Molineria capitulata	0.774	0	0.66	0	0.797	0	0.792	0		
Momordica balsamina	0.75	0	0.775	0	0.838	0	0.821	0		
Momordica charantia	0.742	0	0.751	0	0.841	0	0.829	0		
Momordica cochinchinensis	0.908	0	0.801	0	0.907	0	0.883	0		
Monarda fistulosa	0.824	0	0.863	0	0.91	0	0.879	0		
Monarda punctata	0.918	0	0.926	0	0.947	0	0.946	0		
Monochoria vaginalis	0.868	0	0.843	0	0.9	0	0.884	0		
Moraea flaccida	NaN	100	0.947	0	0.969	0	0.953	0		
Moraea fugax	0.942	0	0.925	0	0.975	0	0.949	0		
Moraea miniata	NaN	100	0.922	0	0.951	0	0.948	20		
Moraea polystachya	0.968	0	0.947	0	0.94	0	0.923	0		
Moraea setifolia	0.954	0	0.948	0	0.969	0	0.963	0		
Morinda citrifolia	0.877	0	0.885	0	0.895	0	0.89	0		
Moringa oleifera	0.769	0	0.746	0	0.806	0	0.813	0		
Mucuna pruriens	0.791	0	0.813	0	0.848	0	0.848	0		
Muehlenbeckia axillaris	0.994	0	0.983	0	0.984	0	0.978	0		
Mukia maderaspatana	0.667	0	0.748	0	0.857	0	0.838	0		
Musa acuminata	0.57	0	0.831	0	0.789	0	0.789	3.3		
Myrica rubra	0.961	0	0.943	0	0.964	0	0.96	0		
Myrmecophila tibicinis	0.949	0	0.936	0	0.939	0	0.919	0		
Nandina domestica	0.855	0	0.832	0	0.884	0	0.864	0		
Nepeta racemosa	0.851	0	0.902	0	0.925	0	0.918	0		
Neptunia oleracea	0.833	0	0.847	0	0.845	0	0.833	0		
Neptunia plena	0.831	0	0.822	0	0.838	0	0.829	0		
Nertera granadensis	0.927	0	0.911	0	0.949	0	0.944	0		
Nicotiana acuminata	0.915	0	0.906	0	0.928	0	0.915	0		
Nicotiana longiflora	0.644	0	0.677	0	0.819	0	0.796	0		
Nicotiana glauca	0.718	0	0.743	0	0.847	0	0.833	0		
Nothoscordum bivalve	0.846	0	0.89	0	0.891	0	0.869	0		
Nymphaea nouchali	0.86	0	0.852	0	0.889	0	0.875	0		
Nymphaea odorata	0.778	0	0.822	0	0.879	0	0.839	0		
Ochroma pyramidale	0.844	0	0.836	0	0.88	0	0.872	0		
Ocimum americanum	0.734	0	0.758	0	0.812	0	0.793	0		
Ocimum gratissimum	0.775	0	0.762	0	0.845	0	0.837	0		
Ocimum kilimandscharicum	0.891	0	0.844	0	0.887	0	0.871	0		
Ocimum tenuiflorum	0.821	0	0.815	0	0.865	0	0.854	0		
Odontonema tubaeforme	0.817	0	0.813	0	0.86	0	0.861	0		
Oeceoclades maculata	0.804	0	0.767	0	0.845	0	0.837	0		
Oenothera drummondii	0.63	0	0.865	0	0.899	0	0.897	0		
Oenothera perennis	0.951	0	0.915	0	0.946	0	0.928	0		
Opuntia aurantiaca	0.959	0	0.944	0	0.978	0	0.969	0		
Opuntia basilaris	0.777	0	0.912	0	0.948	0	0.926	0		
Opuntia humifusa	0.92	0	0.941	0	0.916	0	0.911	0		
Opuntia leucotricha	0.91	0	0.805	0	0.948	0	0.939	0		
Opuntia polyacantha	0.911	0	0.923	0	0.927	0	0.917	0		
Ornithogalum thyrsoides	0.877	0	0.84	0	0.933	0	0.909	0		
Orthrosanthus chimboracensis	0.917	0	0.888	0	0.96	0	0.948	0		
Osmanthus heterophyllus	0.898	0	0.907	0	0.937	0	0.92	0		
Osteospermum ecklonis	0.896	0	0.881	0	0.922	0	0.911	0		
Oxalis depressa	0.939	0	0.933	0	0.949	0	0.932	0		
Oxalis spiralis	0.932	0	0.91	0	0.943	0	0.943	0		
Oxalis tuberosa	0.915	0	0.857	0	0.93	0	0.933	0		
Pachira aquatica	0.845	0	0.854	0	0.893	0	0.883	0		
Paeonia lactiflora	0.854	0	0.855	33.3	0.908	0	0.886	0		
Pandanus tectorius	0.918	0	0.933	0	0.889	0	0.888	0		
Pandorea jasminoides	0.843	0	0.829	0	0.955	0	0.949	0		
Pandorea pandorana	0.952	0	0.958	0	0.975	0	0.964	0		
Papaver aculeatum	0.933	0	0.922	0	0.957	0	0.954	0		
Papaver nudicaule	0.779	0	0.839	0	0.91	0	0.896	0		
Papaver orientale	0.894	0	0.908	0	0.942	0	0.926	0		
Parmentiera aculeata	0.852	0	0.859	0	0.893	0	0.888	0		

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
Parochetus communis	0.888	0	0.897	0	0.906	0	0.892	0
Passiflora amethystina	0.869	0	0.858	0	0.938	0	0.931	0
Passiflora coccinea	0.853	0	0.852	0	0.904	0	0.905	0
Passiflora foetida	0.734	0	0.756	0	0.861	0	0.832	0
Passiflora laurifolia	0.878	0	0.833	0	0.931	0	0.933	0
Passiflora ligularis	0.836	0	0.814	0	0.91	0	0.904	0
Passiflora mixta	0.96	0	0.949	0	0.978	0	0.975	0
Passiflora quadrangularis	0.861	0	0.848	0	0.862	0	0.844	0
Passiflora vitifolia	0.889	0	0.865	0	0.919	0	0.914	0
Pavonia hastata	0.91	0	0.894	0	0.963	0	0.948	0
Pelargonium alchemilloides	0.967	0	0.965	0	0.941	0	0.936	0
Pelargonium grossularioides	0.882	0	0.88	0	0.931	0	0.927	0
Pennisetum alopecuroides	0.858	0	0.878	0	0.922	0	0.912	0
Pennisetum orientale	0.774	0	0.776	0	0.817	0	0.815	0
Penstemon gentianoides	0.961	0	0.872	0	0.936	0	0.93	0
Pentas lanceolata	0.81	0	0.834	0	0.832	0	0.829	0
Peperomia obtusifolia	0.816	0	0.84	0	0.893	0	0.892	0
Pereskia aculeata	0.885	0	0.875	0	0.902	0	0.884	0
Perovskia atriplicifolia	0.551	33.3	0.636	0	0.794	10	0.788	6.7
Persea americana	0.711	0	0.734	0	0.833	0	0.799	0
Petrea volubilis	0.803	0	0.825	0	0.871	0	0.866	26.7
Petunia axillaris	0.802	0	0.788	0	0.866	0	0.848	0
Petunia integrifolia	0.928	0	0.945	0	0.89	0	0.875	0
Philadelphus mexicanus	0.903	0	0.826	0	0.945	0	0.939	0
Philadelphus pubescens	0.86	0	0.9	0	0.925	0	0.92	0
Philodendron bipinnatifidum	0.836	0	0.785	0	0.856	0	0.833	0
Philodendron ornatum	0.894	0	0.885	0	0.93	0	0.926	0
Phlox drummondii	0.823	0	0.814	0	0.836	0	0.833	0
Phoenix reclinata	0.777	0	0.771	0	0.855	0	0.854	0
Photinia glabra	0.882	0	0.873	0	0.889	0	0.883	0
Phyllanthus amarus	0.794	0	0.798	0	0.857	0	0.847	63.3
Phyllanthus emblica	0.787	0	0.83	0	0.886	0	0.872	0
Pimenta dioica	0.83	0	0.813	0	0.872	0	0.863	0
Pinellia ternata	0.92	0	0.804	0	0.933	0	0.913	0
Piper aduncum	0.825	0	0.816	0	0.896	0	0.889	0
Piscidia piscipula	0.876	0	0.872	0	0.892	0	0.896	0
Pistacia chinensis	0.77	0	0.775	0	0.852	0	0.827	0
Pithecellobium dulce	0.732	0	0.766	0	0.818	0	0.802	0
Pittosporum bicolor	0.963	0	0.963	0	0.982	0	0.972	0
Pittosporum eugenoides	0.965	0	0.928	0	0.988	0	0.983	0
Plantago rugelii	0.956	0	0.977	0	0.973	0	0.97	33.3
Plectranthus amboinicus	0.777	0	0.799	0	0.854	0	0.839	0
Plectranthus ciliatus	0.989	0	0.954	0	0.976	0	0.959	0
Plectranthus scutellarioides	0.836	0	0.863	0	0.892	0	0.877	0
Plectranthus verticillatus	0.882	0	0.876	0	0.897	0	0.876	0
Plumbago zeylanica	0.695	0	0.73	0	0.846	0	0.816	0
Plumeria obtusa	0.93	0	0.952	0	0.932	0	0.917	0
Plumeria rubra	0.727	0	0.76	0	0.814	0	0.795	0
Polygala lancifolia	0.864	0	0.894	0	0.983	0	0.952	0
Polygala senega	0.711	33.3	0.938	0	0.9	0	0.891	0
Pomaderris lanigera	0.971	0	0.963	0	0.981	0	0.978	0
Populus acuminata	0.703	33.3	0.831	0	0.987	0	0.969	0
Portulacaria afra	0.955	0	0.987	0	0.93	0	0.903	0
Pouteria caimito	0.877	0	0.875	0	0.922	0	0.93	0
Pratia repens	0.999	0	0.944	0	0.975	0	0.958	0
Prosopis chilensis	0.649	0	0.749	0	0.864	0	0.846	0
Prosopis juliflora	0.624	0	0.651	0	0.766	0	0.761	0
Prunus munsoniana	0.895	0	0.874	0	0.97	0	0.97	0
Prunus pumila	0.902	0	0.928	0	0.928	0	0.921	0
Prunus salicina	0.881	0	0.798	0	0.887	0	0.881	0
Psoralea pinnata	0.89	0	0.87	0	0.935	0	0.933	0
Pueraria montana	0.814	0	0.811	0	0.862	0	0.851	0
Pyracantha fortuneana	0.897	0	0.935	0	0.884	0	0.87	0
Pyracantha koidzumii	0.644	33.3	0.645	0	0.841	0	0.807	0
Pyrus calleryana	0.818	0	0.771	0	0.85	0	0.835	0

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
<i>Pyrus pyrifolia</i>	0.885	0	0.846	0	0.892	0	0.873	0
<i>Quassia amara</i>	0.834	0	0.836	0	0.88	0	0.876	0
<i>Quercus acutissima</i>	0.875	0	0.873	0	0.917	0	0.909	0
<i>Rauvolfia tetraphylla</i>	0.83	0	0.853	0	0.87	0	0.859	0
<i>Rauvolfia vomitoria</i>	0.864	0	0.883	0	0.929	0	0.917	0
<i>Rhamnus japonica</i>	0.939	0	0.921	0	0.976	0	0.976	0
<i>Rhaphiolepis indica</i>	0.898	0	0.823	0	0.915	0	0.91	0
<i>Rheum rhabarbarum</i>	0.904	0	0.916	0	0.95	0	0.943	0
<i>Rhipsalis baccifera</i>	0.828	0	0.832	0	0.905	0	0.894	0
<i>Rhodanthe chlorocephala</i>	0.892	0	0.916	0	0.932	0	0.922	0
<i>Rhododendron japonicum</i>	0.737	0	0.769	0	0.942	0	0.925	0
<i>Romneya coulteri</i>	0.907	0	0.873	0	0.913	0	0.903	0
<i>Romulea flava</i>	0.959	0	0.958	0	0.949	0	0.936	0
<i>Rosa banksiae</i>	0.902	0	0.847	0	0.92	0	0.89	0
<i>Rosa chinensis</i>	0.832	0	0.758	0	0.819	0	0.767	0
<i>Rosenbergiodendron formosum</i>	0.855	0	0.815	0	0.918	0	0.918	0
<i>Rubus ellipticus</i>	0.909	0	0.88	0	0.905	0	0.889	0
<i>Rubus rosifolius</i>	0.875	0	0.903	0	0.934	0	0.931	0
<i>Rudbeckia triloba</i>	0.944	0	0.941	33.3	0.976	0	0.971	0
<i>Ruellia brevifolia</i>	0.802	0	0.828	0	0.891	0	0.868	0
<i>Ruellia tuberosa</i>	0.827	0	0.845	0	0.815	0	0.809	0
<i>Russelia equisetiformis</i>	0.661	0	0.751	0	0.853	0	0.817	0
<i>Russelia sarmentosa</i>	0.853	0	0.874	0	0.891	0	0.882	0
<i>Sageretia thea</i>	0.702	0	0.818	0	0.841	0	0.835	0
<i>Sagittaria graminea</i>	0.856	0	0.888	0	0.929	0	0.921	0
<i>Sagittaria montevidensis</i>	0.8	0	0.791	0	0.875	0	0.856	0
<i>Salix gracilistyla</i>	0.957	0	0.945	0	0.991	0	0.988	0
<i>Salix humboldtiana</i>	0.741	0	0.777	0	0.855	0	0.835	0
<i>Salix nigra</i>	0.901	0	0.896	0	0.915	0	0.901	0
<i>Salvia africana lutea</i>	0.946	0	0.935	0	0.997	0	0.985	0
<i>Salvia leucantha</i>	0.651	33.3	0.688	0	0.813	0	0.802	0
<i>Salvia leucophylla</i>	0.948	0	0.901	0	0.925	0	0.908	0
<i>Salvia microphylla</i>	0.875	0	0.881	0	0.908	0	0.902	0
<i>Salvia plebeia</i>	0.829	0	0.8	0	0.851	0	0.837	0
<i>Salvia splendens</i>	0.516	66.7	0.569	33.3	0.782	0	0.751	0
<i>Sansevieria hyacinthoides</i>	0.818	0	0.869	0	0.867	0	0.857	0
<i>Santalum album</i>	0.862	0	0.839	0	0.888	0	0.891	0
<i>Sanvitalia procumbens</i>	0.772	0	0.889	0	0.909	0	0.888	0
<i>Sauropus androgynus</i>	0.832	0	0.834	0	0.877	0	0.871	0
<i>Scadoxus multiflorus</i>	0.778	0	0.803	0	0.851	0	0.84	0
<i>Scaevola taccada</i>	0.885	0	0.896	0	0.906	0	0.903	0
<i>Schefflera arboricola</i>	0.89	0	0.83	0	0.933	0	0.918	0
<i>Schisandra chinensis</i>	0.71	0	0.77	0	0.951	0	0.945	0
<i>Schotia brachypetala</i>	0.951	0	0.949	0	0.975	0	0.955	0
<i>Senecio radicans</i>	0.943	0	0.961	0	0.961	0	0.942	0
<i>Senecio tamoides</i>	0.871	0	0.944	0	0.969	0	0.956	0
<i>Senna artemisioides</i>	0.927	0	0.943	0	0.976	0	0.967	0
<i>Senna italica</i>	0.806	0	0.846	0	0.899	0	0.88	0
<i>Senna siamea</i>	0.792	0	0.785	0	0.831	0	0.82	0
<i>Sesbania grandiflora</i>	0.853	0	0.712	0	0.842	0	0.825	0
<i>Sesbania sesban</i>	0.762	0	0.759	0	0.867	0	0.855	0
<i>Sisyrinchium atlanticum</i>	0.893	0	0.946	0	0.946	0	0.934	0
<i>Sisyrinchium micranthum</i>	0.867	0	0.893	0	0.91	0	0.906	0
<i>Sisyrinchium mucronatum</i>	0.916	0	0.869	0	0.948	0	0.924	0
<i>Solandra maxima</i>	0.85	0	0.763	33.3	0.818	0	0.791	0
<i>Solanum aviculare</i>	0.91	0	0.933	0	0.949	0	0.936	0
<i>Solanum betaceum</i>	0.873	0	0.782	0	0.826	0	0.836	0
<i>Solanum capsicoides</i>	0.802	0	0.794	0	0.855	0	0.85	0
<i>Solanum chrysotrichum</i>	0.873	0	0.625	33.3	0.92	0	0.9	0
<i>Solanum lanceifolium</i>	0.832	0	0.827	0	0.87	0	0.869	0
<i>Solanum mammosum</i>	0.828	0	0.814	0	0.845	0	0.834	0
<i>Solanum quitense</i>	0.925	0	0.885	0	0.9	0	0.91	0
<i>Solanum retroflexum</i>	0.925	0	0.901	0	0.935	0	0.924	0
<i>Solanum seforthianum</i>	0.757	0	0.789	0	0.846	0	0.834	0

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
Solanum sessiliflorum	0.87	0	0.858	0	0.925	0	0.918	0
Solanum wendlandii	0.813	0	0.878	0	0.898	0	0.857	0
Solidago altissima	0.801	0	0.824	0	0.885	0	0.864	0
Solidago ptarmicoides	0.731	33.3	0.847	0	0.857	0	0.857	0
Sophora tetraptera	0.888	0	0.887	0	0.956	0	0.947	0
Sorbus alnifolia	0.932	0	0.843	0	0.929	0	0.926	0
Sparaxis grandiflora	0.94	0	0.965	0	0.987	0	0.973	0
Spathiphyllum cannifolium	0.903	0	0.904	0	0.929	0	0.932	0
Spathodea campanulata	0.803	0	0.781	0	0.836	0	0.836	0
Spathoglottis plicata	0.898	0	0.709	0	0.91	0	0.91	0
Spiraea prunifolia	0.802	0	0.84	0	0.886	0	0.874	0
Spondias dulcis	0.795	0	0.724	0	0.881	0	0.857	0
Spondias mombin	0.829	0	0.824	0	0.887	0	0.877	0
Stachytarpheta jamaicensis	0.837	0	0.851	0	0.884	0	0.881	6.7
Stachytarpheta mutabilis	0.806	0	0.679	33.3	0.819	0	0.809	0
Stapelia grandiflora	0.953	0	0.946	0	0.948	0	0.929	3.3
Stenocarpus sinuatus	0.685	0	0.857	0	0.895	0	0.869	0
Sterculia apetala	0.819	0	0.837	0	0.897	0	0.887	0
Stigmaphyllon ellipticum	0.891	0	0.877	0	0.875	0	0.874	0
Stipa tenuissima	0.875	0	0.85	0	0.886	0	0.881	0
Streptosolen jamesonii	0.903	0	0.8	0	0.927	0	0.881	13.3
Strophanthus gratus	0.894	0	0.911	0	0.933	0	0.929	0
Strophanthus preussii	0.819	0	0.753	0	0.902	0	0.898	0
Styrax japonicus	0.958	0	0.865	0	0.968	0	0.953	0
Syagrus romanzoffiana	0.867	0	0.848	0	0.914	0	0.889	0
Symplocos paniculata	0.903	0	0.806	0	0.95	0	0.935	0
Syngonium angustatum	0.905	0	0.857	0	0.921	0	0.92	0
Syngonium podophyllum	0.827	0	0.849	0	0.899	0	0.894	0
Syringa reticulata	0.703	0	0.849	0	0.906	0	0.881	0
Syzygium paniculatum	0.863	0	0.839	0	0.931	0	0.924	0
Tabebuia aurea	0.742	0	0.742	0	0.88	0	0.869	0
Tabernaemontana divaricata	0.8	0	0.787	0	0.817	0	0.803	0
Tacca leontopetaloides	0.874	0	0.872	0	0.911	0	0.903	0
Tagetes lucida	0.911	0	0.915	0	0.913	0	0.903	0
Tagetes tenuifolia	0.858	0	0.921	0	0.883	0	0.857	0
Tamarindus indica	0.77	0	0.793	0	0.843	0	0.833	0
Tamarix aphylla	0.804	0	0.807	0	0.828	0	0.812	0
Tamarix chinensis	0.748	0	0.732	0	0.822	0	0.806	0
Tanacetum coccineum	0.835	0	0.809	0	0.939	0	0.933	0
Tecoma stans	0.671	0	0.7	0	0.838	0	0.794	0
Tephrosia candida	0.766	0	0.712	0	0.839	0	0.839	0
Tephrosia grandiflora	0.937	0	0.89	0	0.95	0	0.938	0
Tephrosia purpurea	0.756	0	0.763	0	0.82	0	0.809	0
Tephrosia vogelii	0.806	0	0.786	0	0.854	0	0.85	0
Terminalia catappa	0.806	0	0.806	0	0.859	0	0.853	0
Thalia geniculata	0.797	0	0.8	0	0.878	0	0.87	0
Theobroma cacao	0.868	0	0.865	0	0.907	0	0.907	0
Thunbergia alata	0.744	0	0.764	0	0.862	0	0.854	0
Thunbergia erecta	0.778	0	0.745	0	0.786	0	0.796	0
Thunbergia fragrans	0.844	0	0.816	0	0.843	0	0.834	0
Tigridia pavonia	0.889	0	0.839	0	0.881	0	0.872	0
Tillandsia stricta	0.927	0	0.915	0	0.923	0	0.92	0
Tillandsia usneoides	0.718	0	0.75	0	0.843	0	0.831	40
Tithonia rotundifolia	0.767	0	0.748	0	0.835	0	0.822	0
Toona ciliata	0.867	0	0.856	0	0.908	0	0.901	0
Trachelospermum asiaticum	0.947	0	0.942	0	0.957	0	0.958	40
Trachelospermum jasminoides	0.768	0	0.762	0	0.86	0	0.845	0
Tradescantia spathacea	0.749	0	0.749	0	0.84	0	0.831	0
Triadica sebifera	0.893	0	0.847	0	0.928	0	0.915	0
Trichocentrum carthagenense	0.881	0	0.87	0	0.902	0	0.891	0
Trichosanthes cucumerina	0.875	0	0.903	0	0.924	0	0.914	0
Trichosanthes kirilowii	0.803	0	0.801	0	0.948	0	0.957	0
Tripsacum dactyloides	0.777	0	0.81	0	0.894	0	0.848	0

species	GLM		GAM		RF		GBM	
	Mean TSS	% TSS < 0.5						
Tulbaghia violacea	0.888	0	0.852	0	0.906	0	0.897	0
Ullucus tuberosus	0.935	0	0.901	0	0.954	0	0.954	0
Ulmus parvifolia	0.781	0	0.718	0	0.827	0	0.814	0
Ursinia anthemoides	0.988	0	0.944	0	0.988	0	0.976	0
Ursinia speciosa	0.961	0	0.946	0	0.971	0	0.962	0
Utricularia livida	0.862	0	0.869	0	0.918	0	0.886	63.3
Vallisneria americana	0.751	0	0.838	0	0.876	0	0.871	0
Vallisneria nana	0.591	0	0.824	0	0.832	0	0.816	20
Verbena stricta	0.944	0	0.943	0	0.98	0	0.975	0
Vernicia fordii	0.904	0	0.877	0	0.906	0	0.896	0
Veronica americana	0.748	0	0.798	0	0.895	0	0.833	0
Viburnum dilatatum	0.927	0	0.911	0	0.965	0	0.962	0
Viburnum plicatum	0.918	0	0.88	0	0.951	0	0.949	0
Viburnum sieboldii	0.933	0	0.918	0	0.959	0	0.938	0
Vigna caracalla	0.797	0	0.714	0	0.857	0	0.837	0
Viola hederacea	0.981	0	0.976	0	0.986	0	0.973	0
Viola sororia	0.835	0	0.845	0	0.924	0	0.886	0
Vitex negundo	0.772	0	0.782	0	0.85	0	0.835	0
Vitis coignetiae	0.823	0	0.848	0	0.854	3.3	0.846	3.3
Washingtonia robusta	0.768	0	0.856	0	0.872	0	0.847	0
Weigela floribunda	0.841	0	0.852	0	0.953	0	0.931	0
Westringia fruticosa	0.97	0	0.931	0	0.947	0	0.94	0
Wisteria floribunda	0.922	0	0.91	0	0.919	0	0.916	0
Xanthosoma sagittifolium	0.839	0	0.783	0	0.872	0	0.86	0
Ximenia americana	0.73	0	0.745	0	0.839	0	0.824	0
Zapoteca portoricensis	0.818	0	0.8	0	0.861	0	0.859	0
Zelkova serrata	0.912	0	0.874	0	0.916	0	0.905	0
Zingiber officinale	0.871	0	0.688	0	0.827	0	0.803	0
Zingiber zerumbet	0.821	0	0.738	0	0.83	0	0.84	0
Zinnia angustifolia	0.727	0	0.761	0	0.876	0	0.864	0
Zinnia elegans	0.465	66.7	0.624	0	0.718	3.3	0.697	3.3
Zinnia peruviana	0.827	0	0.845	0	0.901	0	0.888	0
Ziziphus mauritiana	0.713	0	0.732	0	0.796	0	0.799	0
Ziziphus spina-christi	0.837	0	0.776	0	0.857	0	0.843	0

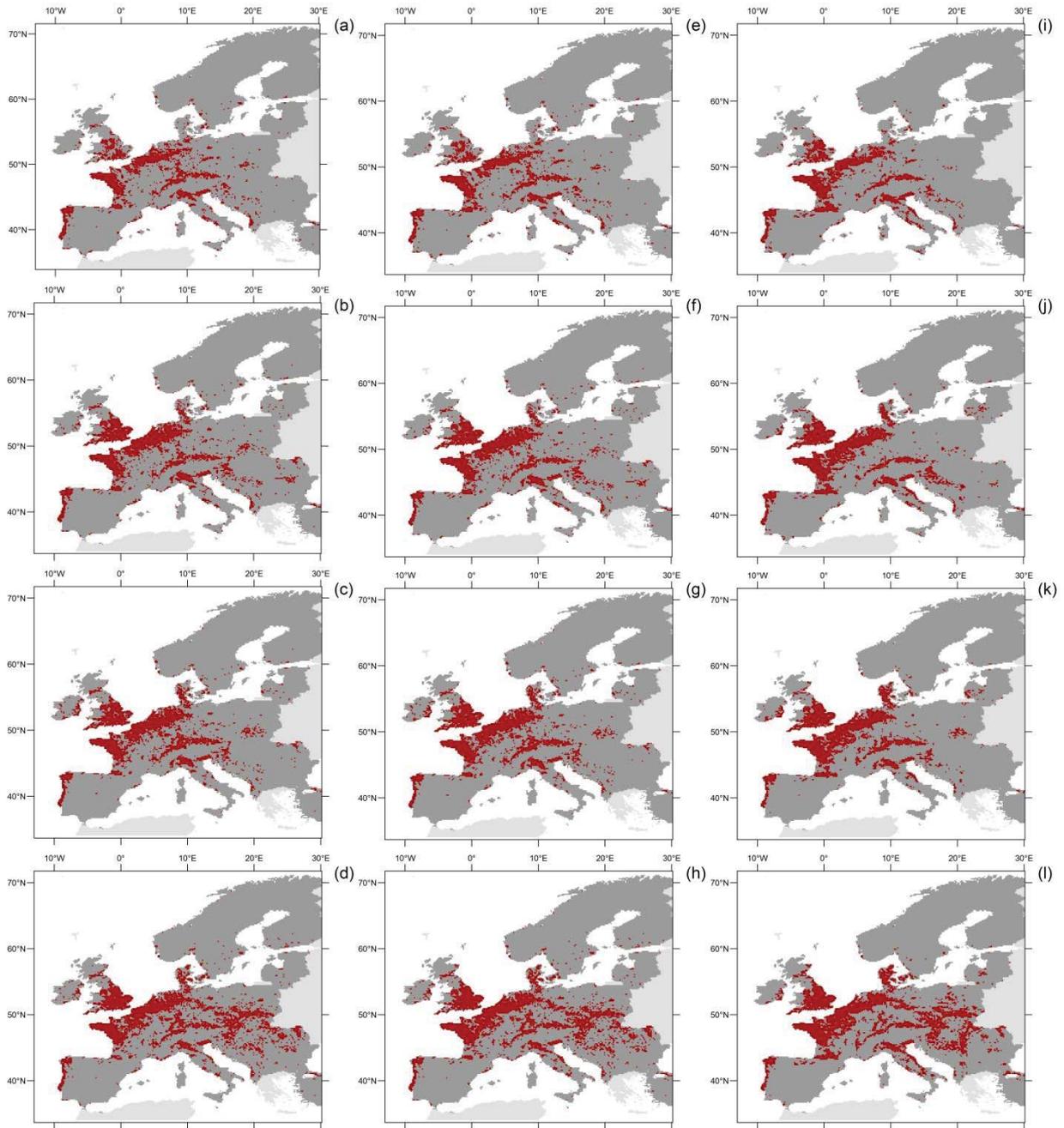
**SUPPORTING INFORMATION**

**Climate change will increase the naturalization risk from garden plants in Europe**

Iwona Dullinger, Johannes Wessely, Oliver Bossdorf, Wayne Dawson, Franz Essl, Andreas Gattringer, Günther Klöner, Holger Kreft, Michael Kuttner, Dietmar Moser, Jan Pergl, Petr Pyšek, Wilfried Thuiller, Mark van Kleunen, Patrick Weigelt, Marten Winter, Stefan Dullinger

**Appendix S5.** Naturalization risk maps calculated according to three different weighting schemes.

Naturalization risk maps calculated by combining climatic and land cover suitability for 783 ornamental species currently not naturalized in, but somewhere outside of Europe. Land cover suitability was quantified by weighting CORINE land cover types according to the estimated area available for ornamental plant cultivation according to three different weighting schemes (A: (a)-(d), B: (e)-(h), C: (i)-(l), see Appendix S3 for details). Climatic suitability is quantified by projections of species distribution models under current climate ((a), (e), (i)) and three scenarios of climate warming: mild scenario (RCP2.6: (b), (f), (j)), intermediate scenario (RCP4.5: (c), (g), (k)) and strong scenario (RCP8.5: (d), (h), (l)).



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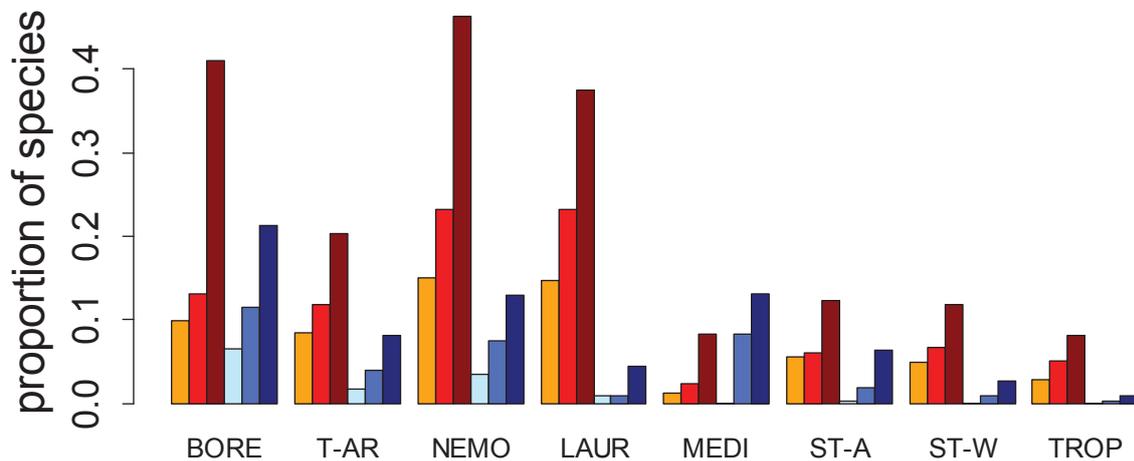
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Appendix S6. Species predicted gain or loss of area under climate change.

The proportion of species predicted to gain or lose > 1600 cells (~ 5 % of the study area) of climatically suitable area under three different climate scenarios as compared to current climatic conditions. Orange, red and dark red bars represent ‘winners’, and light blue, blue and dark blue bars represent ‘losers’ under the RCP2.6, RCP4.5, RCP8.5 scenarios, respectively. BORE: boreal, T-AR: temperate-arid, NEMO: nemoral (= temperate), LAUR: laurophyllous, MEDI: Mediterranean, ST-A: subtropical-arid, ST-W: subtropical seasonally dry, TROP: tropical.



## Chapter 2

### Will climate change increase hybridization risk between potential plant invaders and their congeners in Europe?

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#### Publication Reference

Klöner, G., Dullinger, I., Wessely, J., Bossdorf, O., Carboni, M., Dawson, W., Essl, F., Gattlinger, A., Haeuser, E., van Kleunen, M., Kreft, H., Moser, D., Pergl, J., Pyšek, P., Thuiller, W., Weigelt, P., Winter, M., Dullinger, S. (2017): Will climate change increase hybridization risk between potential plant invaders and their congeners in Europe? *Diversity and Distributions*, 23, 934-943.

#### Status

Published

#### Contribution

I prepared the SDMs and contributed to writing the manuscript.

# Will climate change increase hybridization risk between potential plant invaders and their congeners in Europe?

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## Funding information

ERA-Net BiodivERsA; Austrian Science Fund, Grant/Award Number: I-1443-B25; DFG (German Research Foundation); ANR; Centre of Excellence PLADIAS (Czech Science Foundation), Grant/Award Number: 504/11/1028 and 14-36079G

Editor: Marcel Rejmanek

## Abstract

**Aim:** Interspecific hybridization can promote invasiveness of alien species. In many regions of the world, public and domestic gardens contain a huge pool of non-native plants. Climate change may relax constraints on their naturalization and hence facilitate hybridization with related species in the resident flora. Here, we evaluate this possible increase in hybridization risk by predicting changes in the overlap of climatically suitable ranges between a set of garden plants and their congeners in the resident flora.

**Location:** Europe.

**Methods:** From the pool of alien garden plants, we selected those which (1) are not naturalized in Europe, but established outside their native range elsewhere in the world; (2) belong to a genus where interspecific hybridization has been previously reported; and (3) have congeners in the native and naturalized flora of Europe. For the resulting set of 34 alien ornamentals as well as for 173 of their European congeners, we fitted species distribution models and projected suitable ranges under the current climate and three future climate scenarios. Changes in range overlap between garden plants and congeners were then assessed by means of the true skill statistic.

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**Results:** Projections suggest that under a warming climate, suitable ranges of garden plants will increase, on average, while those of their congeners will remain constant or shrink, at least under the more severe climate scenarios. The mean overlap in ranges among congeners of the two groups will decrease. Variation among genera is pronounced; however, and for some congeners, range overlap is predicted to increase significantly.

**Main conclusions:** Averaged across all modelled species, our results do not indicate that hybrids between potential future invaders and resident species will emerge more frequently in Europe when climate warms. These average trends do not preclude, however, that hybridization risk may considerably increase in particular genera.

#### KEYWORDS

alien ornamental plants, climate change, interspecific hybridization, invasion biology, range overlap, species distribution models

## 1 | INTRODUCTION

Biological invasions are an important component of global environmental change and may have severe ecological as well as economic impacts (Bellard, Cassey, & Blackburn, 2016; Vilà et al., 2011). Owing to intensified trade and traffic, the global redistribution of species and their subsequent establishment outside their native range (=their naturalization) have considerably increased during the recent decades and are likely to further increase in the future (Seebens et al., 2015). Pro-active management of such invasions is, however, hampered by the difficulty of predicting which species may become invasive and where. Such predictions are difficult because of the complex causes of invasions, which include biological traits of the invading species, biotic and abiotic characteristics of the recipient environment, and historical contingencies (Catford, Jansson, & Nilsson, 2009; Richardson & Pyšek, 2006). There are, however, a number of factors known to facilitate invasions such as early reproduction, rapid growth rate, efficient long-distance dispersal or specific trait profiles which are complementary to those of the resident biota (Buhk & Thielsch, 2015; Carboni et al., 2016; van Kleunen, Weber, & Fischer, 2010; Küster, Kühn, Bruelheide, & Klotz, 2008; Pyšek et al., 2015).

Apart from these factors, interspecific hybridization has been assumed to foster invasions since a seminal paper of Ellstrand and Schierenbeck (2000). Indeed, there are prominent examples of highly invasive hybrids. For instance, several species of the genus *Tamarix* have been introduced to North America during the 19th century. Although all of these species have escaped cultivation, by far the most successful and widespread invader is the hybrid between *T. ramosissima* × *T. chinensis* (Gaskin & Kazmer, 2009; Gaskin & Schaal, 2002). The same Eurasian *T. ramosissima* has recently started to hybridize with native *T. usneoides* in South Africa (Mayonde, Cron, Gaskin, & Byrne, 2015). Other examples of genera that have produced successful invasive hybrids include *Rhododendron* (Milne & Abbott, 2000), *Spartina* (Thompson, 1991), *Senecio* (Abbott et al., 2009) and

*Helianthemum* (Rieseberg et al., 2007). More generally, the idea that interspecific hybrids may be especially successful invaders has been corroborated by a recent meta-analysis (Hovick & Whitney, 2014). The possible reasons for hybrid success include increased phenotypic or genotypic variability, phenotypic novelty arising from transgressive segregation or adaptive introgression, and heterosis effects (Prentis, Wilson, Dormontt, Richardson, & Lowe, 2008). Heterosis effects may be maintained especially when hybridization is accompanied by allopolyploidization and/or a shift to apomictic reproduction, which sustain heterozygosity.

As species are transported around the world with increasing intensity, barriers to gene flow between once geographically separated species are reduced and new hybrids between introduced and resident species will probably emerge more frequently (Thomas, 2013). For the British Isles, a recent overview has already demonstrated a rise in the number of hybrids during the last few decades (Stace, Preston, & Pearman, 2015). Apart from the risk that the new hybrids include particularly successful future invaders, rising hybridization rates also raise conservation concerns (Bohling, 2016). In particular, genetic introgression and outbreeding depression may severely threaten native species (Todesco et al., 2016), especially those that are rare and only exist in small populations (Bleeker, Schmitz, & Ristow, 2007).

Disregarding deliberate crossings (e.g., for horticultural reasons), the risk of hybridization between introduced and resident species will depend on the introduced species' ability to naturalize, that is to establish self-sustaining populations in the wild, because naturalization intensifies the spatial contact of the newcomers with their potential hybridization partners in the regional flora and hence increases mating opportunities. The likelihood of naturalization of an introduced species is mainly determined by propagule pressure (Simberloff, 2009) and the suitability of abiotic and biotic conditions (Pyšek et al., 2012; Shea & Chesson, 2002). Among the abiotic factors, climatic suitability has been repeatedly shown to play a

prominent role (e.g., Feng et al., 2016; Hayes & Barry, 2007; Thuiller et al., 2005). As a corollary, predicted climate change is also likely to alter the naturalization odds of introduced alien species and thus the likelihood that they hybridize with resident species (e.g., Bellard et al., 2013).

The alien flora of a region consists, first, of plant species that have already become naturalized or invasive. In addition, there is an often much larger group of alien species that have been introduced to a region and are grown there but have not escaped from cultivation yet. The latter group of species forms a massive pool of potential future additions to the regional wild flora. In many regions, this pool is dominated by non-native plants used for public and domestic gardening (Hulme et al., 2008; Niinemets & Penuelas, 2008; Pergl et al., 2016). In Europe, for example, more than 16,000 species from more than 200 families are currently in cultivation for ornamental purposes, with many of them being alien to Europe (Cullen, Knees, & Cubey, 2011). Some of these non-native garden plant species have already become naturalized or invasive elsewhere in the world (van Kleunen et al., 2015) and can hence be considered particularly likely to do so in Europe too (Williamson, 1999).

In a recent paper, Dullinger et al. (2016) showed that this latter group of "alien garden plants naturalized elsewhere" will benefit from a changing climate in Europe in as much as the area climatically suitable to them will increase. Given that climatic suitability is an important prerequisite to alien species' naturalization and that naturalization facilitates hybridization of introduced and resident species, the risk that new hybrids emerge may thus also be expected to increase in the future. The newly establishing garden plants may thereby hybridize with resident (i.e., native and already naturalized or even invasive) species (e.g., Ayres, Smith, Zaremba, Klohr, & Strong, 2004). However, a climate-driven modification of regional hybridization risk does not only depend on the naturalization odds of garden plants, but also on changes in climatically suitable ranges of their potential hybridization partners (Dehnen-Schmutz, 2011). In other words, the changing spatial overlap in areas climatically suitable for alien garden plants and for their potential resident hybridization partners in the wild (both native and naturalized) flora will determine possible changes in the risk of hybridization between these two groups.

Here, we evaluated whether climate change may lead to an increase in this spatial overlap. We studied a group of 783 alien ornamental plants not yet naturalized in Europe, but established outside their native range elsewhere in the world, as identified in Dullinger et al. (2016). From this group of 783 species, we first selected all those belonging to genera with hybridization documented in the literature. We then fitted species distribution models for this subset of non-native ornamentals as well as for all their congeners in the native and naturalized European flora. We restricted our analysis to congeners because hybridization risk is strongly linked to genetic distance (Mallet, 2005), and intergeneric hybrids are rare (Whitney, Ahern, Campbell, Albert, & King, 2010). Finally, we assessed to what extent the range matching between the selected garden plants and their congeners will increase under three different climate change scenarios.

## 2 | METHODS

### 2.1 | Species selection

Our initial pool of study species was the same as used by Dullinger et al. (2016). These authors aligned the European Garden Flora (EGF; Cullen et al., 2011), the most comprehensive encyclopaedia of ornamental plants in Europe, with the Global Naturalised Alien Flora (GloNAF; van Kleunen et al., 2015; <https://glonaf.org/>), a global database of naturalized alien plant species. They thereby identified non-native ornamental plants cultivated in Europe which have naturalized somewhere outside of Europe, but not yet in Europe. For species distribution modelling (SDM) purposes, this list was then reduced to those 783 species with more than 50 occurrences found in a search of the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org/>) database.

Here, we used a systematic web-based literature search to further narrow this group of candidate species to those particularly relevant in the context of both invasion and hybridization. We used all possible combinations of the following keywords in the Web-of-Science (<http://apps.webofknowledge.com>): #hybridization, #hybridisation, #invasion, #alien, #invasive species, #plant. The records were subsequently limited to the following categories: agriculture, biodiversity, conservation, ecology, environmental sciences, evolutionary biology and reproductive biology. We screened the abstracts of the 1,220 papers found and finally identified 66 plant genera that fulfil the following criteria: (1) interspecific hybridization has been documented and (2) they contain invasive species (even if these are not identical with the hybrids or if only intraspecific hybrids have so far been reported to be invasive, for example in *Pyrus* (Hardiman & Culley, 2010)). Twenty-three of these genera were represented by at least one species in the list of Dullinger et al. (2016), of which 18 were also represented by at least one species (native and naturalized) in the flora of Europe (Tutin et al., 1964–1980). From these, we discarded the genera *Rosa* and *Rubus* because of taxonomic difficulties with a large number of apomictic species. As a result of these consecutive filtering steps, we ended up with 16 genera. These 16 genera contain 34 alien plants currently cultivated in Europe with the potential to escape into the wild (indicated by their naturalization in other continents) and at least one congeneric species in the native and naturalized flora of Europe which shares the same life form (assuming that only mating partners of the same life form are likely to produce viable hybrid offspring; see Tables S1, S3, S6). Most of these species are planted for ornamental purposes only, but some, like *Chenopodium quinoa* or several *Eucalyptus* spp., are also of commercial interest beyond horticulture. After a final screening in GBIF for those species with more than 50 occurrence records (see Table S2), the group of congeneric species within Europe contained 133 native and 40 alien naturalized spp (see Table S6).

### 2.2 | Species distribution data and climatic maps

Data on the world-wide distribution of the 34 alien garden plants and their 173 native and naturalized congeners were taken from GBIF.

All species lists were taxonomically harmonized using The Plant List (<http://www.theplantlist.org>). Multiple occurrences within 10' × 10' grid cells and clearly erroneous records, that is those in water bodies, were removed. We did not limit records to those from the native range because species are known to partly expand their realized climatic niches in the naturalization range (Dellinger et al., 2016; Early & Sax, 2014; Petitpierre et al., 2012).

For characterizing the means and annual variability of the current temperature and precipitation patterns, we used six bioclimatic variables (climatic data averaged for the baseline period 1950–2000) provided by WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005): BIO4—Temperature Seasonality, BIO5—Max Temperature of Warmest Month, BIO6—Min Temperature of Coldest Month, BIO16—Precipitation of Wettest Quarter, BIO17—Precipitation of Driest Quarter, BIO18—Precipitation of Warmest Quarter. All these variables are known to potentially influence species distributions (Root et al., 2003). All climatic variables were provided by WORLDCLIM at a spatial resolution of 10 min.

Possible future climates in Europe were represented by three emission scenarios of the IPCC5-scenario family: the milder RCP2.6, the medium RCP4.5 and the severe RCP8.5 (IPCC, 2013). The respective monthly temperature and precipitation time series, already regionalized for Europe, were taken from the Cordex portal (<http://cordexsg.dmi.dk/esgf-web-fe/live>) and used to recalculate 10' resolution maps of the above six bioclimatic variables for possible future climates of the 21st century. A 50-year average of the period 2050–2100 was then used as the climate of the future in model projections (see below).

### 2.3 | Species distribution models

We used the BIOMOD2 platform (Thuiller, Lafourcade, Engler, & Araujo, 2009) in R (R Core Team, 2015) to quantify species' climatic niches and subsequently project current and future spatial distributions. The following modelling algorithms were used: generalized linear model (GLM), general additive model (GAM), boosted regression tree (BRT) and random forest (RF). For applying these species distribution models (SDMs) with presence-only data as provided by GBIF, we generated "pseudo-absences" following recommendations of Barbet-Massin, Jiguet, Albert, and Thuiller (2012): for regression technique models (GLM and GAM), we used 10,000 randomly distributed absences, and for machine-learning technique models (BRT and RF), we used a number of pseudo-absences equal to the number of occurrences found in GBIF and selected outside a radius of 200 km around these occurrences. In the latter case, pseudo-absence generation, and hence model calibration, was repeated 10 times per species to ensure that selected pseudo-absences did not bias the final predictions. For all models, the weighted sum of presences equalled the weighted sum of pseudo-absences. The predictive performance of the models was evaluated by means of the true skill statistic (TSS; Allouche, Tsoar, & Kadmon, 2006) based on a repeated (three times) split-sampling approach in which models were calibrated with 80% of the data and evaluated over the remaining 20%. Evaluated models were then used for two different average projections of the spatial distribution of

each of the 34 garden plants and their 173 native and naturalized congeners under current climatic conditions and the three climate change scenarios: one comprised the two regression-based techniques and one comprised the two machine-learning techniques. The probabilistic output of the two ensemble models was aggregated to a weighted mean, with weights determined by their respective TSS scores. Similarly, binary outputs of each of the two ensemble projections were generated based on a threshold that maximizes the TSS score (Liu, Berry, Dawson, & Pearson, 2005; Liu, White, & Newell, 2013) and then aggregated to a conservative consensus map; that is, 10' resolution cells were only classed as climatically suitable to a species if both ensemble models agreed on the potential presence of the species in the cell.

### 2.4 | Overlap of climatically suitable ranges

Geographic overlap between the climatically suitable ranges of the 34 alien garden plants and their 173 congeners under current and future climatic conditions was quantified by calculating the TSS from binary projections. Further, range overlap was quantified by the total number of overlapping grid cells, again based on binary projections. Both metrics were calculated for each possible species pair; that is, each of the 34 garden plants was combined with any of its congeners. Overlap metrics were subsequently averaged per species of garden plant (i.e., the average range overlap of each garden plant species and all its congeners in the wild flora was computed), separately for each climate change scenario. These average overlaps were then compared among the current climate and each climate change scenario using linear mixed-effects models (LMMs). Each LMM used the 34 ratios of current-to-future climatic range overlaps as the response, which was regressed against a fixed intercept, that is we tested whether the mean of the logarithm of these ratios was significantly larger or smaller than 0. A random intercept for genus was estimated to account for the fact that some genera were represented by more than one species of garden plant.

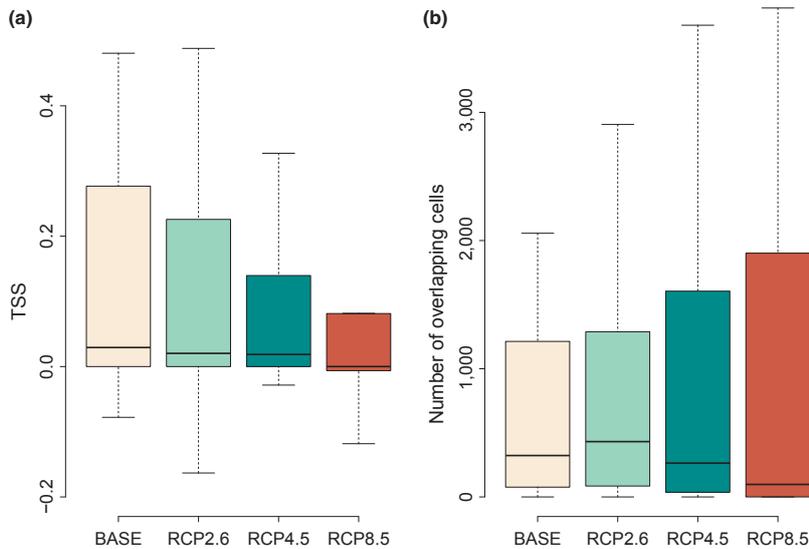
All analyses were carried out in R (R Core Team, 2015) mainly using the packages RASTER (Hijmans & van Etten, 2012) for handling of SDM gridded outputs, PRESENCEABSENCE (Freeman & Moisen, 2008) for calculating TSS and evaluation metrics and NLME (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2015) for LMMs.

## 3 | RESULTS

### 3.1 | Geographic overlap of suitable ranges

Species distribution models for both the 34 alien garden plants and their 173 congeners in the native and naturalized European flora produced accurate projections in most cases (see Table S6).

True skill statistic scores suggest that the mean geographical overlap between the climatically suitable ranges of the 34 garden plants and their congeners will decrease under a warming climate (Figure 1a): the overlap is lowest under the strongest scenario (RCP8.5) and also significantly different from current climatic conditions under the



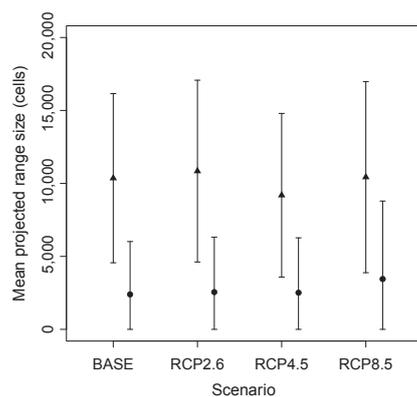
**FIGURE 1** Mean overlap in areas climatically suitable to 34 alien garden plants and their congeners in the native and naturalized flora of Europe. Overlap was quantified by the true skill statistic-TSS (a), or the number of overlapping cells (b), and calculated for current climate (BASE) and under three scenarios of climate change (RCP2.6, RCP4.5, RCP8.5) for the second half of the 21st century (2050–2100)

mild and intermediate scenarios (RCP2.6 and RCP4.5; see Table S4). When overlap is measured as the number of  $10' \times 10'$  cells that are climatically suitable to both the garden plants and their congeners (i.e., the absolute size of their overlapping range, see Table S5), the results suggest that a warmer climate will not change the size of overlapping ranges in a statistically significant way in any of the scenarios (Figure 1b, see Table S4).

Looking at climatically suitable ranges of the 34 garden plant species and their 173 congeners separately indicates that these results are partly driven by opposite effects of climate change on the two species groups: while average range size (=number of suitable cells) is projected to increase for the garden plants (statistically significantly only for scenario RCP8.5, see Table S4), it will remain constant or even decrease for their congeners in the wild European flora, at least under

the more severe scenarios (RCP4.5 and RCP8.5, Figure 2 and see Table S4). These opposite trends apparently result in no net change in overlap or in a slight reduction depending on scenario and overlap measure used, but never in a significant increase in overlap.

These average trends mask strong differences among genera. Figure 3 demonstrates that the number of cells climatically suitable to both the 34 garden plants and their European congeners can either strongly decrease or increase under each of the future climate scenarios, and variation among individual species pairs (i.e., a particular garden plant species with all its individual congener species) is even more pronounced. In particular, under each of the scenarios, there are a number of genera for which spatial overlap of suitable ranges between non-native ornamental plants and their European congeners will increase markedly. This is especially true for the genera *Solidago*, *Fraxinus*, *Lonicera* and *Prunus*.

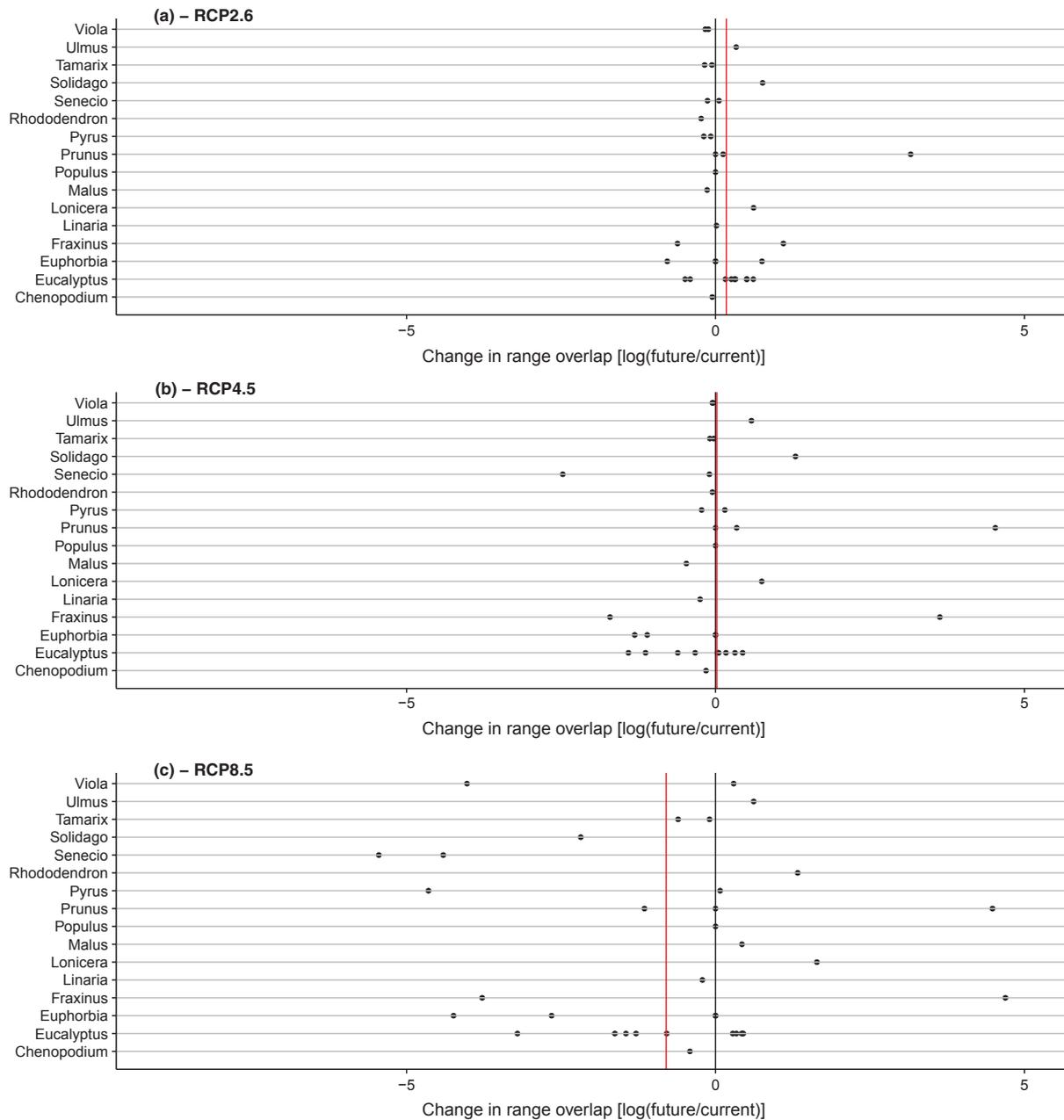


**FIGURE 2** Mean projected range size of 34 alien garden plants (circles) and of their 173 congeners in the native and naturalized flora of Europe (triangles) under current climate (BASE) and under three different scenarios of climate change (RCP2.6, RCP4.5, RCP8.5) for the second half of the 21st century (2050–2100). The error bars indicate the standard deviation

## 4 | DISCUSSION

Taken together, our results do not support the expectation that the area suitable to both the group of potential future invaders among European garden plants and their congeners in the resident flora of the continent will increase under a changing climate. Potential range overlap between these two groups of species will rather decrease under all warming scenarios. This is partly due to opposing trends in the size of climatically suitable ranges among the two groups: while potential invaders on average expand their suitable ranges, those of resident congeners remain constant or shrink, at least under moderate and severe warming. However, there is pronounced variation among the different species pairs and for some of them the predicted increase in range overlap is significant, suggesting that the risk of hybridization between them will also increase.

Climate change has already allowed many alien species to expand their non-native ranges (e.g., IPCC, 2014). For ornamental plants, the



**FIGURE 3** Change in overlap of areas climatically suitable to 34 alien garden plants and their 173 congeners in the native and naturalized flora of Europe. Overlap in areas is measured by the log of the ratio of the number of  $10 \times 10'$  cells suitable to both species in a possible species pair. Each point represents the average change in overlap between one of the 34 garden plants and all its congeners under the respective climate scenario (some points represent more than one pair because of identical values). Values  $<0$  represent a decrease, values  $>0$  an increase, values  $= 0$  no change in overlap. The three panels refer to climate change scenarios RCP2.6 (a), RCP4.5 (b) and RCP8.5 (c). The red line represents the mean over all pairs

main reason for this trend is probably their widespread commercial use beyond climatic conditions they would tolerate in the wild, which gives them a head start when the climate warms (Van der Veken, Hermy, Vellend, Knapen, & Verheyen, 2008). Predictions of increasing suitable range sizes of ornamental plants in a warming Europe likely

have similar underlying reasons. Many ornamentals currently cultivated on the continent come from warm(er) regions and hence tend to expand towards north-eastern and north-western Europe, in particular, if climatic constraints in these regions are relaxed (cf. Bellard et al., 2013; Dullinger et al., 2016). The 34 non-native ornamental

plants used in this study are also mostly native to warm regions and hence their potentially suitable ranges in Europe tend to increase, on average, despite pronounced idiosyncratic differences. Although the pool of their European congeners contains many warm-adapted species too (e.g., most species from the genera *Euphorbia* and *Tamarix*), it also includes a considerable number of montane or even alpine species (e.g., from the genera *Linaria*, *Rhododendron*, *Senecio* and *Viola*). For montane species, climatically suitable ranges are particularly likely to shrink under climate warming (Engler et al., 2011; Thuiller et al., 2014). The share of montane species is thus probably a factor restricting range increases of congeners in the more severe climate scenarios.

We emphasize that our estimate of changing range overlaps does not include a temporal dimension. Real changes in overlap of species distribution over the 21st century may actually deviate from those projected here. On the one hand, wild populations of species (both native and naturalized) will likely lag behind the changing climate due to dispersal and migration constraints (e.g., Corlett & Westcott, 2013; Dullinger et al., 2015). These constraints are less relevant or even irrelevant for ornamental plants in horticultural trade. Actually, garden plants may even “overtake” climate change when regional demand of gardeners anticipates future climatic alterations (Bradley et al., 2012). On the other hand, remnant populations of species in the wild may still occupy an area long after the average climate has become unsuitable to them (Eriksson, 2000). Actual range overlap over the next decades will hence not only be a function of changes in suitable ranges, but will be co-determined by the behaviour of gardeners and by migration lags and extinction debts of wild populations (Dullinger et al., 2012). Thus, we may expect that our SDM-based projections will underestimate real overlap near the wild species’ trailing edges (because of delayed extinctions), but overestimate it near the wild species’ leading edges (because of lagged migration).

An average decrease in range overlap among all the species pairs tested here does not necessarily imply a general decrease in hybridization risk from invasive plants in Europe. First, we deliberately restricted our approach to hybridization among potential future invaders and resident species but did not consider the possible emergence of hybrids within the resident (i.e., native and already naturalized or even invasive) species. Among the latter, several hybrids come from genera well-known to hybridize such as *Fallopia* (Parepa, Fischer, Krebs, & Bossdorf, 2014) or *Epilobium* (Gregor et al., 2013). For an exhaustive evaluation of climate-driven changes in hybridization risk of non-native plants, these species would have to be included into the models. Second, the probability of hybridization risk will likely vary widely among the species pairs included in this study. Successful establishment of allopolyploid hybrids, for example, depends on plant traits (Mallet, 2007). In addition, the genetic distance between species certainly differs a lot among the pairs studied and hence also the likelihood that reproductive barriers break down (Mallet, 2005). A more precise evaluation of hybridization risk under climate warming would therefore have to weight changing range overlaps by the likelihood that particular species pairs hybridize at all—and, in an additional step, by the probability that a particularly successful invader emerges from

such hybridization (e.g., Abbott et al., 2009; Hovick & Whitney, 2014). Such weighting might significantly modify expected changes in hybridization as individual species pairs with increasing range overlap are to be found in almost all genera. Although data for reliable estimation of these weights are lacking, we emphasize that among the genera with increasing average range overlaps in at least some scenarios, species in *Solidago* and *Rhododendron* have already produced invasive hybrids in Europe (Abbott et al., 2009; Erfmeier, Tsaliki, Ross, & Bruelheide, 2011; Karpaviciene & Radusiene, 2016) and may hence be particularly likely to do so in the future again. In addition, among the genera which were both identified to have produced invasive hybrids in the meta-analysis of Hovick and Whitney (2014) and used in our study, three include species pairs with increasing average range overlaps in at least some climate change scenarios (*Rhododendron*, *Ulmus*, *Viola*) and only one solely contains pairs with decreasing average overlap (*Tamarix*).

Although we consider the change in suitable range overlap to be a sensible indicator of changing hybridization risk, the emergence of hybrids does not necessarily depend on the contact of the species in the wild. Some of the native or already naturalized congeners in our study are species that frequently occur at ruderal sites or even as garden weeds (e.g., *Euphorbia peplus*, *Senecio vulgaris*) and hence also potentially reproduce with plants cultivated in gardens or parks. For these species, changing hybridization risk might more realistically be estimated from how their future suitable ranges overlap with the possible area where potential hybridization partners among ornamental plants can be cultivated when climate warms. These areas are usually much larger than those suitable for establishment of wild populations (Van der Veken et al., 2008) and hence risk assessments based on the latter may actually be underestimates.

Apart from potentially fostering invasiveness, hybridization between alien and native plants may threaten native populations of rare species through outbreeding depression (Bleeker et al., 2007), gene swamping (Todesco et al., 2016) or pollen competition (Arceo-Gomez & Ashman, 2016). Among the genera included in this study, introgressive hybridization has been documented in several cases (e.g., *Tamarix* (Gaskin & Kazmer, 2009), *Rhododendron* (Stace et al., 2015), *Viola* (Stace et al., 2015)). Conversely, Bleeker et al. (2007) have identified 18 native species red-listed in Germany, which potentially suffer from outbreeding depression when hybridizing with more abundant aliens. Among the 13 genera these species belong to, six are also included in our study (*Euphorbia*, *Malus*, *Populus*, *Prunus*, *Solidago*, *Viola*) with two of them (*Solidago*, *Prunus*) tending towards increased range overlap with native congeners under a warming climate (these results are very similar when the climatic area of natives that is also suitable to their non-native congeners among garden plants is calculated as a measure of threat to the native plants, see Fig. S3). In addition, Bleeker et al. (2007) listed threatened native *Viola* spp. as sensitive to gene introgression from alien congeners. Similar evaluations for other European countries are largely lacking. However, across Europe, the congeners of our 34 potential future invaders include many regionally endangered or even globally rare species such as Mediterranean endemics in the genera *Linaria*, *Senecio* or *Viola*. Although the magnitude of threat to rare species from outbreeding depression and introgression with

hybridizing aliens is not well documented yet (Bohling, 2016), future escape and expansion of ornamental plants into the range of these endemics may actually put additional pressure on them, beyond the challenges they face under a warming climate. Most of these species are not included in our study as their distribution is not represented well enough in GBIF, but this issue certainly warrants further investigation.

Finally, as a last caveat, we note that the models this study is based on were fitted using data taken from GBIF. This source combines the advantage of a global coverage, and hence the possibility to fit niches of species comprehensively, with the disadvantage of the errors and biases implicit to this database (Meyer, Weigelt, & Kreft, 2016). Uncertainties in species distribution estimates and models resulting from these caveats have a clear geographical bias and are least pronounced in the well represented regions of Europe, North- and Central America, and Australia (Meyer et al., 2016). The majority of the ornamental plants and all congeners modelled here come from these areas, and we hence assume that data problems are of limited importance for them. Several of the ornamental plants are native to temperate Asia and Africa, however, and these regions have notoriously low data coverage. The most likely consequence of this low coverage is an underestimate of these species' niches and hence of their potential distribution in Europe as well as their overlap with native and already naturalized congeners. Such underestimation may have been reinforced by the restrictive rules of our consensus projections. As a result, range overlap estimates computed here are probably conservative. We do not, however, think that these data problems affect our main result, namely that the average potential range overlap between ornamental plants and congeners does not increase under a warming climate. This is because predicted trends for species of Asian and African origin are similar to those of the remaining species (see Fig. S1 and Fig. S2 respectively).

## 5 | CONCLUSION

Climate warming will potentially increase the area suitable for the naturalization of many non-native ornamental plants in Europe (Dullinger et al., 2016), but the mean geographical overlap of climatic ranges between the selection of ornamentals and their native and naturalized congeners modelled here is unlikely to increase in the future. Thus, the average risk that garden plants and their wild congeners in the European flora will hybridize does not appear to rise when climate warms. We emphasize, however, that suitable range overlaps do increase for many individual congener pairs and that the pair-specific likelihood of successful hybrid establishment is unknown. A decreasing average range overlap does not, therefore, preclude increasing invasion risk from hybrids between particular species pairs.

## ACKNOWLEDGEMENTS

This research was funded by the ERA-Net BiodivERsA, with the national funders FWF (Austrian Science Fund, project "Who Is Next" I-1443-B25 to G.K., I.D., F.E., D.M., S.D.), DFG (German Research Foundation: O.B., E.H., M.vK.) and ANR (French National Research Agency: M.C., W.T.),

part of the 2012-2013 BiodivERsA call for research proposals. P.P. and J.P. were supported by projects 504/11/1028 and 14-36079G Centre of Excellence PLADIAS (Czech Science Foundation), long-term research development project RVO 67985939 and Praemium Academiae award (The Czech Academy of Sciences).

## AUTHOR CONTRIBUTIONS

S.D. and G.K. conceived the ideas; G.K. and A.G. analysed the data; I.D. and J.W. contributed to the analyses; G.K. and S.D. led the writing of the manuscript; all authors contributed to the discussion of ideas and revised the text.

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## BIOSKETCH

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

**How to cite this article:** Klonner G, Dullinger I, Wessely J, et al. Will climate change increase hybridization risk between potential plant invaders and their congeners in Europe?. *Diversity Distrib.* 2017;23:934–943. <https://doi.org/10.1111/ddi.12578>

## (A) APPENDIX

Table S1: Overview of plant genera for which interspecific hybridization is documented, which contain garden plant species cultivated in Europe and naturalized somewhere in the world but not yet in Europe, which have at least one congener in the native or already naturalized European flora, and which are represented by > 50 occurrence records in GBIF. The taxonomically difficult genera *Rosa* and *Rubus* were excluded. FE indicates the number of congeneric species in the native or already naturalized European flora according to the Flora Europea (Tutin et al. 1964-1980). “Hybrid” indicates whether a genus contains interspecific hybrids that have naturalized somewhere (1). In addition, examples of references to articles in ISI-listed journals that report successful interspecific hybridization are given under “source”.

genus	FE	hybrid	source
<i>Chenopodium</i>	27	1	e.g. (Bleeker <i>et al.</i> , 2007)
<i>Eucalyptus</i>	11	0	e.g. (Barbour <i>et al.</i> , 2006, 2007; 2010)
<i>Euphorbia</i>	106	1	e.g. (Bleeker <i>et al.</i> , 2007)
<i>Fraxinus</i>	5	1	e.g. (Thomasset <i>et al.</i> , 2014)
<i>Linaria</i>	70	1	e.g. (Ward <i>et al.</i> , 2009)
<i>Lonicera</i>	17	1	e.g. (Bleeker <i>et al.</i> , 2007)
<i>Malus</i>	6	1	e.g. (Bleeker <i>et al.</i> , 2007)
<i>Populus</i>	11	1	e.g. (Bleeker <i>et al.</i> , 2007)
<i>Prunus</i>	21	1	e.g. (Bleeker <i>et al.</i> , 2007)
<i>Pyrus</i>	12	0	e.g. (Yamamoto <i>et al.</i> , 2002; Hardiman & Culley, 2010; Bell & Itai, 2011)
<i>Rhododendron</i>	6	1	e.g. (Erfmeier <i>et al.</i> , 2011)
<i>Senecio</i>	67	1	e.g. (Pelser <i>et al.</i> , 2012)
<i>Solidago</i>	5	1	e.g. (Bleeker <i>et al.</i> , 2007)
<i>Tamarix</i>	14	1	e.g. (Gaskin & Schaal, 2002; Gaskin & Kazmer, 2009; Lindgren <i>et al.</i> , 2010; Mayonde <i>et al.</i> , 2015)
<i>Ulmus</i>	6	1	e.g. (Zalapa <i>et al.</i> , 2010)
<i>Viola</i>	92	1	e.g. (Bleeker <i>et al.</i> , 2007)

Table S2: List of model species (i.e. those alien garden plants cultivated in Europe and naturalized somewhere in the world but not yet in Europe, which have at least one congener in the native or already naturalized European flora, which stem from genera for which hybridization is documented) and which are represented by > 50 occurrence records in GBIF together with their life form (cf. Tab. 3) and their native range (GloNAF; van Kleunen *et al.*, 2015; <https://glonaf.org/>).

<b>spec</b>	<b>life form</b>	<b>native range</b>	<b>GBIF points</b>
<i>Chenopodium quinoa</i>	annual	S-America	96
<i>Eucalyptus cinerea</i>	tree	Australia	84
<i>Eucalyptus cladocalyx</i>	tree	Australia	88
<i>Eucalyptus cornuta</i>	tree	Australia	78
<i>Eucalyptus dalrympleana</i>	tree	Australia	277
<i>Eucalyptus goniocalyx</i>	tree	Australia	296
<i>Eucalyptus leucoxydon</i>	tree	Australia	382
<i>Eucalyptus nitens</i>	tree	Australia	73
<i>Eucalyptus ovata</i>	tree	Australia	407
<i>Eucalyptus rubida</i>	tree	Australia	405
<i>Euphorbia balsamifera</i>	shrub	Africa (+ Canary Islands)	69
<i>Euphorbia leucocephala</i>	shrub	N-America, S-America	52
<i>Euphorbia mauritanica</i>	herb	Africa	175
<i>Euphorbia tithymaloides</i>	shrub	N-America, S-America	188
<i>Fraxinus nigra</i>	tree	N-America	118
<i>Fraxinus uhdei</i>	tree	N-America, S-America	151
<i>Linaria maroccana</i>	herb	Africa	206
<i>Lonicera sempervirens</i>	herb	N-America	123
<i>Malus prunifolia</i>	tree	Asia	59
<i>Populus acuminata</i>	tree	N-America	65
<i>Prunus munsoniana</i>	tree	N-America,	57
<i>Prunus pumila</i>	shrub	N-America	152
<i>Prunus salicina</i>	tree	Asia	90
<i>Pyrus calleryana</i>	tree	Asia	88
<i>Pyrus pyrifolia</i>	tree	Asia	102
<i>Rhododendron japonicum</i>	shrub	HYBRID	58
<i>Senecio radicans</i>	herb	Africa	57
<i>Senecio tamoides</i>	herb	Africa	73
<i>Solidago ptarmicoides</i>	herb	N-America	89
<i>Tamarix aphylla</i>	tree	Africa, Asia	205
<i>Tamarix chinensis</i>	tree	Asia	216
<i>Ulmus parvifolia</i>	tree	Asia	146
<i>Viola hederacea</i>	herb	Asia	354
<i>Viola sororia</i>	herb	N-America	849

Table S3: Reclassification of life forms reported in the Global Naturalized Flora database (GloNAF; van Kleunen *et al.*, 2015; <https://glonaf.org/>) used for assessing correspondence between alien garden plants and potential hybridization partners in the resident flora of Europe.

Life form	Conversion
phanerophyte, macrophanerophyte,	tree
hemiphanerophyte, nanophanerophyte, shrub	shrub
shrub/vine	shrub/vine
Chamaephyte	scrub
herb, succulent herb	herb
forb/vine, herb + forb/herb, geophyte, forb/herb,	forb/herb
forb annual, therophyte	annual

Table S4: Linear Mixed Effects Models (LMMs) testing either climate-driven changes in the overlap of climatically suitable ranges (by 2050-2100) of alien garden plants and their congeners in the naturalized and native flora of Europe; or climate-driven changes in the number of cells suitable either to the garden plants or their congeners. Overlap was measured by the True Skill statistic (TSS) and the number of overlapping cells. The column “model” gives the representation of the model in the statistical programming language R. The other columns document fixed effects estimates (est) with lower and upper .95 confidence intervals (lower; upper), standard error (std.error), degrees of freedom (df), t-values and p-values. Significant models (p-value < 0.05) are in bold.

Model	lower	est	upper	std.error	df	t-value	p-value
TSS							
<b>RCP2.6/BASE ~ 1  genus</b>	<b>-0.043</b>	<b>-0.020</b>	<b>0.004</b>	<b>0.009</b>	<b>18</b>	<b>-2.488</b>	<b>0.023*</b>
<b>RCP4.5/ BASE ~ 1  genus</b>	<b>-0.049</b>	<b>-0.026</b>	<b>0.004</b>	<b>0.011</b>	<b>18</b>	<b>-2.465</b>	<b>0.024*</b>
<b>RCP8.5/ BASE ~ 1  genus</b>	<b>-0.096</b>	<b>-0.061</b>	<b>-0.025</b>	<b>0.017</b>	<b>18</b>	<b>-3.622</b>	<b>0.0019*</b>
<i>Cell overlap</i>							
RCP2.6/BASE ~ 1  genus	-183	-6	171	83	15	-0.071	0.944

RCP4.5/ BASE ~ 1  genus	-679	-163	354	242	15	-0.671	0.512
RCP8.5/ BASE ~ 1  genus	-434	-319	1073	354	15	0.903	0.381
<i>Cells natives</i>							
<b>RCP2.6/ BASE ~ 1  genus</b>	<b>264</b>	<b>510</b>	<b>756</b>	<b>125</b>	<b>157</b>	<b>4.088</b>	<b>0.0001*</b>
<b>RCP4.5/ BASE ~ 1  genus</b>	<b>-1621</b>	<b>-1041</b>	<b>-460</b>	<b>294</b>	<b>157</b>	<b>-3.540</b>	<b>0.0005*</b>
RCP8.5/ BASE ~ 1  genus	-526	71	667	294	157	-0.234	0.815
<i>Cells potential invasives</i>							
RCP2.6/ BASE ~ 1  genus	-226	195	617	200	18	0.975	0.342
RCP4.5/ BASE ~ 1  genus	-572	213	998	374	18	0.569	0.576
<b>RCP8.5/ BASE ~ 1  genus</b>	<b>-268</b>	<b>1713</b>	<b>3429</b>	<b>826</b>	<b>18</b>	<b>2.098</b>	<b>0.05*</b>

Table S5: Range overlap of 34 alien garden plants and their native and already naturalized European congeners under current climate and three climate change scenarios (by 2050-2100) measured as number of cells potentially suitable to both species in each pair. Numbers represent averages over all possible combinations of each of the listed garden plants with each of their possible congeneric species (see Table S6).

species	base	RCP2.6	RCP4.5	RCP8.5
<i>Chenopodium quinoa</i>	4710	3912	3478	3622
<i>Eucalyptus cinerea</i>	731	1263	1411	1638
<i>Eucalyptus cladocalyx</i>	975	705	344	374
<i>Eucalyptus cornuta</i>	219	175	95	0
<i>Eucalyptus dalrympleana</i>	373	577	631	462
<i>Eucalyptus goniocalyx</i>	453	914	670	48
<i>Eucalyptus leucoxydon</i>	651	862	594	630
<i>Eucalyptus nitens</i>	513	842	874	399
<i>Eucalyptus ovata</i>	774	1217	939	236
<i>Eucalyptus rubida</i>	186	237	122	0
<i>Euphorbia balsamifera</i>	0	0	0	0
<i>Euphorbia leucocephala</i>	0	0	0	0
<i>Euphorbia mauritanica</i>	44	54	9	1
<i>Euphorbia tithymaloides</i>	16	7	6	0
<i>Fraxinus nigra</i>	32	102	86	766
<i>Fraxinus uhdei</i>	0	0	0	0
<i>Linaria maroccana</i>	9660	10280	8104	7947
<i>Lonicera sempervirens</i>	977	1458	1888	9
<i>Malus prunifolia</i>	7626	3765	4498	2
<i>Populus acuminata</i>	0	0	0	0
<i>Prunus munsoniana</i>	1	60	240	88
<i>Prunus pumila</i>	0	0	0	0
<i>Prunus salicina</i>	1609	1636	1951	844
<i>Pyrus calleryana</i>	2083	1924	2775	3170
<i>Pyrus pyrifolia</i>	15	24	24	0
<i>Rhododendron japonicum</i>	761	919	1262	1454
<i>Senecio radicans</i>	133	81	35	0
<i>Senecio tamoides</i>	110	153	170	0
<i>Solidago ptarmicoides</i>	216	353	526	1168
<i>Tamarix aphylla</i>	3357	2812	2758	434
<i>Tamarix chinensis</i>	1338	1106	897	690
<i>Ulmus parvifolia</i>	1963	2699	3703	2445
<i>Viola hederacea</i>	283	336	375	334
<i>Viola sororia</i>	1357	1106	1268	649

Table S6: List of the two species sets modelled: 1) 34 alien garden plants 2) 173 native or already naturalized plant species of Europe which are congeneric and share life forms with the 34 alien garden plants listed in Table S2, and which are represented in GBIF by > 50 occurrences. Further the table reflects model evaluation statistics for all modelled species. Reported is the mean TSS over all replicates and the percentage of replicates that have a TSS < 0.5, respectively, for each modelling technique.

species	model life form	GLM		GAM		RF		GBM	
		TSS	%< 0.5						
<i>Chenopodium quinoa</i>	annual	0.835	0.0	0.778	0.0	0.900	0.0	0.902	0.0
<i>Eucalyptus cinerea</i>	tree	0.921	0.0	0.897	0.0	0.910	0.0	0.908	0.0
<i>Eucalyptus cladocalyx</i>	tree	0.957	0.0	0.949	0.0	0.939	0.0	0.933	0.0
<i>Eucalyptus cornuta</i>	tree	0.975	0.0	0.955	0.0	0.979	0.0	0.971	3.3
<i>Eucalyptus dalrympleana</i>	tree	0.992	0.0	0.987	0.0	0.987	0.0	0.982	0.0
<i>Eucalyptus gonicalyx</i>	tree	0.977	0.0	0.986	0.0	0.978	0.0	0.975	0.0
<i>Eucalyptus leucoxydon</i>	tree	0.961	0.0	0.968	0.0	0.979	0.0	0.976	0.0
<i>Eucalyptus nitens</i>	tree	0.875	0.0	0.879	0.0	0.949	0.0	0.942	0.0
<i>Eucalyptus ovata</i>	tree	0.979	0.0	0.983	0.0	0.981	0.0	0.979	0.0
<i>Eucalyptus rubida</i>	tree	0.974	0.0	0.978	0.0	0.978	0.0	0.971	0.0
<i>Euphorbia balsamifera</i>	shrub	0.907	0.0	0.897	0.0	0.933	0.0	0.919	0.0
<i>Euphorbia leucocephala</i>	shrub	0.777	0.0	0.837	0.0	0.793	0.0	0.800	0.0
<i>Euphorbia mauritanica</i>	herb	0.942	0.0	0.960	0.0	0.959	0.0	0.947	0.0
<i>Euphorbia thymaloides</i>	shrub	0.777	0.0	0.798	0.0	0.817	0.0	0.813	0.0
<i>Fraxinus nigra</i>	tree	0.947	0.0	0.950	0.0	0.964	0.0	0.951	0.0
<i>Fraxinus uhdei</i>	tree	0.831	0.0	0.822	0.0	0.889	0.0	0.881	0.0
<i>Linaria maroccana</i>	herb	0.824	0.0	0.854	0.0	0.915	0.0	0.906	0.0
<i>Lonicera sempervirens</i>	herb	0.924	0.0	0.933	0.0	0.967	0.0	0.961	0.0
<i>Malus prunifolia</i>	tree	0.909	0.0	0.766	0.0	0.892	0.0	0.850	0.0
<i>Populus acuminata</i>	tree	0.972	0.0	0.970	0.0	0.959	0.0	0.951	0.0
<i>Prunus munsoniana</i>	tree	0.938	0.0	0.842	0.0	0.964	0.0	0.970	0.0
<i>Prunus pumila</i>	shrub	0.910	0.0	0.936	0.0	0.936	0.0	0.926	0.0
<i>Prunus salicina</i>	tree	0.781	0.0	0.767	0.0	0.898	0.0	0.880	0.0
<i>Pyrus calleryana</i>	tree	0.802	0.0	0.870	0.0	0.868	0.0	0.850	0.0
<i>Pyrus pyrifolia</i>	tree	0.870	0.0	0.790	0.0	0.888	0.0	0.872	0.0
<i>Rhododendron japonicum</i>	shrub	0.893	0.0	0.792	0.0	0.947	0.0	0.922	0.0
<i>Senecio radicans</i>	herb	0.844	0.0	0.768	0.0	0.958	0.0	0.939	0.0
<i>Senecio tamoides</i>	herb	0.940	0.0	0.950	0.0	0.969	0.0	0.951	0.0
<i>Solidago ptarmicoides</i>	herb	0.861	0.0	0.845	0.0	0.867	0.0	0.859	0.0
<i>Tamarix aphylla</i>	tree	0.727	0.0	0.758	0.0	0.834	0.0	0.826	0.0
<i>Tamarix chinensis</i>	tree	0.722	0.0	0.799	0.0	0.836	0.0	0.824	0.0
<i>Ulmus parvifolia</i>	tree	0.827	0.0	0.732	0.0	0.815	0.0	0.817	0.0
<i>Viola hederacea</i>	herb	0.978	0.0	0.976	0.0	0.986	0.0	0.974	0.0
<i>Viola sororia</i>	herb	0.860	0.0	0.863	0.0	0.925	0.0	0.893	0.0
<i>Chenopodium album</i>	annual	0.881	0.0	0.907	0.0	0.935	0.0	0.909	0.0
<i>Chenopodium capitatum</i>	annual	0.724	0.0	0.794	0.0	0.887	0.0	0.848	0.0
<i>Chenopodium ficifolium</i>	annual	0.917	0.0	0.944	0.0	0.969	0.0	0.960	0.0
<i>Chenopodium foliosum</i>	annual	0.809	0.0	0.831	0.0	0.889	0.0	0.876	0.0
<i>Chenopodium glaucum</i>	annual	0.820	0.0	0.830	0.0	0.925	0.0	0.891	0.0
<i>Chenopodium hybridum</i>	annual	0.955	0.0	0.948	0.0	0.963	0.0	0.961	0.0
<i>Chenopodium murale</i>	annual	0.801	0.0	0.850	0.0	0.909	0.0	0.887	0.0
<i>Chenopodium opulifolium</i>	annual	0.867	0.0	0.884	0.0	0.932	0.0	0.898	0.0
<i>Chenopodium polyspermum</i>	annual	0.930	0.0	0.946	0.0	0.973	0.0	0.967	0.0
<i>Chenopodium rubrum</i>	annual	0.902	0.0	0.919	0.0	0.956	0.0	0.941	0.0
<i>Chenopodium strictum</i>	annual	0.796	0.0	0.842	0.0	0.925	0.0	0.878	0.0
<i>Chenopodium sueticum</i>	annual	0.942	0.0	0.956	0.0	0.972	0.0	0.964	0.0
<i>Chenopodium urbicum</i>	annual	0.914	0.0	0.914	0.0	0.956	0.0	0.929	0.0
<i>Chenopodium vulvaria</i>	annual	0.883	0.0	0.889	0.0	0.941	0.0	0.933	0.0

<i>Eucalyptus botryoides</i>	tree	0.913	0.0	0.896	0.0	0.940	0.0	0.928	0.0
<i>Eucalyptus camaldulensis</i>	tree	0.788	0.0	0.859	0.0	0.887	0.0	0.881	0.0
<i>Eucalyptus globulus</i>	tree	0.888	0.0	0.891	0.0	0.957	0.0	0.953	0.0
<i>Eucalyptus gomphocephalus</i>	tree	0.885	0.0	0.883	0.0	0.959	0.0	0.957	0.0
<i>Eucalyptus resinifer</i>	tree	0.911	0.0	0.887	0.0	0.936	0.0	0.933	0.0
<i>Eucalyptus robusta</i>	tree	0.888	0.0	0.859	0.0	0.898	0.0	0.895	0.0
<i>Eucalyptus rudis</i>	tree	0.892	0.0	0.898	0.0	0.936	0.0	0.933	0.0
<i>Eucalyptus tereticornis</i>	tree	0.924	0.0	0.938	0.0	0.946	0.0	0.937	0.0
<i>Eucalyptus viminalis</i>	tree	0.962	0.0	0.959	0.0	0.972	0.0	0.962	0.0
<i>Euphorbia acanthothamnos</i>	scrub	0.926	0.0	0.993	0.0	0.970	0.0	0.955	0.0
<i>Euphorbia amygdaloides</i>	scrub	0.958	0.0	0.965	0.0	0.979	0.0	0.969	0.0
<i>Euphorbia angulata</i>	forb/herb	0.943	0.0	0.973	0.0	0.969	0.0	0.966	0.0
<i>Euphorbia biumbellata</i>	forb/herb	0.946	0.0	0.920	0.0	0.956	0.0	0.949	0.0
<i>Euphorbia boetica</i>	forb/herb	0.939	0.0	0.940	0.0	0.982	0.0	0.968	0.0
<i>Euphorbia brittingeri</i>	shrub	0.970	0.0	0.978	0.0	0.967	0.0	0.963	0.0
<i>Euphorbia characias</i>	forb/shrub	0.957	0.0	0.952	0.0	0.969	0.0	0.962	0.0
<i>Euphorbia clementei</i>	forb/herb	0.980	0.0	0.927	0.0	0.973	0.0	0.973	0.0
<i>Euphorbia cyparissias</i>	forb/herb	0.912	0.0	0.932	0.0	0.962	0.0	0.953	0.0
<i>Euphorbia dendroides</i>	shrub	0.955	0.0	0.932	0.0	0.963	0.0	0.955	0.0
<i>Euphorbia dracunculoides</i>	forb/herb	0.761	0.0	0.777	0.0	0.810	0.0	0.810	0.0
<i>Euphorbia dulcis</i>	forb/herb	0.946	0.0	0.947	0.0	0.971	0.0	0.963	0.0
<i>Euphorbia duvalii</i>	forb/herb	0.992	0.0	0.974	0.0	0.993	0.0	0.974	0.0
<i>Euphorbia epithymoides</i>	forb/herb	0.913	0.0	0.909	0.0	0.949	0.0	0.940	0.0
<i>Euphorbia esula</i>	forb/herb	0.858	0.0	0.854	0.0	0.924	0.0	0.899	0.0
<i>Euphorbia helioscopia</i>	forb/herb	0.939	0.0	0.944	0.0	0.965	0.0	0.955	0.0
<i>Euphorbia humifusa</i>	forb/herb	0.859	0.0	0.868	0.0	0.879	0.0	0.881	0.0
<i>Euphorbia hyberna</i>	shrub	0.962	0.0	0.957	0.0	0.979	0.0	0.971	0.0
<i>Euphorbia isatidifolia</i>	forb/herb	0.940	0.0	0.939	0.0	0.984	0.0	0.972	0.0
<i>Euphorbia lathyris</i>	forb/herb	0.920	0.0	0.927	0.0	0.962	0.0	0.958	0.0
<i>Euphorbia minuta</i>	forb/herb	0.956	0.0	0.972	0.0	0.967	0.0	0.960	0.0
<i>Euphorbia myrsinites</i>	forb/herb	0.897	0.0	0.877	0.0	0.916	0.0	0.907	0.0
<i>Euphorbia nevadensis</i>	forb/herb	0.984	0.0	0.967	0.0	0.991	0.0	0.987	0.0
<i>Euphorbia nicaeensis</i>	forb/herb	0.924	0.0	0.924	0.0	0.961	0.0	0.955	0.0
<i>Euphorbia oblongata</i>	forb/herb	0.951	0.0	0.911	0.0	0.925	0.0	0.914	0.0
<i>Euphorbia palustris</i>	forb/herb	0.940	0.0	0.947	0.0	0.961	0.0	0.951	0.0
<i>Euphorbia paralias</i>	forb/herb	0.964	0.0	0.966	0.0	0.956	0.0	0.944	0.0
<i>Euphorbia peplis</i>	forb/herb	0.950	0.0	0.952	0.0	0.941	0.0	0.933	0.0
<i>Euphorbia pithyusa</i>	scrub	0.930	0.0	0.919	0.0	0.974	0.0	0.968	0.0
<i>Euphorbia polygalifolia</i>	forb/herb	0.836	0.0	0.893	0.0	0.905	0.0	0.885	0.0
<i>Euphorbia portlandica</i>	shrub	0.983	0.0	0.979	0.0	0.976	0.0	0.971	0.0
<i>Euphorbia prostrata</i>	forb/herb	0.594	0.0	0.692	0.0	0.812	0.0	0.774	0.0
<i>Euphorbia pubescens</i>	forb/herb	0.874	0.0	0.924	0.0	0.908	0.0	0.897	0.0
<i>Euphorbia serrata</i>	forb/herb	0.905	0.0	0.961	0.0	0.967	0.0	0.960	0.0
<i>Euphorbia serrulata</i>	forb/herb	0.781	0.0	0.833	0.0	0.901	0.0	0.888	0.0
<i>Euphorbia spinosa</i>	scrub	0.968	0.0	0.940	0.0	0.970	0.0	0.961	0.0
<i>Euphorbia squamigera</i>	shrub	0.981	0.0	0.975	0.0	0.968	0.0	0.961	0.0
<i>Euphorbia taurinensis</i>	forb/herb	0.860	0.0	0.854	0.0	0.902	0.0	0.897	0.0
<i>Euphorbia terracina</i>	forb/herb	0.952	0.0	0.955	0.0	0.966	0.0	0.956	0.0
<i>Fraxinus angustifolia</i>	tree	0.959	0.0	0.960	0.0	0.966	0.0	0.959	0.0
<i>Fraxinus excelsior</i>	tree	0.957	0.0	0.960	0.0	0.977	0.0	0.969	0.0
<i>Fraxinus ornus</i>	tree	0.934	0.0	0.944	0.0	0.962	0.0	0.957	0.0
<i>Fraxinus pennsylvanica</i>	tree	0.807	0.0	0.835	0.0	0.927	0.0	0.900	0.0
<i>Linaria aeruginea</i>	forb/herb	0.953	0.0	0.961	0.0	0.965	0.0	0.958	0.0
<i>Linaria alpina</i>	forb/herb	0.940	0.0	0.935	0.0	0.971	0.0	0.968	0.0
<i>Linaria angustissima</i>	forb/herb	0.987	0.0	0.993	0.0	0.972	0.0	0.960	0.0
<i>Linaria canadensis</i>	annual	0.781	0.0	0.778	0.0	0.880	0.0	0.864	0.0
<i>Linaria genistifolia</i>	forb/herb	0.931	0.0	0.925	0.0	0.906	0.0	0.888	0.0
<i>Linaria incarnata</i>	forb/herb	0.860	0.0	0.875	0.0	0.880	0.0	0.886	0.0
<i>Linaria purpurea</i>	forb/herb	0.971	0.0	0.975	0.0	0.974	0.0	0.967	0.0
<i>Linaria repens</i>	forb/herb	0.941	0.0	0.965	0.0	0.975	0.0	0.964	0.0
<i>Linaria saxatilis</i>	forb/herb	0.959	0.0	0.987	0.0	0.976	0.0	0.969	0.0
<i>Linaria supina</i>	forb/herb	0.911	0.0	0.924	0.0	0.964	0.0	0.947	0.0

<i>Linaria vulgaris</i>	forb/herb	0.880	0.0	0.894	0.0	0.948	0.0	0.929	0.0
<i>Lonicera etrusca</i>	shrub/vine	0.949	0.0	0.955	0.0	0.965	0.0	0.957	0.0
<i>Lonicera implexa</i>	shrub/vine	0.973	0.0	0.977	0.0	0.981	0.0	0.968	0.0
<i>Lonicera japonica</i>	shrub/vine	0.833	0.0	0.860	0.0	0.934	0.0	0.915	0.0
<i>Malus domestica</i>	tree	0.900	0.0	0.911	0.0	0.941	0.0	0.926	0.0
<i>Malus sylvestris</i>	tree	0.931	0.0	0.953	0.0	0.974	0.0	0.962	0.0
<i>Populus alba</i>	tree	0.922	0.0	0.917	0.0	0.950	0.0	0.938	46.7
<i>Populus candicans</i>	tree	0.984	0.0	0.992	0.0	0.977	0.0	0.961	0.0
<i>Populus canescens</i>	tree	0.923	0.0	0.935	0.0	0.970	0.0	0.960	0.0
<i>Populus deltoides</i>	tree	0.769	0.0	0.830	0.0	0.935	0.0	0.910	0.0
<i>Populus euphratica</i>	tree	0.711	0.0	0.747	0.0	0.806	0.0	0.792	0.0
<i>Populus grandidentata</i>	tree	0.960	0.0	0.942	0.0	0.968	0.0	0.960	0.0
<i>Populus nigra</i>	tree	0.916	0.0	0.930	0.0	0.963	0.0	0.958	0.0
<i>Populus simonii</i>	tree	0.785	0.0	0.789	0.0	0.839	0.0	0.814	0.0
<i>Populus tremula</i>	tree	0.922	0.0	0.943	0.0	0.964	0.0	0.956	76.7
<i>Prunus armeniaca</i>	tree	0.735	0.0	0.728	0.0	0.823	0.0	0.807	0.0
<i>Prunus avium</i>	tree	0.953	0.0	0.953	0.0	0.966	0.0	0.957	0.0
<i>Prunus cerasifera</i>	tree	0.912	0.0	0.924	0.0	0.967	0.0	0.964	0.0
<i>Prunus cerasus</i>	tree	0.903	0.0	0.936	0.0	0.964	0.0	0.949	0.0
<i>Prunus domestica</i>	tree	0.918	0.0	0.936	0.0	0.961	0.0	0.947	0.0
<i>Prunus dulcis</i>	tree	0.896	0.0	0.901	0.0	0.929	0.0	0.920	0.0
<i>Prunus fruticosa</i>	tree	0.774	0.0	0.794	0.0	0.927	0.0	0.917	0.0
<i>Prunus laurocerasus</i>	shrub	0.962	0.0	0.957	0.0	0.980	0.0	0.971	0.0
<i>Prunus lusitanica</i>	shrub	0.940	0.0	0.956	0.0	0.976	0.0	0.972	0.0
<i>Prunus mahaleb</i>	tree	0.915	0.0	0.912	0.0	0.950	0.0	0.940	0.0
<i>Prunus padus</i>	tree	0.927	0.0	0.932	0.0	0.969	0.0	0.955	0.0
<i>Prunus persica</i>	tree	0.789	0.0	0.801	0.0	0.881	0.0	0.866	0.0
<i>Prunus prostrata</i>	shrub	0.935	0.0	0.936	0.0	0.950	0.0	0.948	0.0
<i>Prunus serotina</i>	tree	0.902	0.0	0.930	0.0	0.959	0.0	0.952	0.0
<i>Prunus spinosa</i>	tree	0.961	0.0	0.961	0.0	0.980	0.0	0.970	0.0
<i>Prunus virginiana</i>	tree	0.801	0.0	0.825	0.0	0.928	0.0	0.874	0.0
<i>Pyrus bourgaeana</i>	tree	0.979	0.0	0.978	0.0	0.982	0.0	0.972	0.0
<i>Pyrus pyraster</i>	tree	0.967	0.0	0.966	0.0	0.980	0.0	0.972	0.0
<i>Rhododendron ferrugineum</i>	shrub	0.978	0.0	0.964	0.0	0.983	0.0	0.972	0.0
<i>Rhododendron hirsutum</i>	shrub	0.973	0.0	0.976	0.0	0.964	0.0	0.958	0.0
<i>Rhododendron lapponicum</i>	shrub	0.754	0.0	0.764	0.0	0.887	0.0	0.870	0.0
<i>Rhododendron luteum</i>	shrub	0.947	0.0	0.928	0.0	0.949	0.0	0.937	0.0
<i>Rhododendron ponticum</i>	shrub	0.956	0.0	0.957	0.0	0.976	0.0	0.965	0.0
<i>Senecio cacaliaster</i>	forb/herb	0.993	0.0	0.996	0.0	0.974	0.0	0.965	0.0
<i>Senecio carpetanus</i>	forb/herb	0.991	0.0	0.993	0.0	0.990	0.0	0.979	0.0
<i>Senecio doronicum</i>	forb/herb	0.941	0.0	0.949	0.0	0.954	0.0	0.945	0.0
<i>Senecio erucifolius</i>	forb/herb	0.967	0.0	0.962	0.0	0.987	0.0	0.982	0.0
<i>Senecio inaequidens</i>	forb/herb	0.969	0.0	0.971	0.0	0.980	0.0	0.973	0.0
<i>Senecio lagascanus</i>	forb/herb	0.966	0.0	0.942	0.0	0.977	0.0	0.972	0.0
<i>Senecio lividus</i>	annual	0.942	0.0	0.953	0.0	0.965	0.0	0.956	0.0
<i>Senecio nebrodensis</i>	forb/herb	0.927	0.0	0.924	0.0	0.929	0.0	0.911	0.0
<i>Senecio nemorensis</i>	forb/herb	0.899	0.0	0.907	0.0	0.932	0.0	0.925	0.0
<i>Senecio nevadensis</i>	forb/herb	0.954	0.0	0.985	0.0	0.968	0.0	0.955	0.0
<i>Senecio pyrenaicus</i>	forb/herb	0.985	0.0	0.982	0.0	0.970	0.0	0.959	0.0
<i>Senecio smithii</i>	forb/herb	0.991	0.0	0.945	0.0	0.988	0.0	0.995	0.0
<i>Senecio squalidus</i>	forb/herb	0.939	0.0	0.946	0.0	0.956	0.0	0.948	0.0
<i>Senecio sylvaticus</i>	forb/herb	0.937	0.0	0.952	0.0	0.960	0.0	0.948	0.0
<i>Senecio viscosus</i>	forb/herb	0.934	0.0	0.956	0.0	0.970	0.0	0.964	0.0
<i>Senecio vulgaris</i>	forb/herb	0.894	0.0	0.928	0.0	0.947	0.0	0.930	0.0
<i>Solidago canadensis</i>	forb/herb	0.898	0.0	0.905	0.0	0.946	0.0	0.935	0.0
<i>Solidago gigantea</i>	forb/herb	0.903	0.0	0.906	0.0	0.950	0.0	0.944	0.0
<i>Solidago sempervirens</i>	forb/herb	0.885	0.0	0.895	0.0	0.912	0.0	0.905	0.0
<i>Solidago virgaurea</i>	forb/herb	0.924	0.0	0.944	0.0	0.964	0.0	0.951	0.0
<i>Tamarix africana</i>	tree	0.942	0.0	0.941	0.0	0.958	0.0	0.950	0.0
<i>Tamarix boveana</i>	tree	0.991	0.0	0.992	0.0	0.990	0.0	0.990	0.0
<i>Tamarix canariensis</i>	tree	0.947	0.0	0.957	0.0	0.952	0.0	0.935	0.0
<i>Tamarix gallica</i>	tree	0.898	0.0	0.901	0.0	0.916	0.0	0.905	0.0

<i>Tamarix parviflora</i>	tree	0.781	0.0	0.782	0.0	0.910	0.0	0.890	0.0
<i>Tamarix ramosissima</i>	tree	0.740	0.0	0.769	0.0	0.883	0.0	0.857	0.0
<i>Ulmus glabra</i>	tree	0.965	0.0	0.968	0.0	0.967	0.0	0.961	0.0
<i>Ulmus laevis</i>	tree	0.922	0.0	0.928	0.0	0.968	0.0	0.960	0.0
<i>Ulmus minor</i>	tree	0.951	0.0	0.950	0.0	0.976	0.0	0.968	0.0
<i>Viola arvensis</i>	forb/herb	0.923	0.0	0.924	0.0	0.957	0.0	0.947	0.0
<i>Viola biflora</i>	forb/herb	0.927	0.0	0.940	0.0	0.960	0.0	0.950	0.0
<i>Viola bubanii</i>	forb/herb	0.992	0.0	0.993	0.0	0.969	0.0	0.960	0.0
<i>Viola calcarata</i>	forb/herb	0.956	0.0	0.952	0.0	0.946	0.0	0.934	0.0
<i>Viola canina</i>	forb/herb	0.907	0.0	0.931	0.0	0.964	0.0	0.950	0.0
<i>Viola cenisia</i>	forb/herb	0.996	0.0	0.971	0.0	0.961	0.0	0.953	0.0
<i>Viola collina</i>	forb/herb	0.917	0.0	0.923	0.0	0.942	0.0	0.938	0.0
<i>Viola cornuta</i>	forb/herb	0.923	0.0	0.933	0.0	0.947	0.0	0.943	0.0
<i>Viola elatior</i>	forb/herb	0.906	0.0	0.930	0.0	0.972	0.0	0.964	0.0
<i>Viola epipsila</i>	forb/herb	0.892	0.0	0.958	0.0	0.973	0.0	0.962	0.0
<i>Viola hirta</i>	forb/herb	0.976	0.0	0.980	0.0	0.987	0.0	0.981	0.0
<i>Viola jordanii</i>	forb/herb	0.864	0.0	0.832	0.0	0.957	0.0	0.953	0.0
<i>Viola kitaibeliana</i>	forb/herb	0.939	0.0	0.947	0.0	0.964	0.0	0.950	0.0
<i>Viola lactea</i>	forb/herb	0.960	0.0	0.964	0.0	0.983	0.0	0.974	0.0
<i>Viola lutea</i>	forb/herb	0.993	0.0	0.993	0.0	0.990	0.0	0.984	0.0
<i>Viola mirabilis</i>	forb/herb	0.935	0.0	0.956	0.0	0.970	0.0	0.959	0.0
<i>Viola odorata</i>	forb/herb	0.932	0.0	0.940	0.0	0.962	0.0	0.948	0.0
<i>Viola palustris</i>	forb/herb	0.907	0.0	0.937	0.0	0.966	0.0	0.952	0.0
<i>Viola parvula</i>	forb/herb	0.974	0.0	0.947	0.0	0.937	0.0	0.928	0.0
<i>Viola persicifolia</i>	forb/herb	0.960	0.0	0.977	0.0	0.980	0.0	0.973	0.0
<i>Viola pumila</i>	forb/herb	0.939	0.0	0.959	0.0	0.987	0.0	0.979	0.0
<i>Viola pyrenaica</i>	forb/herb	0.978	0.0	0.981	0.0	0.971	0.0	0.965	0.0
<i>Viola reichenbachiana</i>	forb/herb	0.979	0.0	0.981	0.0	0.984	0.0	0.978	36.7
<i>Viola riviniana</i>	forb/herb	0.933	0.0	0.951	0.0	0.961	0.0	0.955	36.7
<i>Viola rupestris</i>	forb/herb	0.889	0.0	0.908	0.0	0.943	0.0	0.923	0.0
<i>Viola selkirkii</i>	forb/herb	0.862	0.0	0.871	0.0	0.947	0.0	0.935	0.0
<i>Viola suavis</i>	forb/herb	0.930	0.0	0.944	0.0	0.964	0.0	0.959	0.0
<i>Viola tricolor</i>	forb/herb	0.923	0.0	0.941	0.0	0.954	0.0	0.938	0.0
<i>Viola uliginosa</i>	forb/herb	0.949	0.0	0.956	0.0	0.978	0.0	0.963	0.0
<i>Viola willkommii</i>	forb/herb	0.984	0.0	0.977	0.0	0.974	0.0	0.964	0.0

Figure S1

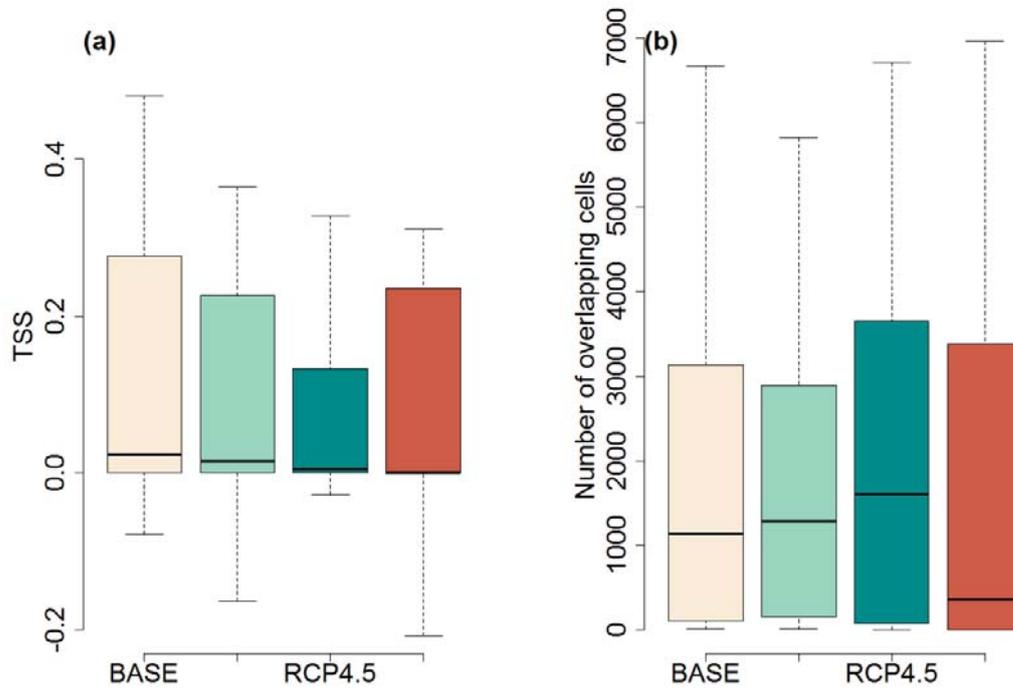


Fig. S1: Mean overlap in areas climatically suitable to 15 alien garden plants and their congeners in the native and naturalized flora of Europe. Only garden plant species native to Africa or Asia and their congeners are included. Overlap was quantified by using True Skill Statistic - TSS (A), or the number of overlapping cells (B), and calculated for current climate (BASE) and under three scenarios of climate change (RCP2.6, RCP4.5, RCP8.5) for the second half of the 21st century (2050-2100).

Figure S2

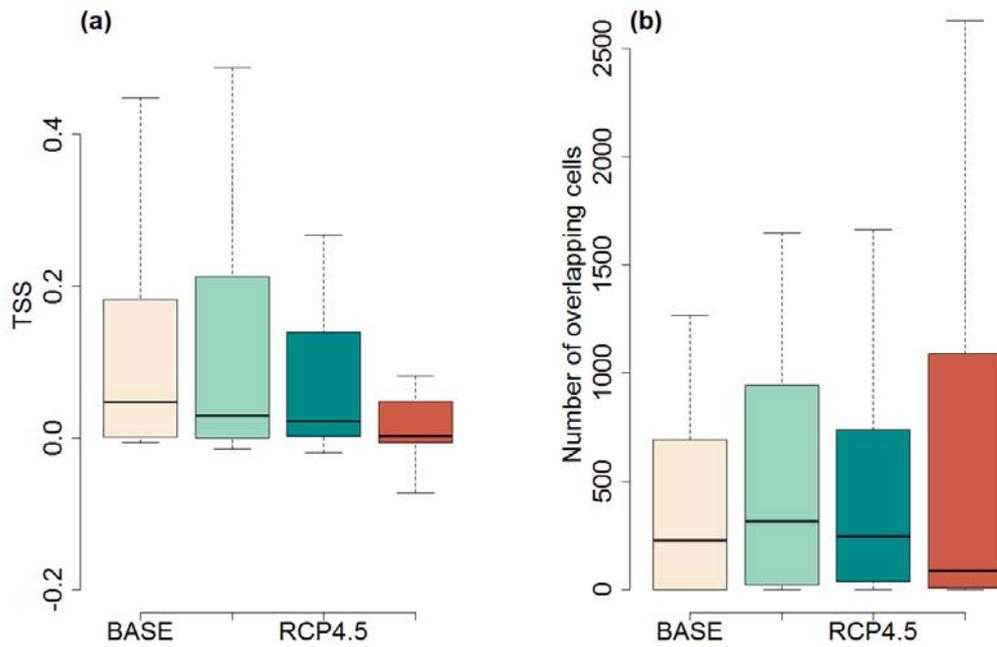


Fig. S2: Mean overlap in areas climatically suitable to 19 alien garden plants and their congeners in the native and naturalized flora of Europe. Only garden plant species not native to Africa or Asia and their congeners are included. Overlap was quantified by using True Skill Statistic - TSS (A), or the number of overlapping cells (B), and calculated for current climate (BASE) and under three scenarios of climate change (RCP2.6, RCP4.5, RCP8.5) for the second half of the 21st century (2050-2100).

**Figure S3**

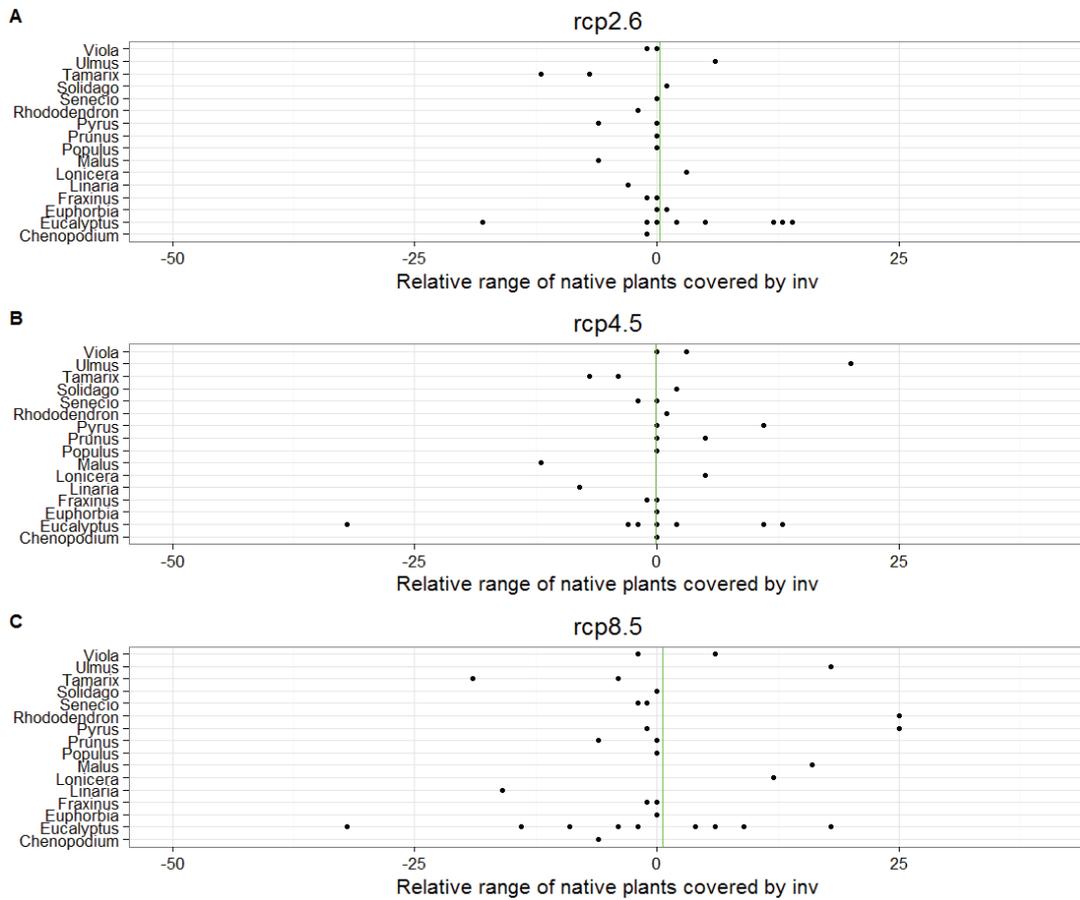


Fig. S3: Climate-driven changes in the share of the ranges of native and naturalized plant species in Europe which is also suitable to congeners among the modelled 34 alien garden plants. Share of range is measured by the ratio of 10 x 10' cells suitable to both species in a possible species pair. Each point represents the average share of range between one of the 34 garden plants and all its congeners under the respective climate scenario (some points represent more than one pair because of identical values). Values < 0 represent decreasing, values > 0 increasing, values = 0 no change in share. The three panels refer to climate change scenarios RCP2.6 (A), RCP4.5 (B) and RCP8.5 (C). The green line represents the mean over all pairs.

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## **Chapter 3**

### **Towards better integration of land use into models of species distribution and diversity**

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#### **Publication Reference**

Dullinger, I., Essl, F., Moser, D., Erb, K., Haberl, H., Dullinger, S. (in prep.): Towards better integration of land use into models of species distribution and diversity

#### **Status**

In preparation

#### **Contribution**

I conceived the idea and led the writing of the manuscript together with Stefan Dullinger.  
I conducted the literature review.

## **Towards better integration of land use into models of species distribution and diversity**

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Keywords: biodiversity, land use, land-use change, land-use intensity, predictive modelling, species distribution, species diversity

### **ABSTRACT**

1. Human land use is the most important driver of species loss, but its impact is not appropriately reflected in predictive models of species distribution and diversity so far. Possible reasons include the complex nature of land use – biodiversity relations, which is in contrast to the strive towards simple predictor variables, and the apparent lack of appropriate data.

2. Here, we discuss some important issues towards a more systematic integration of land use into predictive biodiversity models. We therefore introduce conceptual distinctions of land-use facets and dimensions from land-use science. Using land-use intensity as an example, we review the literature to evaluate the representation of these different dimensions in biodiversity research. We moreover highlight the importance of scaling issues for modelling land use – biodiversity relations and discuss issues of data availability.

3. We emphasize that biodiversity models should routinely use sets of variables that represent all of land cover, land management practice and land-use intensity, and that further account for the multi-dimensionality of land-use intensity. With respect to land-use intensity, we show that biodiversity research has been

strongly biased towards particular dimensions and qualitative indicators so far. We outline how relationships of land use and biodiversity may depend on interactions among spatial, thematic and temporal scales that are insufficiently understood and represented in models. Finally, we suggest that data to proceed towards better integration of land use into biodiversity models are at least partly there.

4. Predictive models of biodiversity need to re-focus efforts on land-use change as the currently most important threat to biological populations. Appropriately representing the complexity of land use – biodiversity relationships in such models will be key for making progress in this field. Improving data availability is another important issue, but available data also appear insufficiently used.

## **INTRODUCTION**

Rankings of drivers of global environmental change in terms of the threat they pose to biodiversity clearly identify human land use as by far the most relevant one (Pimm & Raven 2000; Maxwell *et al.* 2016). Land-use impacts on biological populations already affect approximately three-quarters of the earth's ice-free land mass (Ellis *et al.* 2013) and are predicted to further rise in extent and intensity, driven by the rapidly growing human population, economic growth, as well as changes in lifestyle and diets (Tilman *et al.* 2011; Erb *et al.* 2016).

The huge impact of land use on biodiversity is in salient contrast to the modest attention it receives by predictive biodiversity models: forecasts of how biodiversity may develop in the 21<sup>st</sup> century have concentrated on the effects of climate change while land-use change has been neglected, in comparison, with this imbalance even increasing over time (Titeux *et al.* 2016; Sirami *et al.* 2017). As a consequence, model-based biodiversity scenarios for the 21<sup>st</sup> century are potentially inappropriate or even misleading (de Chazal & Rounsevell 2009; Pereira *et al.* 2010). The reasons for this relative neglect are probably manifold. Two aspects, however, appear pivotal. First, mechanistic interrelations between land use and biodiversity are complex. While climatic parameters directly control the physiology and behaviour of organisms, land use is a complicated interplay of socioeconomic activities and ecological processes which can have manifold and

possibly interacting direct and indirect consequences for biological populations. This complexity is in contrast to the strive towards models that favour simple representations of biodiversity ‘predictors’ or the need to rely on a limited number of input datasets.

Second, biodiversity modellers commonly project expected occurrence, abundance or diversity of species in space and time to highlight regional differences of future changes in the magnitude of threats (e.g. Engler *et al.* 2011; Newbold *et al.* 2015), to inform mitigation strategies (e.g. Kehoe *et al.* 2017; Kok *et al.* 2017), or to guide particular conservation decisions (e.g. Guisan *et al.* 2013). These applications require predictor variables mapped in space and time. With respect to climatic conditions a tradition of providing appropriate maps that are often freely and easily accessible for ‘naïve users’ like biodiversity modellers has been developed by the climate modelling community (e.g. Hijmans *et al.* 2005; Overpeck *et al.* 2011). With respect to land use, comparable datasets either do not exist or are scattered across different sources and often have inappropriate resolution, especially with respect to scenarios of future development (Harfoot *et al.* 2014; Titeux *et al.* 2016).

With this article, we primarily address biodiversity modellers and want to stimulate a more widespread, systematic and conscient integration of land use into predictive models of species distribution and diversity. We therefore (1) introduce conceptual distinctions from land-use science to foster comprehensive selection of predictor variables in such models; (2) emphasize the importance of interacting scaling issues for land use – biodiversity relations, and (3) briefly discuss issues of data availability.

### **THREE FACETS OF LAND USE TO INFORM BIODIVERSITY MODELS**

The complex human agency called land use impacts many processes which potentially control the presence or abundance of particular species or emergent community properties like species richness, functional or phylogenetic diversity. Such processes include changes in the availability of resources (water, nitrogen, light, prey etc.), ambient conditions (e.g. microclimate, soil chemistry), disturbance regimes (e.g. fire, grazing), habitat structure (vertical structure, nesting sites, hiding places etc.), habitat configuration (habitat area and fragmentation), or the metacommunity of potentially interacting species (local

extinction, biological invasions). It is unlikely that any single metric or indicator of land use will ever be sufficient to comprehensively represent spatio-temporal variation in all those possible controls of species distribution and diversity. We hence suggest that land use should generally be represented in biodiversity models by a combination of several variables, similar to the sets of bioclimatic descriptors used for predicting the response of species to climate change (e.g. Engler *et al.* 2011; Thuiller *et al.* 2011). Based on recent conceptual developments in land-use science (e.g. Jansen & Gregorio 2002; Erb *et al.* 2017), we propose that these variable sets shall include metrics from three essential dimensions or 'facets' of land use which, in combination, contain information about most of the processes by which land use affects biological populations (cf. Fig. 1). First, variables describing land cover must be distinguished from those characterizing land management. While changes in land cover lead to land cover conversions, variation of land management may additionally result in land modifications, i.e. in ecologically important variation of human intervention within the same land-cover type (Erb *et al.* 2017). Within land management, distinction must further be made between descriptors of management practice and indicators or metrics of the intensity of land management (or land-use intensity, Erb *et al.* 2013; Kuemmerle *et al.* 2013). In the following, we briefly characterize these three facets. We then zoom on the land-use intensity facet to exemplarily review common practice and research gaps with respect to the interrelation of land use and biodiversity.

*Land cover*, classed according to various different schemes (e.g. EEA 2000; Tuanmu & Jetz 2014), is the so far most frequently used descriptor of land use in biodiversity models (Luoto, Virkkala & Heikkinen 2007; Barbet-Massin, Thuiller & Jiguet 2012; Dullinger *et al.* 2017). Land cover is undoubtedly important for biological populations since land-cover conversions can profoundly change biophysical and biochemical habitat characteristics (e.g. He *et al.* 2015), and because many species are adapted to structural habitat properties e.g. via specific nesting or foraging habits, microclimatic or light requirements (e.g. forest vs. non-forest). Moreover, particular types of human disturbance are implicit in certain land cover types (e.g. ploughing vs grazing/mowing), and land cover maps can serve as a basis for calculating variables that represent spatial habitat

configuration, a feature especially important for species organized as metapopulations (Hanski & Ovaskainen 2000; Krauss *et al.* 2010). The central role of land cover data in existing models of land-use effects on biodiversity is moreover motivated by the pervasive effects that land conversions, and in particular deforestation, currently have in the species rich terrestrial biomes, especially in the tropics (e.g. Fearnside 2005; Wearn, Reuman & Ewers 2012). Nevertheless, there are differences in *land management practices* that are important for species but leave no, or only subtle marks in land cover (Erb *et al.* 2017). Examples include the distinction between mowing and pasturing of grasslands (Schläpfer, Zoller & Körner 1998), the selection of crop species (Seifert, Leuschner & Culmsee 2015), the selection of tree species for afforestation (Bremer & Farley 2010), the artificial drainage respectively irrigation of land (Smart *et al.* 2006), or the use of fire as a management tool of rangeland (Fuhlendorf *et al.* 2006). These management practices may e.g. alter disturbance types, modify biotic interaction and prey availability, or change soil water and nutrient contents and the impact of such practices on species will be context dependent but is potentially severe (e.g. Paillet *et al.* 2010). For example, Bremer and Farley (2010) showed in their review that replacement of primary forest by forest plantations reduces overall plant diversity by 35% on average, but native plant diversity by 65%. Other even more subtle management differences with potentially huge impact on biological populations of at least some taxonomical groups include, e.g., dead wood management in forests (Christensen *et al.* 2005) or organic vs. non-organic farming styles (Bengtsson, Ahnström & Weibull 2005). While ecological implications of management practices have often been addressed in experimental and observational studies, appropriate descriptors are so far rarely used in predictive models biodiversity (e.g. Welsh, Dunk & Zielinski 2006; Pulsford, Lindenmayer & Driscoll 2017).

In many parts of the world changes to *land-use intensity* have been the most important type of land-use change during the recent decades (Krausmann *et al.* 2013) and intensification will likely be a prevalent trend in the future (Tilman *et al.* 2011). Land-use intensity is well known to have strong environmental impacts, for example by modifying disturbance frequency and intensity (Blüthgen *et al.* 2012), vegetation structure, nutrient, water, prey, or, more generally, energy availability (Haberl, Erb & Krausmann 2014), or the input of agrochemicals to ecosystems

(Firbank *et al.* 2003). Not surprisingly, land-use intensity has hence also strong effects on biodiversity (e.g. Laliberté *et al.* 2010; Newbold *et al.* 2015; Gossner *et al.* 2016). Nevertheless, the use of land-use intensity descriptors in predictive models of biodiversity or species distributions is relatively uncommon (but see Newbold *et al.* 2015; Kehoe *et al.* 2017).

Land-use intensity is itself a complex concept that comprises different aspects. Instead of providing a one-dimensional definition, land-use scientists have thus suggested a classification scheme of land-use intensity indicators which essentially distinguishes (Erb *et al.* 2013): (1) Inputs to the production system (input intensity; e.g. amount of fertilizer input, intensity of irrigation); (2) Outputs from the production system (output intensity; e.g. agricultural yield, stocking density of livestock, mowing frequency); and (3) Changes in system properties (i.e. the associated system-level properties of land-based production; e.g. structure or complexity of ecosystems, net primary production and its human appropriation (cf. Haberl *et al.* 2007).

Although these different aspects of land-use intensity may have distinct effects on biodiversity (Kehoe *et al.* 2015), there has so far been little reflection on this complexity in biodiversity research, and even less so in predictive biodiversity modelling. To highlight this gap, we conducted a selective literature review. We therefore searched for documents in SCOPUS by applying the following criteria: any combination of the terms 'land-use intensity' and 'biodiversity' in title, abstract and keywords of documents belonging to the type 'article'. This search yielded 291 publications which we screened in detail and retained all those that actually report data on differences in biodiversity (genetic, taxonomic, functional, phylogenetic) or population abundance in dependence on some measure of land-use intensity within terrestrial ecosystems. From the remaining studies, we selected every second (chronologically) yielding 95 articles in total. We then assigned the land-use intensity metrics used in each study to one of the above-mentioned three dimensions (see Supplementary Material). In doing so, we realized that the 'system' dimension is in need of a further distinction since land-use intensity was actually "measured" in many studies by contrasting land cover classes and/or management practices with assumed implicit differences of land-use intensity (i.e. primary forest vs. agroforestry or forest vs. agricultural land). We classified the land-use intensity 'metric' of such studies as 'implicit system'

variable as opposed to 'explicit system' variables which directly measure some system properties like HANPP or spatial habitat configuration parameters associated with land-use intensity such as patch shape complexity (Moser *et al.* 2002).

We found that more than half of the studies focus on only one of three dimensions of LU-intensity (c. 51% studies, see Fig. 2a) and only 19% integrate over all three dimensions. Moreover, the representation of dimensions is highly imbalanced with a huge majority concentrating on system variables, in particular on implicit ones. And, third, from those 45% focusing solely on system variables, more than half explore biodiversity differences among land cover types and/or management practices which are interpreted as correlates of land-use intensity and do not provide any quantitative measure of any of the three dimensions of land-use intensity (Fig. 2b). Input and output variables are seldom used on their own (1% and respectively 4% of the studies), but relatively often are metrics representing these two dimensions in combination (21%, see Fig. 2a). This is due to a frequently applied LUI-index comprising input and output variables (i.e. fertilization, mowing and grazing) developed by Blüthgen *et al.* (2012). In summary, these results suggest that research on the biodiversity – land-use intensity relationship would profit from a more integrative and systematic approach that is based on a proper conceptualization of the complex land-use intensity phenomenon and represents its different dimensions by quantitative rather than qualitative indicators. Obviously, the same applies with respect to predictive models of biodiversity.

### **ISSUES OF SCALE: INTERACTING DIMENSIONS AGAIN**

Scaling issues play a key role in ecology (Wiens 1989; McGill 2015) and are also an important topic in predictive biodiversity models (e.g. Austin & Van Niel 2011; Anderson 2018). With respect to climate impact modelling, the mismatch between the grain size at which predictor variables in such models are represented and the spatial and temporal scales at which they actually influence organisms in the real world has been intensively debated (e.g. Randin *et al.* 2009; Potter, Arthur Woods & Pincebourde 2013; Hülber *et al.* 2016). Similar problems occur when modelling land-use effects on species (e.g. Barbet-Massin, Thuiller & Jiguet 2012; Riordan & Rundel 2014). Moreover, there is an additional

scaling dimension relevant to at least two of the ‘facets’ of land use introduced above: land cover and management practice are commonly represented as categorical variables. The resolution of these variables can hence also vary in a thematic sense, i.e. with respect to the degree of differentiation offered by the underlying classification schemes (Verburg, Neumann & Nol 2011).

We suggest that the different dimensions of scale – spatial, temporal and thematic – likely interact with each other in determining the importance of land-use variables for species distribution and diversity and propose that scaling issues are in need of a more systematic exploration and discussion in the context of modelling land-use effects on biodiversity. For example, the effect of spatial resolution of land cover data in biodiversity models has repeatedly been evaluated (e.g. Luoto, Virkkala & Heikkinen 2007; Keil *et al.* 2012). The common view emerging from such studies is that climate determines species distribution at broader spatial scales, whereas land cover becomes increasingly important at finer resolution (e.g. Pearson, Dawson & Liu 2004; Newbold *et al.* 2015).

However, effects of land cover variables may disappear even at fine spatial grain if thematic resolution is insufficient (Martin *et al.* 2013). Nevertheless, while the lack of sufficient thematic resolution of land cover maps has repeatedly been bemoaned by biodiversity modellers (e.g. Thuiller, Araújo & Lavorel 2004; Barbet-Massin, Thuiller & Jiguet 2012; Riordan & Rundel 2014), systematic analyses of how varying thematic resolutions affect model outcomes have hardly been conducted – and even less work has been dedicated to the interactive effects of thematic and spatial resolutions.

The issue of thematic resolution of land cover data is closely linked to the different facets of land use as introduced above. In fact, recent progress in remote sensing has made land cover data available at very fine spatial and thematic resolutions and these remote sensing products are already increasingly used by biodiversity modellers (e.g. He *et al.* 2015; Skowronek *et al.* 2017).

However, as discussed above, there are biologically important aspects of human land use which are hardly detectable in land cover features. There are hence inherent constraints for increasing the biologically relevant information content by further differentiating land cover data (e.g. Kuemmerle *et al.* 2013). What is needed instead, is coupling land cover data with information on management practice and land-use intensity at an appropriate spatial resolution.

Spatial scaling issues may not only interact with thematic ones, but also with temporal ones. For example, the tenet that land use affects species distributions only at fine spatial grain is at odds with the well-established importance of landscape-scale habitat area and fragmentation for many species, especially those organized as metapopulations (Hanski & Ovaskainen 2000). In fact, the apparent lower importance of land use at larger spatial grain sizes may at least partly result from delays in the response of biological populations and diversity patterns to land-use change. Indeed, complete extinction of a species can lag behind responsible land-use change for decades (Wearn, Reuman & Ewers 2012; Essl *et al.* 2015). As these time lags are often caused by processes at the metapopulation level (Tilman *et al.* 1994; Hanski & Ovaskainen 2000), they likely blur the the relationship between (current) land-use patterns and the distribution of biological populations at landscape scales in particular. The importance of spatial scale for modelling species' occurrence may hence be a function of the temporal scale of observation or prediction (Fig. 3). Landscape-scale variables may turn out to be important predictors of species distribution and diversity if they appropriately represent the relevant time horizon of cause-effect relationships (Krauss *et al.* 2010). To put it differently, with increasing temporal extent of the data, thematic resolution may become important for biodiversity models even at large spatial scales. Indeed, in a global and long-term perspective, land use has already driven many species to extinction even at a coarse grain size (Ellis, Antill & Kreft 2012).

In summary, we think that the relationship between land use and patterns of species distribution and diversity is subject to complex scaling issues that are insufficiently explored by and hardly incorporated into predictive biodiversity models so far. Focussing on these issues more intensively is certainly timely because remote sensing products become available at ever finer spatial resolution on the one hand, and time series of such products now span several decades. As a consequence, data for studying at least part of these issues are already available. The results from such studies are potentially relevant for both theory and applications. Finding, for example, that land cover patterns of the past have strong effects on current species distributions even at large spatial scales may obviously alter our projections of future biodiversity patterns profoundly, even if we assume land use to remain constant.

## DO WE HAVE THE DATA TO MOVE FORWARD?

More frequent, more systematic and more comprehensive integration of land use into predictive biodiversity models will critically depend on the availability of data that cover all the biologically relevant facets and dimensions of the land-use phenomenon at appropriate scales. In an ideal world, such data should be compiled on a common data portal with consistency issues (Verburg, Neumann & Nol 2011) removed as far as possible. Biodiversity modellers could then choose from this portfolio the subset of predictors most relevant for their particular study as they do with climatic maps.

Such a ready-to-use portfolio is probably less illusory than it may seem. As far as current land cover is concerned, it is clearly within reach already, even at fine spatial resolution for a global extent (Hansen *et al.* 2013; Chen *et al.* 2015). The spatial distribution of management practices is much less well documented globally, often only in national inventories or census documents, if at all, but land-use scientists are increasingly addressing this knowledge gap (Erb *et al.* 2017). For several metrics of land-use intensity such as crop yields, livestock density, fertilizer input, or HANPP, global datasets are actually available at relatively fine grain sizes (300 m - 5 arc min, cf. Kehoe *et al.* 2017), even if many inaccuracies and problems are associated with these maps (Verburg, Neumann & Nol 2011). Based on these data, integrated classification systems that couple land cover with land-use intensity metrics have been developed and downscaled to a 1 km resolution recently ('land system' maps, van Asselen & Verburg 2012; Kehoe *et al.* 2017). Other aspects of land-use intensity, such as mowing or harvest frequency, are less well documented, but remote sensing products with high temporal resolution now allow reconstruction of phenological time series and thus potentially offer a way forward here (He *et al.* 2015; Senf *et al.* 2015). For specific regions such as Europe, additional though yet underexplored sources may provide important information on management practice and land-use intensity at even finer spatial resolution. In the European Union, a system for the identification of agricultural parcels in member states is being developed as part of the Integrated Administration and Control System (IACS) for channeling subsidies to farmers ([https://ec.europa.eu/agriculture/direct-support/iacs\\_en](https://ec.europa.eu/agriculture/direct-support/iacs_en)). Associated national GIS databases contain information on management practices and land-use intensity metrics (such as mown vs. pastured, frequency of mowing,

livestock density, crop species, fertilizer input) for each parcel of cropland and grassland within their territory. Although usage of this information is subject to privacy laws, these data are highly relevant for biodiversity modelling even after appropriate anonymization and aggregation (e.g. Lomba *et al.* 2017).

Complementarily, many countries conduct regular forest inventories which provide information on tree species composition and forest harvesting on a fine mesh of sampling points. While these data are increasingly used in ecological studies (e.g. Seidl *et al.* 2014; García-Valdés *et al.* 2015), their relevance for modelling effects of forest management on species from taxonomic groups other than trees is rarely exploited (Müller *et al.* 2009; Martínez-Jauregui, Soliño & Díaz 2016). In summary, important data gaps certainly remain in the spatial documentation of biologically relevant land-use metrics, but a lot of information is already available, or will become so in the foreseeable future.

However, predictive biodiversity modelling needs information on future land use in addition to information on the current status. Unfortunately, most future land-use scenarios have been developed within Integrated Assessment Models (IAMs) which did not focus on biodiversity effects and are very coarse in both thematic and spatial resolution (de Chazal & Rounsevell 2009; Harfoot *et al.* 2014; Titeux *et al.* 2016). Even these coarse scenarios might be useful for a rough estimate of how land use will affect certain facets of biodiversity in the future (Newbold *et al.* 2015; Kehoe *et al.* 2017). However, more detailed models that project the fate of individual species or different aspects of biodiversity associated with varied scales (McGill 2015; Gossner *et al.* 2016) will require scenarios at finer spatial and thematic resolutions. Establishing such scenarios will need complex approaches that account for human decision making on the background of economic and biophysical environments as well as of regionally varying cultural contexts and traditions (Giupponi *et al.* 2006; Rounsevell & Reay 2009). Until such scenarios become available, global or continental scale models will have to rely on coarse simplifying assumptions to explore 'option spaces' (Kehoe *et al.* 2017). At regional scales, we suggest that coupling of predictive biodiversity models with forecast techniques that allow incorporation of such decision making such as Agent Based Modelling should be intensified (Gaube *et al.* 2009; Rounsevell *et al.* 2014). While such model-coupling is laborious and requires interdisciplinary work, it is likely the most adequate way to represent possible

future effects of the complex socio-ecological phenomenon 'land use' on biodiversity.

## **CONCLUSIONS**

Predictive models of biodiversity need to re-focus efforts on land-use change as the currently most important threat to biological populations. Here, we have emphasized several important points that we consider crucial for such an undertaking (see Table 1 for a summary). First, models of species distribution and diversity should better acknowledge the complex nature of the land use – biodiversity interrelation by not using one-dimensional land-use indicators but variable sets that represent all of land cover, management practice and land-use intensity, and that further account for the multi-dimensionality of land-use intensity. Second, the land use – biodiversity relationship is subject to complex scaling issues that are in need of better exploration and consequent integration into modelling. And third, predictive modelling of future land-use change on species distribution and diversity should intensify interdisciplinary collaboration with land-use scientists to develop coupled models of human agency and the associated response of biological populations. Data to proceed along these lines are at least partly there already. Compiling them into comprehensive and readily available data sets that cover all the above-mentioned facets of land use will likely promote representation of land-use variables in biodiversity models considerably.

## **Authors' contributions**

ID and SD conceived the idea; ID conducted the literature review; ID and SD led the writing of the manuscript with the support of FE, DM, KE and HH.

## **Acknowledgements**

ID was funded by the Austrian Academy of Sciences (project 'LUBIO'). The icons in Fig. 1 were made by Freepik from [www.flaticon.com](http://www.flaticon.com).

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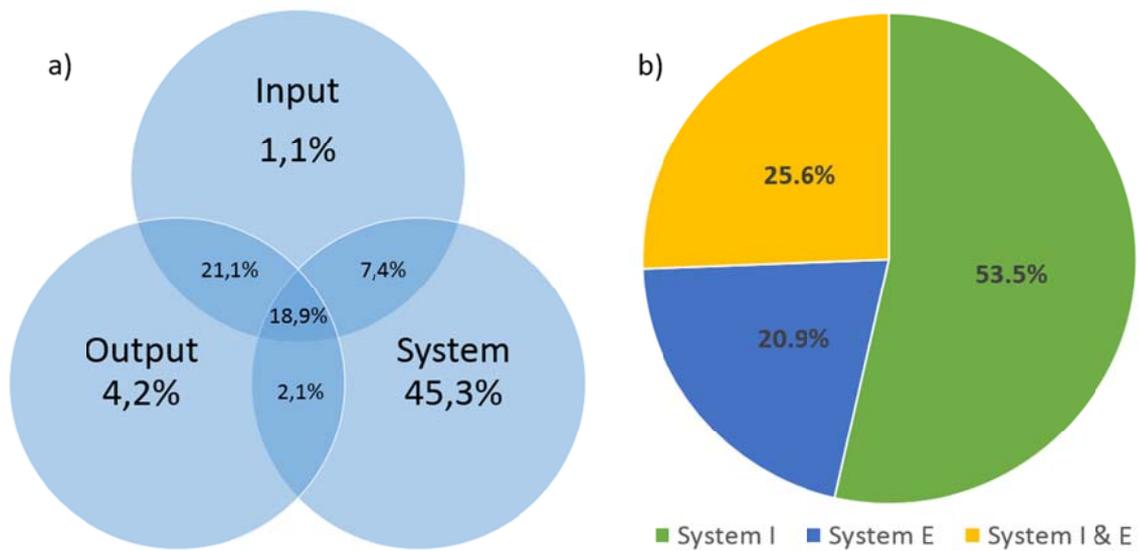
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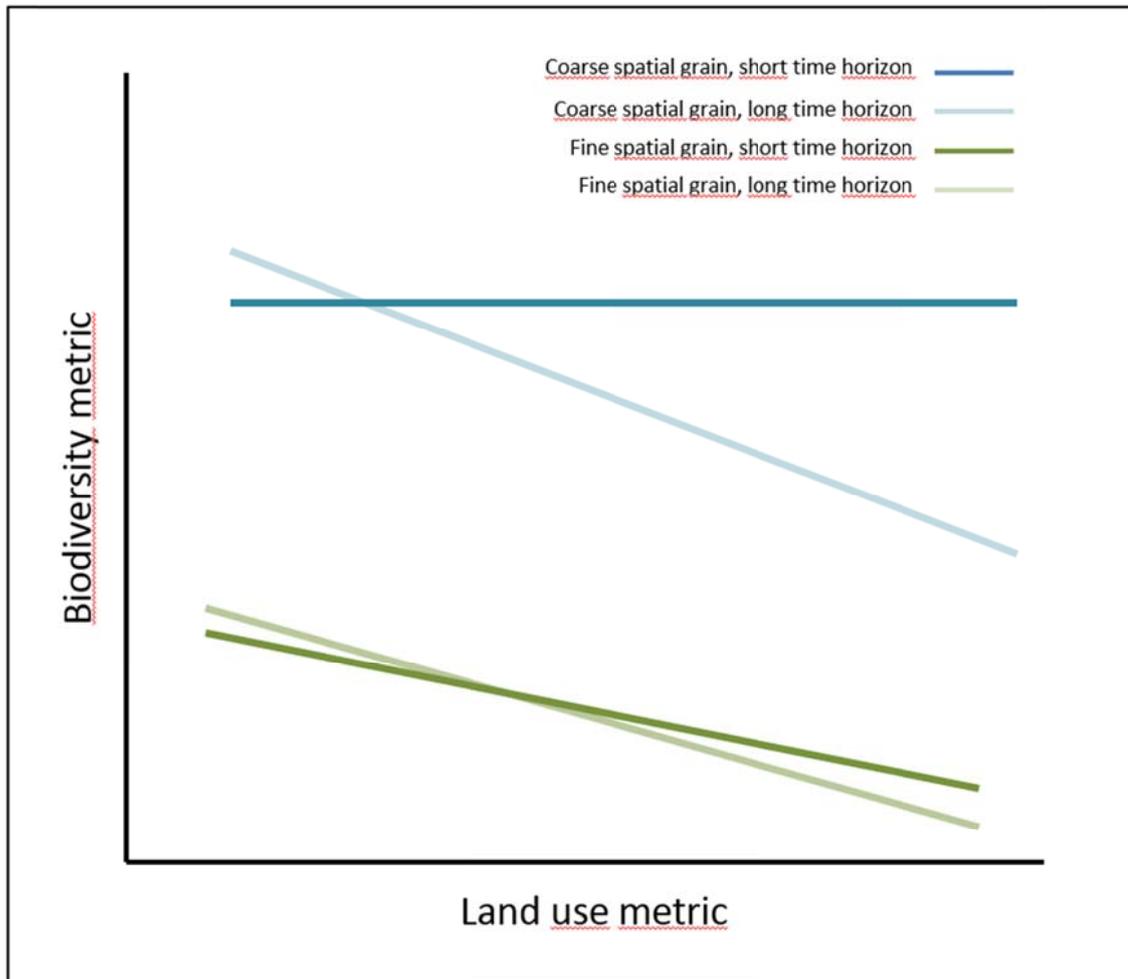
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**Figure 1:** Three facets of ‘land use’. Symbols within the triangle represent examples of processes important for the distribution of individual species and for biodiversity patterns. Their position is relative to the information that data about the three facets provide on these processes.



**Figure 2:** **a)** Overview on how often different kinds of land-use intensity variables (Erb *et al.* 2013) have been used within a sample of studies on the effects of land-use intensity on biodiversity. **b)** Overview on how often different system variables (explicit, implicit or both) have been used within all studies that have solely applied any system variable.



**Figure 3:** Possible interactions between spatial and temporal scales in land use – biodiversity relationships. The x-axis represents some metric of land use (e.g. percentage area of intensively used cropland), the y-axis some metric of biodiversity (e.g. some measure of taxonomic, functional or phylogenetic diversity). With current land-use metric data (short time horizon), correlations are only detectable at fine spatial grain. With land-use metric data from several decades back into the past (long time horizon), correlations emerge at both resolutions. Depending on the main mechanisms responsible for delays in cause-effect relationships (cf. Hylander & Ehrlén 2013), this interaction may be more or less pronounced.

## Supplementary Material

### Towards better integration of land use into models of species distribution and diversity

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List of the 95 studies used for the review of research on land-use intensity – biodiversity relations. For each of the studies, we assigned the land-use intensity metrics applied in the study to one of these dimensions: input, output, system E (explicit) or system I (implicit). For details see text.

Citation	Dimension
Bestelmeyer and Wiens (1996)	output
Daily, Ehrlich and Sánchez-Azofeifa (2001)	system E, system I
Zeidler, Hanrahan and Scholes (2002)	output
Zechmeister <i>et al.</i> (2003)	input, output, system E, system I
Mulder <i>et al.</i> (2003)	input, output, system E
Gillison <i>et al.</i> (2004)	system E, system I
Shahabuddin, Schulze and Tschardt (2005)	system E, system I
Schmitzberger <i>et al.</i> (2005)	input, output, system I
Hoffmann and Zeller (2005)	output
Glück and Deuschle (2005)	output
Michel, Burel and Butet (2006)	system E, system I
Økland <i>et al.</i> (2006)	system E, system I
Dietschi <i>et al.</i> (2007)	input, output
Hendrickx <i>et al.</i> (2007)	input, output, system E
Vermaat, Goosen and Omtzigt (2007)	input, system E
Dormann <i>et al.</i> (2007)	input, system E

Citation	Dimension
Dormann <i>et al.</i> (2008)	input, output, system E
Winfree <i>et al.</i> (2008)	input, output, system E
Jangid <i>et al.</i> (2008)	input, system I
Batáry, Kovács and Báldi (2008)	input, output, system E
Alkemade <i>et al.</i> (2009)	system E, system I
Brady <i>et al.</i> (2009)	system E
Sovu <i>et al.</i> (2009)	input, system E
Laliberté <i>et al.</i> (2010)	system I
Batáry <i>et al.</i> (2010)	input, output
Louzada <i>et al.</i> (2010)	system I
Hamre <i>et al.</i> (2010)	system E, system I
De Souza <i>et al.</i> (2010)	system I
Faude, Feilhauer and Schmidlein (2010)	system E
Teodoro <i>et al.</i> (2011)	system I
Weiner <i>et al.</i> (2011)	input, output
Armengot <i>et al.</i> (2011)	input, output, system E
José-María and Sans (2011)	input, output
Kleijn <i>et al.</i> (2012)	input
Pinho <i>et al.</i> (2012)	output, system E
Schneiders <i>et al.</i> (2012)	system I
Vačkář, Chobot and Orlitová (2012)	system E
Wachira <i>et al.</i> (2013)	system I

Citation	Dimension
Newbold <i>et al.</i> (2013)	system I
Rizali <i>et al.</i> (2013)	system E
Dullinger <i>et al.</i> (2013)	system E
Klaus <i>et al.</i> (2013a)	system E
Macchi <i>et al.</i> (2013)	system I
Klaus <i>et al.</i> (2013b)	input, output, system I
Overmars <i>et al.</i> (2013)	input, system E, system I
de Lima <i>et al.</i> (2013)	system E, system I
Moura <i>et al.</i> (2013)	system E, system I
Diekötter <i>et al.</i> (2014)	system E
Rader <i>et al.</i> (2014)	system I
Simons <i>et al.</i> (2014)	input, output
Van Meerbeek, Helsen and Hermy (2014)	system I
Allan <i>et al.</i> (2014)	input, output
Liu <i>et al.</i> (2014)	input, output, system E
Egorov <i>et al.</i> (2014)	input, output
Gossner <i>et al.</i> (2014)	input, output, system E, system I
Soliveres <i>et al.</i> (2015)	input, output, system E
Vályi, Rillig and Hempel (2015)	input, output
Perović <i>et al.</i> (2015)	input, output, system E
Allan <i>et al.</i> (2015)	input, output
Simons <i>et al.</i> (2015)	input, output
Sreekar <i>et al.</i> (2015)	system I
Mammides <i>et al.</i> (2015)	system I
Birkhofer <i>et al.</i> (2015)	input, output, system I
Braun and Koch (2015)	input, system E, system I
Heinrichs and Pauchard (2015)	system I
Tardy <i>et al.</i> (2015)	input, output, system E

Citation	Dimension
Kehoe <i>et al.</i> (2015)	input, output, system E
Rüdiger <i>et al.</i> (2015)	system E, system I
Wagner, Yap and Yap (2015)	system I
Gossner <i>et al.</i> (2016a)	input, output
Perry <i>et al.</i> (2016)	system I
Marull <i>et al.</i> (2016)	system E
Simons, Weisser and Gossner (2016)	input, output
Oldén <i>et al.</i> (2016)	output, system I
Tonkin <i>et al.</i> (2016)	system I
Hevia <i>et al.</i> (2016)	system I
De Carvalho <i>et al.</i> (2016)	system I
Chisté <i>et al.</i> (2016)	input, output
Oliver <i>et al.</i> (2016)	input, output, system E
Gossner <i>et al.</i> (2016b)	input, output
Simons <i>et al.</i> (2017)	input, output
Elsen <i>et al.</i> (2017)	system E, system I
Birkhofer <i>et al.</i> (2017)	input, output, system I
Tukiainen <i>et al.</i> (2017)	input, system I
Baumann <i>et al.</i> (2017)	input, output
Estendorfer <i>et al.</i> (2017)	input, output
Phillips, Newbold and Purvis (2017)	system I
Häkkinen <i>et al.</i> (2017)	system E
Oehl <i>et al.</i> (2017)	system I
N'Dri <i>et al.</i> (2017)	system I
Mangels <i>et al.</i> (2017)	input, output
Chisté <i>et al.</i> (2018)	input, output
Nopper <i>et al.</i> (2018)	system I
Joyce <i>et al.</i> (2018)	system I
Boch <i>et al.</i> (2018)	input, output

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## **Chapter 4**

### **A socio-ecological model for predicting land use and climate change impacts on regional plant diversity**

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#### **Publication Reference**

Dullinger, I., Wessely, J., Gattringer, A., Moser, D., Plutzer, C., Willner, W., Egger, C., Gaube, V., Haberl, H., Mayer, A., Böhner, A., Gilli, C., Pascher, K., Essl, F., Dullinger, S. (in prep): A socio-ecological model for predicting land use and climate change impacts on regional plant diversity

#### **Status**

For submission to *Global Change Biology*

#### **Contribution**

I computed the SDMs, analysed the data and led the writing of the manuscript.

# A socio-ecological model for predicting impacts of land-use and climate change on regional plant diversity

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**Keywords:** agent-based model, climate change, land-use change, plant species distribution, species distribution model, Europe

## ABSTRACT

Climate and land-use change will jointly affect the future of biodiversity. Yet, biodiversity scenarios have so far concentrated on climatic effects, most likely because forecasts of land use are rarely available at appropriate spatial and thematic scales. Agent-based models (ABMs) represent a potentially powerful but little explored tool for establishing thematically and spatially fine-grained land-use scenarios. Here, we use an ABM parameterized for 1,329 agents, mostly farmers, in a Central European model region, and simulate the changes to land-use patterns resulting from their response to three scenarios of changing socio-economic conditions and three scenarios of climate change until the mid of the century. Subsequently, we use species distribution models to, first, analyse relationships between the realized niches of 832 plant species and climatic

gradients or land-use types, respectively, and, second, to project changes in potential regional range size of these species as triggered by changes in both the altered land-use patterns and the changing climate. We find that both drivers determine the realized niches of the studied plants, with land use having a stronger effect than any single climatic variable in the model. Nevertheless, the plants' future distributions appear much more responsive to climate than to land-use changes because alternative future socio-economic backgrounds have only modest impact on land-use decisions in the model region. We argue that these results are likely representative for the 'used matrix' of many cultural landscapes in Europe, but may differ drastically in regions that still contain large tracts of natural or semi-natural habitat. We conclude that agent-based modelling of land use is indeed able to provide scenarios at scales relevant to individual species distribution and suggest that coupling such ABMs with models of species' range change should be intensified to provide more realistic biodiversity forecasts.

## INTRODUCTION

Land use is considered the most important human threat to terrestrial biodiversity (Pimm & Raven, 2000; Sala *et al.*, 2000; Baillie *et al.*, 2004; Newbold *et al.*, 2015; Maxwell *et al.*, 2016; Marques *et al.*, 2019). Land use potentially degrades or destroys natural ecosystems and increases the fragmentation of natural or semi-natural habitats. Negative impacts of that kind are already widespread and currently affect approximately three-quarters of the earth's ice-free land mass (Erb *et al.*, 2007; Ellis *et al.*, 2013). They are predicted to further rise in extent and intensity, driven by the rapidly growing human population, economic growth, as well as changes in lifestyle and diets (Foley *et al.*, 2011; Tilman *et al.*, 2011; Erb *et al.*, 2016).

However, human agency threatens biodiversity in multiple, often interacting ways (Vitousek *et al.*, 1997; Ehrlich & Pringle, 2008). Besides habitat conversion through land use, climate change is considered another particularly powerful driver of biodiversity loss (Pereira *et al.*, 2010). Global warming forces species to either adapt to the changing conditions or to shift their distribution to cooler environments (Bellard *et al.*, 2012). So far, the consequences of such forcing on local or regional species richness appear highly context-dependent (e.g. Pauli *et al.*, 2012; Vellend *et al.*, 2017). In the future, however, the possible scale (Foster *et al.*, 2017) and pace (Loarie *et al.*, 2009; Corlett & Westcott, 2013) of climate change may go beyond what many species can tolerate (Urban, 2015), especially those adapted to cold conditions at high latitudes or elevations (e.g. Engler *et al.*, 2011; McElwain, 2018). It has hence been speculated that global warming may

increasingly rival land use as the dominant threat to biodiversity in the future (Maxwell *et al.*, 2016).

To evaluate the possible magnitude of future human impacts on biodiversity, and to guide societal responses, forecasting trajectories of biodiversity under different scenarios of future development has become an active field of research (Pereira *et al.*, 2010; Lurgi *et al.*, 2015; Urban *et al.*, 2016; Zurell *et al.*, 2016). In this context, the predominant impact that land use has had on biodiversity so far is in salient contrast to the modest attention it receives by predictive biodiversity models. Recent reviews document that forecasts of how biodiversity may develop in the 21<sup>st</sup> century have concentrated on the effects of climate change while land-use change has mostly been neglected, with this imbalance even increasing over time (Titeux *et al.*, 2016; Sirami *et al.*, 2017). Similarly, the combination and interaction of both drivers appears understudied (Pimm, 2008; Forero-Medina *et al.*, 2011; Titeux *et al.*, 2016). As a consequence, the relative impacts of land-use and climate change on the unfolding biodiversity crisis are difficult to evaluate, and the presented forecasts for the 21<sup>st</sup> century are potentially inappropriate or even misleading (de Chazal & Rounsevell, 2009; Pereira *et al.*, 2010).

The probably most important reason for the modest attention that land use receives in biodiversity forecasts is the lack of future land-use scenarios (Titeux *et al.*, 2016). In fact, a number of such scenarios has become available over the last one and a half decades (Busch, 2006; Rounsevell *et al.*, 2006; Verburg *et al.*, 2006; Hurtt *et al.*, 2011; Spangenberg *et al.*, 2012) and some of these scenarios have also been used to predict how species richness of local assemblages may develop in the future (Newbold *et al.*, 2015; Kehoe *et al.*, 2017). However, the spatial and thematic resolution of these scenarios is usually considered inappropriate to represent habitat suitability for individual species (Barbet-Massin *et al.*, 2012; Martin *et al.*, 2013). The ecological requirements, or niches, of individual species, are, on the other hand, the basis of most models that predict climate effects on biodiversity such as species distribution models (SDMs, e.g. Araújo *et al.*, 2011; Thuiller *et al.*, 2011), joint SDMs (e.g. Clark *et al.*, 2014; Maguire *et al.*, 2015), hybrid SDMs (e.g. Dullinger *et al.*, 2012a; Wessely *et al.*, 2017), and most other types of dynamic range models (e.g. Lurgi *et al.*, 2015; Zurell *et al.*, 2016; Fordham *et al.*, 2018). Linking climate and land-use effects in such a type of modelling hence requires scenarios of future land use that deliver more fine-grained spatial and thematic information.

At landscape to regional scales, agent-based modelling (ABM) represents a way towards establishing such 'fine-grain' scenarios (Matthews *et al.*, 2007; Valbuena *et al.*, 2010).

ABMs simulate human decision-making against the background of economic and biophysical environments as well as regionally varying cultural contexts and traditions (Rounsevell & Reay, 2009; An, 2012). With individual land owners/users as agents, ABMs can simulate trajectories of usage for individual parcels of land at thematically fine resolutions (e.g. Gaube *et al.*, 2009). Coupling individual- or farm-scale ABMs with models like SDMs or their derivatives hence represents a potentially powerful ‘innovative model architecture’ (Verburg *et al.*, 2016) to integrate land-use and climate effects in biodiversity forecasts. Surprisingly, however, model combinations of that kind have hardly been attempted so far. Here, we present such a model combination and apply it to predict changes in plant distribution across a Central European study region until the mid of the century. Apart from demonstrating the concept, we particularly compare the relative effects of climate and land-use change scenarios on the future shrinkage or expansion of regional species ranges.

## **METHODS**

### **Study region**

The coupled model was developed for a subarea of the long-term socio-ecological research (LTSER) region “Eisenwurzen” in Austria’s Northern Limestone Alps. The area covers the upper part of the valley of the river Enns, which follows approximately a north-south direction (Fig. 1 a). The region encompasses 18 municipalities, spread across 1426 km<sup>2</sup>, is topographically highly diverse and includes a broad variety of land-use systems. The southern parts are characterized by high mountains (highest elevation: 2,309 m), rugged topographic conditions, high annual precipitation (c. 1,200-1,800 mm mean annual precipitation), low mean temperature (c. 5-6 °C mean annual temperature), a short vegetation period, and a dominance of forests and livestock-centred agriculture. Towards the north, elevation and precipitation decline (c. 800 mm mean annual precipitation), mean temperatures rise (c. 9 °C mean annual temperature) and arable land gains importance. The largest city of the region, Steyr (elevation: 310 m a.s.l., c. 40,000 inhabitants), is situated in the northern part of the study area which is dominated by intensive cropland agriculture.

### **Data**

#### *Species selection and data*

We focused on all vascular plant species currently occurring in the study region and its immediate surroundings based on information from the floristic mapping of Austria

(Niklfeld, 1998). The floristic mapping database holds complete species records for each cell of a 3' × 5' raster covering the entire country. Fig. 1 a shows the cells considered for compiling our species list.

For these species, we collated plot-scale distribution data from different existing databases (Office of the State of Upper Austria, 1993-2013; Pascher *et al.*, 2011; Willner *et al.*, 2012). We only included plots that provided full lists of vascular plant species. We used plot data from the entire territory of Austria to get a better representation of the environmental niches of species. We supplemented the collated plots by 155 own records from within the study region and its immediate surroundings to improve representation of under-sampled land-use types in the dataset.

The final dataset included 12,498 plots spread across Austria (Table S1 and Fig. S1). Accuracy of the geographical location of each plot varied between < 10 m and c. 250 m. In case of the data of the Biotope Mapping Upper Austria (Office of the State of Upper Austria, 1993-2013), plots characterize polygons of the biotope map which vary in size between 50 and 100,000 m<sup>2</sup>. In this case, we assigned the concrete plot location to the centre of gravity of the respective polygon.

All taxa names listed for 12,498 plots were cross-checked and a consistent taxonomy following Fischer *et al.* (2008) was applied. Crop species were excluded. Taxonomically critical species or subspecies were combined to aggregates or species, respectively, in several cases (e.g. *Achillea millefolium* agg., *Aconitum variegatum* agg., cf. Table S2). From the remaining taxa, we further excluded all those occurring in < 50 of the 12,498 records because model accuracy may significantly decrease with fewer observations (e.g. Wisz *et al.*, 2008). The final set for modelling included 834 vascular plant taxa which we call species for convenience henceforth (Table S2).

#### *Current and future land-use data*

Land-use information was assigned to the 12,498 in different ways (cf. Table S1). For a subset of 5897 plots land use had been directly classified in the field at the time of recording. This information was harmonized into 22 land-use classes that combine information about type of usage, and for grasslands and arable land additionally intensity of usage (Table 1). The remaining plots were taken from the Austrian Vegetation Database (Willner *et al.*, 2012) and were assigned to these 22 classes based on their assignment to alliances of the European phytosociological system of plant communities that also underlies standard European habitat typologies (Rodwell *et al.*, 2002).

A map of current land use in the study region was compiled by using information from the Integrated Administration and Control System (IACS) which provides spatially explicit

data for agricultural areas (croplands, pastures, meadows, orchards) in Austria. IACS is giving information on land-use type and intensity for each parcel of land for the year 2014, as well as associated information on the farm holds that use these parcels (e.g. farm size, farm type, region, organic vs. conventional mode of farming etc.). Outside of agricultural areas, land-use information was complemented by a fine-scale (10 × 10 m) raster map of EUNIS land cover types for Austria (Umweltbundesamt, 2014). Land-use and land cover information from these sources was cross-tabulated to the same 22 classes as used for the vegetation plots (Table 1). The resulting map was finally re-sampled to a 25 m raster using a majority rule in the case that several land-use categories were overlapping one cell.

Corresponding maps of future land use (year 2050) were modelled by calculating trajectories of future land-use change according to three different scenario projections from the Shared Socioeconomic Pathways (SSPs) family (O'Neill *et al.*, 2014; O'Neill *et al.*, 2017): a scenario describing a world of sustainability-oriented growth and equality (SSP1), another one describing a world of rapid and unconstrained growth in economic output and energy use (SSP5) and a business as usual scenario (BAU). Based on the narratives of the scenarios and information from regional applications of the SSPs (Absar & Preston, 2015; Steininger *et al.*, 2015; Popp *et al.*, 2017), we made different assumptions on the development of yields, prices, subsidies, income, workload and forest development for each of these scenarios (see Table S3). These assumptions set the socio-economic background for human decision-making simulated via ABMs. The ABMs included 1,329 agents (farmers, owners, 2 national parks). We assigned each agent the particular area of land he or she managed at the time of initialization (2014), as derived from the IACS database. Agents then choose from a set of available options for using this land each year until 2050, such as intensification, switch from high to low intensity farming practices, switch to different land-use types, termination etc.), following the main goal of a satisfactory balance between income and workload (= invested time). The probability of selecting a particular option in each year was modelled as dependent on the above scenario assumptions in combination with the particular economic situation of each farm in each year. We developed the list of options and the relevant decision criteria from interviews conducted with a number (n=35) of regional land owners and stakeholders. Results of these decisions were translated into annual updates of the land cover map. Further explanation of the ABM, its design and its parameterization can be found in the Appendix (Additional Methods and Fig. S2).

As decisions of land owners are not modelled in a deterministic, but in a probabilistic way (i.e. options are randomly selected, based on associated, context-dependent

probabilities), we repeated simulations 100 times per land-use scenario. From the resulting 300 land-use maps for the year 2050 we selected five per scenario, i.e. a total of 15, for further modelling of biodiversity response. As these five simulations should span the full breadth of possible land-use change under the respective scenario, we applied the following selection procedure: for each simulated future land-use map two indices were calculated: evenness, i.e. homogeneity of land-use classes in terms of the area they cover, and the total area of intensively used land. Intensively used land was defined as cropland belonging to farms that do not receive subsidies for organic practices, pastures with more than 1.5 livestock units/ ha, and meadows with more than two cuts per year. For each scenario, the values of these two indices resulting from each of the 100 simulation runs were plotted against each other. We then selected the five simulations closest to the centroid and the four corners of a minimum bounding rectangle across all simulations.

#### *Current and future climate data*

Maps of current climatic conditions were derived from combining Worldclim data for temperature with a high-resolution data set for precipitation of the European Alps (Isotta *et al.*, 2014) providing average (1970-2005) monthly precipitation sums at a resolution of 5 km. The precipitation data were downscaled to a resolution of 100 m using ordinary kriging with elevation as co-variable. Worldclim monthly temperature variables (mean, minimal and maximal monthly temperature) were downscaled as in Dullinger *et al.* (2012a). As the Worldclim data represents average values from 1950-2000, these were corrected using the E-OBS climate grids available online (<https://www.ecad.eu/download/ensembles/download.php>) to average values ranging from 1970-2005 to equal the reference period of the precipitation data.

Future climate was characterized by three different IPCC5 scenarios from the Representative Concentration Pathways family (Moss *et al.*, 2010): RCP2.6 ('mild' climate scenario), RCP4.5 ('intermediate' climate scenario) and RCP8.5 ('severe' climate scenario). We therefore downloaded climatic models, which were generated by Météo-France / Centre National de Recherches Météorologiques using the CNRM-ALADIN53 model, fed by output from the global circulation model CNRM-CM5, available at the Cordex portal (<http://www.euro-cordex.net>) for a 35 year period around 2050. These monthly time series were statistically downscaled from the original 11' resolution by (a) calculating differences ("deltas") in monthly temperature and precipitation values between hindcasted historical (mean 1970-2005) and forecasted future climatic parameters (mean 2033-2067) at the original spatial resolution; (b) spatially interpolating

these differences to a resolution of 100 × 100 m using cubic splines and (c) adding these differences to the downscaled current climate data of the same climatic variables (Zimmermann *et al.*, 2009; Dullinger *et al.*, 2012a). Subsequently we used these spatially refined temperature and precipitation grids to derive maps of four bioclimatic variables which, in combination, represent temperature and precipitation conditions together with their seasonal variability, and which are known to influence species distributions (Root *et al.*, 2003): (1) minimum temperature of the coldest month (BIO6), (2) temperature annual range (BIO7), (3) precipitation seasonality (BIO15), (4) precipitation of the warmest quarter (BIO18). Correlations (Pearson's *r*) among these variables were < 0.75 throughout.

#### *Other environmental data*

We used two additional variables to better characterize the environmental niche of the species: solar radiation and percentage of calcareous bedrock substrate. In temperate regions of the northern hemisphere, solar radiation income mainly distinguishes topographically warmer sites facing southern directions from cooler ones facing north. We calculated direct and diffuse solar radiation income (in kWh/m<sup>2</sup>) using the Potential Incoming Solar Radiation Tool of the System for Automated Geoscientific Analyses (version 2.2.0, <http://www.saga-gis.org>). As input data we used a Digital Model of the European Environmental Agency (<https://www.eea.europa.eu/data-and-maps/data/eu-dem>) with a cell-size of 100 meters. Calculations were done for the days March, 20 and June, 21 on an hourly basis, and resulting radiation income values finally summed.

Calcareous substrate is important because many species of the central European flora are known to be sensitive to soil chemistry and especially to the contrast between siliceous and calcareous soils (Ellenberg, 2009). We therefore derived of the presence and absence of calcareous bedrock from a 1:200.000 geological map of Austria (cf. Dullinger *et al.*, 2012b).

### **Species distribution models**

#### *Model calibration and evaluation*

We modelled the realized niche of each species by combining presence/absence at the 12,498 vegetation plots with information on current land use, current climate, solar radiation income and presence/absence of calcareous substrates at the sampling sites. We applied three statistical modelling techniques available in the biomod2 (Thuiller *et al.*, 2009) library in R (R Development Core Team, 2014): Artificial Neural Networks (ANN), Random Forests (RF) and Gradient Boosting Machines (GBM). We selected these

techniques because they are relatively insensitive to a low ratio of the number of occurrences to the number of predictors (land use with 22 categories + 4 climatic variables + 2 additional environmental variables in our case, Cutler *et al.*, 2007; Dasgupta *et al.*, 2011). All models were run with the default settings in biomod2. We evaluated the models by randomly dividing the original dataset into two sub-parts, one for calibrating models (80 %) and one for evaluating them (20 %) using the True Skill Statistic (TSS, Allouche *et al.*, 2006). This process was repeated three times to make sure that the estimated predictive accuracy was not influenced by the random partitioning.

To assess the importance of predictor variables in the fitted models, we used a built-in permutation function which re-shuffles one of the predictor variables among vegetation records in each permutation and calculates a Pearson's correlation between the original prediction (on to the observation points) and the prediction achieved with the re-shuffled variable. The complement of this correlation,  $1-r$ , is used for scoring the impact the respective variable has on the discrimination ability of the model (Thuiller *et al.*, 2009). The number of permutations to estimate variable importance was set to 3.

### *Model projections*

Calibrated models were used to project the occurrence probability of all species across the study region under current and possible future (= year 2050) land use and climatic conditions by means of an ensemble forecast approach (Araújo & New, 2007). The contribution of each of the three models to the ensemble forecast of each species was weighted according to its TSS score. Models with a TSS score  $< 0.5$  were excluded from contributing to projections. To match the resolution of the land-use data, projections were done onto a 25 m raster of the study region, with constant climate, solar radiation and substrate across all cells within a  $100 \times 100$  m cell of these coarser grids of these variables. Solar radiation and calcareous substrates were assumed to remain constant in projections for 2050. The probabilistic ensemble forecasts were translated into binary maps using the value that maximizes the TSS score as the threshold for distinguishing presence and absence predictions.

### **Analysis of projections**

To assess the effects of the different land-use and climate scenarios on the distribution of the 834 species, we first computed the projected range size change (= number of  $25 \times 25$  m cells predicted to be suitable in the future / number of  $25 \times 25$  m cells predicted to be suitable under current land use and climatic conditions) for each species. To evaluate

whether results differ for subsets of species specifically adapted to particular habitats we defined four broad habitat categories: forests, agricultural lands, grasslands, and alpine habitats. All 22 land-use classes were assigned to these categories (see Table 1). Species which had at least 75 % of their occurrences in vegetation plots assigned to one category were defined as specialists of the respective habitat. For the species in each of these four groups, we then calculated a log response ratio as the natural logarithm of projected range size change (as defined above) to make the possible values of suitable area expansion and shrinkage, respectively, symmetric around zero. We repeated computations after defining habitat specialists by lower (50 % of occurrences) and higher (90 %) thresholds, but results were essentially the same and are hence not reported.

To compare the magnitude of effects of land-use and climate scenarios on changes of potential range size of species we fitted Generalized Linear Mixed Effects models, with the natural logarithm of range size change as response, land-use and climate scenarios (including the baseline, i.e. current land use and climate) and their interaction as fixed-effects, and a random intercept term for species identity. We partitioned the variation explained by climate change scenarios, land-use scenarios, and their interaction by recalculating  $R^2$ -values for models that had either one or the other of these two predictors (land use or climate) omitted, or the interaction term replaced by an additive combination.  $R^2$ -values were calculated by means of the 'r.squaredGLMM' function in the 'MuMIn' package of R (Barton, 2018).

## RESULTS

### Trends in land use and climate within the study region

Summarized into broad categories, the study region is currently covered by 67 % deciduous and conifer forests (incl. felling area), 19 % grasslands, 9 % agricultural lands and 6 % alpine areas (see Fig. 1 a). The ABMs simulated low to moderate changes to these percentages until the year 2050, with little differences among scenarios. In general, forests are predicted to increase on the expense of grasslands. The size of agricultural lands remains approximately constant (Fig. 1 b). At the level of the 22 land-use classes, trends differ more strongly among land-use change scenarios (Table 1).

Predicted regional temperature increase is relatively pronounced, with changes in the means of the coldest month (as compared to the references period 1970-2005) of +2.4 °C, +3.0 °C and +3.8 °C for RCP2.6, RCP4.5 and RCP8.5, respectively (Table S4). Only slight changes, which differ among scenarios, are predicted for annual temperature

ranges and precipitation-related variables.

### **Species distribution models**

The discrimination ability of SDMs was high to very high in general. TSS values of the Ensemble Models ranged from 0.647 to 0.995 and ROC values from 0.894 to 0.999 (see Table S2 for full information on model performance). For two of the 834 species we could not fit any single model with a TSS > 0.5 and consequently, they were omitted from further analysis.

### **Variable importance**

The importance of the seven predictor variables in the SDMs varied strongly among species, but also between modelling techniques (ANN, RF, GBM, see Fig. 2). On average across species, however, re-shuffling land-use classes changed model predictions most pronouncedly, i.e. land use was the most important of all single predictor variables included, independent of the modelling technique. The predominance of land use was particularly clear with GBMs, and somewhat less pronounced with ANN and RF. The median importance score of land use was relatively constant (c. 0.6-0.7) across the three modelling techniques (see Fig. 2).

From the four bioclimatic variables used, minimum temperature of the coldest month (BIO6) was consistently the most important one in ANN, GBM and RF. However, its numerical importance value varied considerably among modelling techniques (c. 0.1-0.5). The other bioclimatic variables showed similar variation around a lower level of the median. Solar radiation and substrate were, on average across species, the least important predictors in the SDMs (see Fig. 2).

### **Projected changes in the size of suitable ranges**

#### Under current climate but varying land-use scenarios (Fig. 3 a-c):

If neither the climate nor the socio-economic background conditions would change until 2050 (current climate + BAU land-use scenario), SDMs forecast that a majority of species will lose moderate fractions of their currently suitable ranges. In particular, c. 20 % of the species are predicted to expand their ranges by up to 20 %, 50 % of the species face shrinkage of ranges by up to 20 %, and c. 17 % of species will not see measurable changes to the size of their suitable ranges. More pronounced range losses or gains are rare.

In both the sustainability-oriented (SSP1) and unconstrained growth (SSP5) scenarios, proportions of winners and losers are approximately balanced, but changes are slightly

more pronounced in SSP5. While c. 85 % of the species do not change their range sizes by more than 20 % in SSP1, shrinkage or expansion of up to 60 % are predicted for c. 30 % of the species in SSP5.

Under varying climate but current land use (Fig 3 d-f):

Predictions are vastly different if, by contrast, land use is kept constant (= at current conditions) but climate changes. Under RCP2.6 (Fig. 3 d), there are many more losers (c. 70 %) than winners (c. 25 %), and both losers and winners vary pronouncedly in the magnitude of range loss or gain. In particular, more than 20 % of the species are predicted to even lose 80-100 % of their current ranges while c. 10 % will expand their ranges by more than 200 %. Predictions are similar, in principle, for the stronger climate scenarios, but both extreme 'losers' and 'winners' tend to become more frequent the more severe the climatic scenario (Fig. 3 d-f).

Under varying climate and SSP5 land use (Fig 3 h-i):

When varying both climate and land use in combination, predictions closely resemble those achieved under constant (current) land use and changing climate. We therefore only show results for the SSP5 scenario.

In summary, these predictions indicate a strong impact of climate change on future plant distribution, while land use is projected to have a relatively weak effect. These descriptive results are corroborated by partitioning the variance in range change explained by the GLMR among the land-use and climate scenarios (Table 2). As evidenced by conditional  $R^2$ -values, the big part of the variance is captured by the random effects demonstrating that the amount of range change varies idiosyncratically among species. However, the overall trend, as captured by the marginal  $R^2$ -values, is nearly entirely determined by the climate scenarios which trigger the loss of average range size the more pronounced the more extreme the assumed warming. Interactions among climate and land-use scenarios also had negligible effects on range size changes.

**Loss/gain of suitable area for subsets of species**

Focusing on specialists of forests, agricultural lands, grasslands, and alpine habitats demonstrates that alpine species are those likely suffering most under the predicted changes. The amount of range loss depends on the climatic, but not on the land-use scenario (Fig. 4 b). Forest species rank second among losers (Fig. 4 a). Similar to alpine species, range loss of forest species tends to be more pronounced under strong climate warming, with some additional effect of the business-as-usual land-use scenario under

RCP2.6. Specialists of agricultural lands and grasslands both show moderate increases in range size, with range changes similar across all different land-use and climatic scenarios (Fig. 4 c and d).

## **DISCUSSION**

Taken together, the key findings of our study are, first, that both climate and land use determine the realized niches of the studied plants, with variation in type and intensity of land use having a stronger effect than any single climatic variable in the model. And second, that in contrast to the strong effect that land use has on the current distribution of species, the future distribution of suitable ranges in our study region appears much more responsive to climate than to land-use scenarios. The apparent contradiction arises from the obviously weak effect that alternative future socio-economic backgrounds have on the decision of land users, whereas the regionally pronounced temperature increase has a marked impact on the study area's climate.

### **Land-use change effects**

While expert assessments consistently emphasize the overwhelming effect of human land use on species threat (Baillie *et al.*, 2004; Maxwell *et al.*, 2016), the land-use signal is often relatively weak in species distribution models (e.g. Thuiller *et al.*, 2004; Barbet-Massin *et al.*, 2012; Riordan & Rundel, 2014). This apparent contradiction is usually attributed to a lack of both, spatial and thematic resolution of available land-use information (e.g. Pearson *et al.*, 2004; Austin & Van Niel, 2011; Martin *et al.*, 2013). Indeed, the land-use information underlying many SDM applications is derived from remotely sensed land cover maps that often have spatial resolutions too coarse for matching them with plot-scale species distribution data (e.g. Luoto *et al.*, 2007; Keil *et al.*, 2012). Moreover, these maps do not reflect important distinctions among land management practices (e.g. grazing vs. mowing: Schläpfer *et al.*, 1998) and intensities of usage (Laliberté *et al.*, 2010; Erb *et al.*, 2013; Newbold *et al.*, 2015). Our results corroborate this interpretation. Using a relatively detailed classification that accounts for both the type of usage and its intensity at the spatial scale of local species assemblages, we find that variation in land-use type and intensity has a stronger effect on current plant species distribution in Austria (i.e., the region covered by our vegetation plots) than either temperature or precipitation gradients. This result is particularly remarkable because Austria is a mountaineous country with strong climatic contrasts between the warm and dry eastern lowlands and the cold and humid high elevations of the Alps:

according to the Austrian Zentralanstalt für Meteorologie und Geodynamik, current (2018) mean annual temperatures in the country vary between -5.8 and +14 °C, and annual precipitation sums between 390 mm and more than 2,500 mm (<https://www.zamg.ac.at/cms/de/klima/klima-aktuell/klimamonitoring>). The predominant effect of land use on species distributions reflects pre-adaptation of plant species to particular types of habitats, such as forests or grasslands, and the associated differences in resource availability, ambient conditions and disturbance regimes (Grime, 2001). It is in line with the well-known and well-documented impact that a long history of human usage has had on the present-day distribution of species and the composition of plant communities across Europe (e.g. Ellenberg, 2009) and reflects the fact that variation in type and intensity of usage has strong effects on plant diversity at the local scale (Vellend *et al.*, 2017).

Despite the importance of land use in the SDMs, the impact of land-use scenarios on future plant distribution in the study region is only moderate and much weaker than the impact of climatic scenarios. The apparent contradiction is explained by the modest changes in land use predicted by these land-use scenarios. This relative stability reflects a number of real constraints on land-use development in the area. First, the region's topography, especially in the southern parts, represents terrain not easily accessible by machinery. As a result, establishing production systems other than the currently dominating ones, i.e. permanent grassland based dairy farming and forestry, is difficult (Trnka *et al.*, 2009). Second, there are legal constraints on land-use development as the region overlaps with two national parks which take approximately 8 % of the modelled area, and forests are legally protected in Austria from being converted into other forms of land use. This latter restriction is particularly important in the study region, as forests cover c. 65 % of the area. More generally spoken, the current land-use patterns in the region reflect given socio-economic conditions as well as environmental and legal contexts in combination with the regionally specific tradition of farming systems. These constraints obviously restrict changes to these patterns over the next decades, even under the partly pronounced differences in the assumed future development of prices, subsidies, income, and workload underlying ABM simulations.

However, land-use decisions in the ABM are driven by attitudes derived from interviewing a current generation of farmers and stakeholders. Due to social change, a different economic environment and legal context, as well as technological change, it might be that the "decision space" of future farmers differs profoundly from the one perceived by the current generation. Changing social and environmental conditions might exert strong pressure on traditional land-use forms which might diminish. The

extent of technical development in agriculture might allow for yet unforeseeable changes to farming practices, albeit even techno-optimistic global assessments do not foresee such changes (FAO, 2018), and yield growth in developed world regions might (have) reach(ed) their maximum potential (Ray *et al.*, 2012). Finally, future climate change itself will likely force land owners to consider new farming strategies beyond what currently appears conceivable (Trnka *et al.*, 2009; Li *et al.*, 2018). In fact, except for forestry, current land owners' decisions usually reflect today's immediate socio-economic challenges and short-term reactions to (extreme) weather events, rather than they reflect longer-term changes in climatic constraints (Schermer *et al.*, 2018). To put it differently, we model future land-use decisions based on the options we have empirically assessed through interviews with current land owners. These current land owners may not be aware of options that are available to them, or their successors, 20 or 30 years into the future. As a corollary, the range of simulated land-use changes may underestimate the range of real future changes under the same socio-economic scenarios.

### **Climate change effects**

In contrast to land use, our coupled model suggests a strong effect of future climate on regional plant range sizes. These results corroborate findings of other studies that have modelled consequences of climate warming on species distributions in mountainous environments (e.g. Dirnböck *et al.*, 2003; Randin *et al.*, 2009; Hämmerle *et al.*, 2018). However, the strong climate warming effect is not independent of land use but rather results from an interplay with regional topography and land-use patterns. On the one hand, available area for plant colonization changes with elevation. Both in Austria as a whole (Essl *et al.*, 2009) and in the study region, available area peaks at montane to subalpine elevations and strongly decreases above the treeline (c. 1900 m a.s.l. in the study region). This topographical constraint is mainly responsible for the particular threat that the warming climate poses to alpine species, as found in other studies (Engler *et al.*, 2011; Dullinger *et al.*, 2012a). For all other species, shift of suitable ranges is restricted by both topography and land-use patterns. This is particularly relevant for forest specialists which show declining range sizes even though all land-use scenarios predict an increase of forest cover in the region. This apparent contradiction arises because simulated forest expansion mainly occurs at the expense of abandoned grasslands in montane areas. At the same time, climate warming shifts the ranges of many montane forest species upward to elevations where there is no forest anymore, either because they are above the current climatic treeline, or because the rugged terrain (widespread rock faces, debris cones, and avalanche paths) does not allow for forest establishment, or because the areas are used for summer farming and thus kept free of forest by

pasturing and regular clearing. Consequently, these species cannot make full use of their expanding habitat because the local climate at the 'new' forest sites is not suitable to them anymore. In the long run, this contradiction will likely attenuate with the rise of the climatic treeline. However, this process is likely slow (e.g. Dullinger *et al.*, 2004), and constraints from topography and land use will determine forest expansion at and above the treeline much stronger over the next centuries in the European Alps (Holtmeier & Broll, 2005; Tasser *et al.*, 2017).

At the other end of the elevational gradient, species that are currently restricted to the lowlands are among the potential winners of climate warming. The number of such winners would have further increased, if we had included species from even warmer areas of Austria that do not actually grow within or in the surroundings of the study area. However, where such species are bound to particular land-use forms, they may not be able to realize this potential unless land-use decisions have adapted to the upward shift of climatic conditions. Specialists of agricultural lands, for example, the land-use type most widespread in the warmest part of the study area show no or only moderate expansion of suitable area in our simulations, mainly because ABMs predict agricultural production to remain more or less where it is today.

### **Do we need land-use scenarios for predicting future species distributions?**

The response of species to climate vs. land-use scenarios in our simulations may suggest that the focus on climate instead of land use in future biodiversity forecasts is actually justified. Indeed, for our study region, land-use scenarios do not contribute much to the modelled changes in future plant distribution. However, there are a number of caveats. First, as already discussed, the scenarios developed might underestimate the scale of future land-use change in the area for several reasons. Second, a considerable part of the biodiversity in the study region, and in cultural landscapes of Europe in general, is concentrated in small remnants of natural or semi-natural habitats such as mires, dry and wet grasslands or rock outcrops which are out-of-use or managed for conservation purposes (Tscharntke *et al.*, 2005; Marini *et al.*, 2008; Ellenberg, 2009; Dengler *et al.*, 2014). For these remnants we have assumed that current 'no-land-use' regimes remain unchanged in our simulations, i.e. that they are conserved as such. These assumptions are not unrealistic because at least part of these remnants is under legal protection. However, there will still be many cases where such patches fall victim to competing interests (Henle *et al.*, 2008). Such changes have little effects on area statistics but potentially large ones on regional species pools (Haddad *et al.*, 2015). Consequently, the future of biodiversity in many regions of Europe, including our study

area, may be determined more by the fate of these small patches than by changes to the usage of the matrix (Wessely *et al.*, 2017; Wintle *et al.*, 2019). Further land-use scenario development for biodiversity forecasts should hence particularly address the fate of these remnants. Third, the results achieved in our case-study region are likely representative for many cultural landscapes of Central and Western Europe. These landscapes do not only have a long tradition of usage, they have also undergone at least half a century of intensification including application of fertilizers, herbicides and insecticides, multiple mowing of grasslands, land consolidation or amelioration techniques, or abandonment and afforestation of economically marginal sites (Benton *et al.*, 2003; Poschlod *et al.*, 2005; Graf *et al.*, 2014). In combination with established legal constraints, options for further land-use intensification (apart from destruction of remaining semi-natural remnants, see above) are thus relatively limited, and future alterations may rather result from the abandonment or reforestation of economically marginal parts of the land (Giupponi *et al.*, 2006; Henle *et al.*, 2008). As a consequence, major changes to land-use patterns and thus species distributions are unlikely unless legal or economical frameworks change more drastically than supposed in the SSP scenarios and our ABM assumptions. The situation is completely different, however, where regions still contain large tracts of natural areas that are of agricultural interest, or where low-intensity land-use systems still prevail. In these regions, future habitat transformations resulting from e.g. the clearing of forests (e.g. Wearn *et al.*, 2012), or the intensification of cropland use (Kehoe *et al.*, 2017) will certainly have a drastic impact on the distribution of species and their diversity.

For these reasons we argue that including land-use scenarios into biodiversity forecasts is generally important, even if the relative effects of climate and land-use change may vary considerably across regions. We have shown here that ABMs can represent future land-use patterns at a spatial and thematic scale relevant to species distribution. We hence suggest that the development and implementation of such scenarios via ABMs and their linkage with biodiversity models should be intensified. Moreover, ABMs can potentially be coupled with any type of biodiversity models, not only with SDMs. Links with dynamic range models (Lurgi *et al.*, 2015; Zurell *et al.*, 2016) may be especially attractive as both types of models are able to represent transient change and therefore to link the spatio-temporal dynamics of species' populations with the spatio-temporal dynamics of landscape patterns (Wessely *et al.*, 2017; Fordham *et al.*, 2018). The necessary effort to parameterize and run such combined socio-ecological models is certainly larger, but its forecasts will also be more realistic than those of climate impact models in isolation (Evans *et al.*, 2013; Fordham *et al.*, 2018).

## ACKNOWLEDGEMENTS

ID was funded by the Austrian Academy of Sciences (project 'LUBIO').

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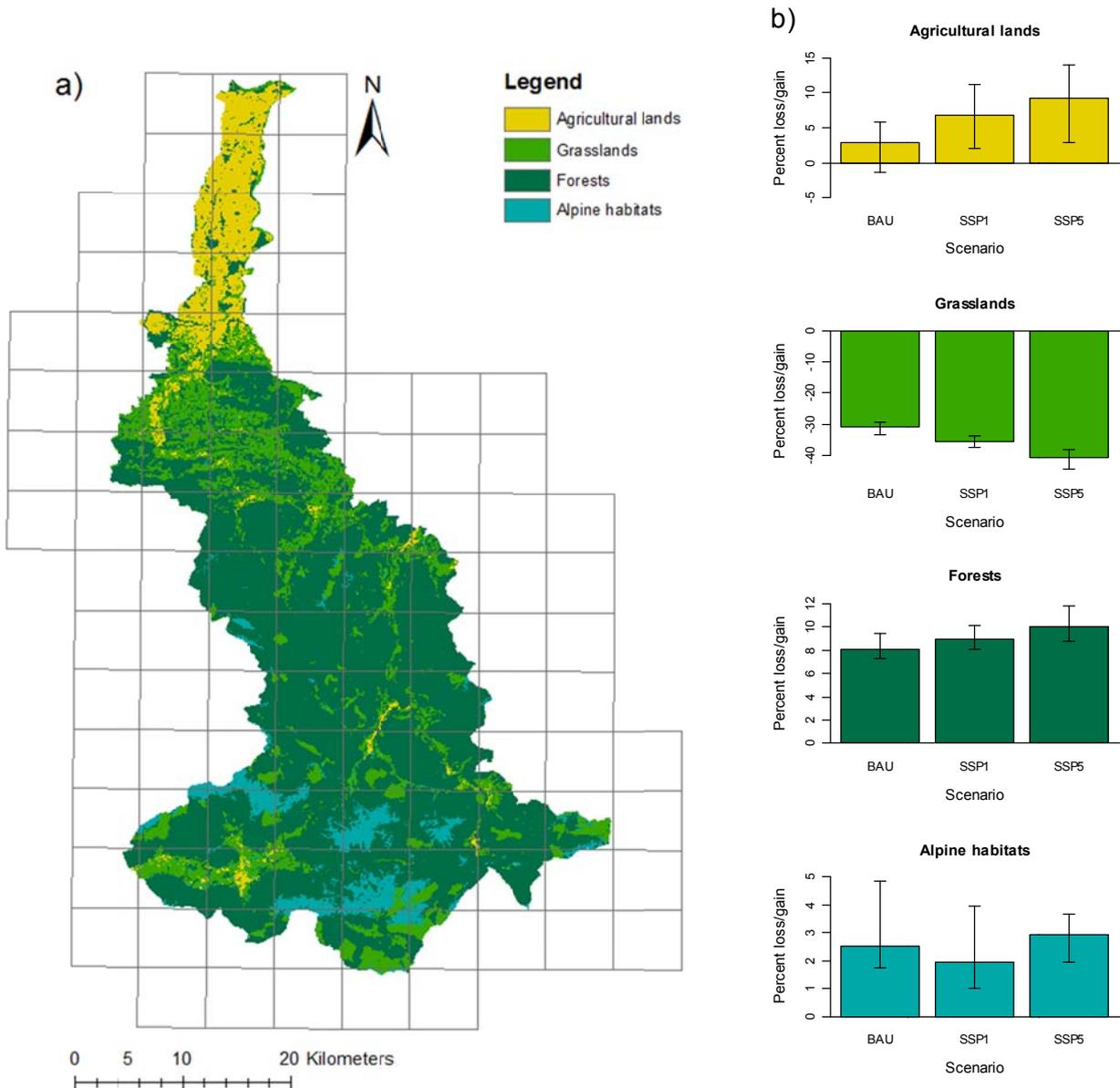
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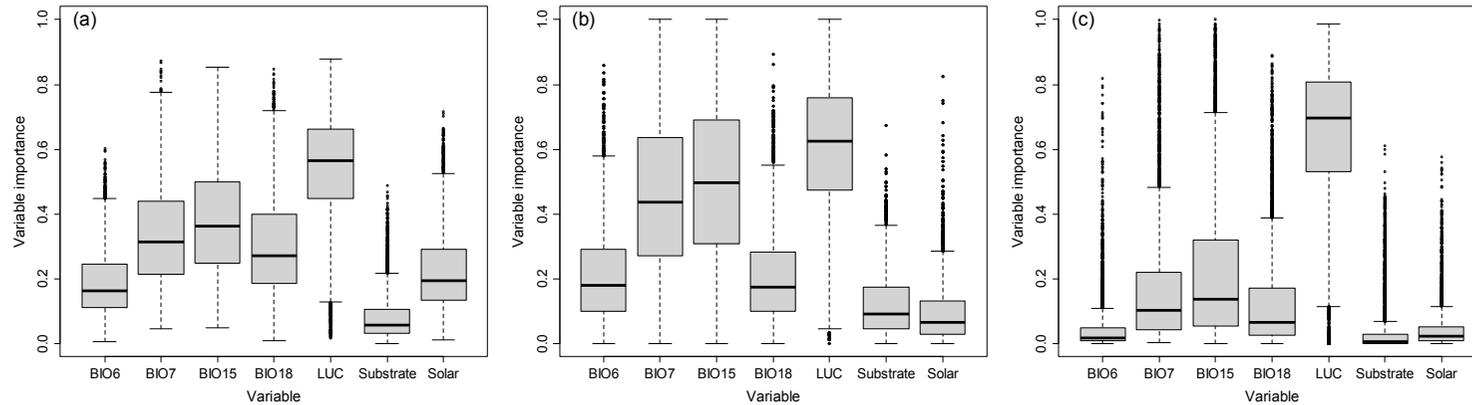
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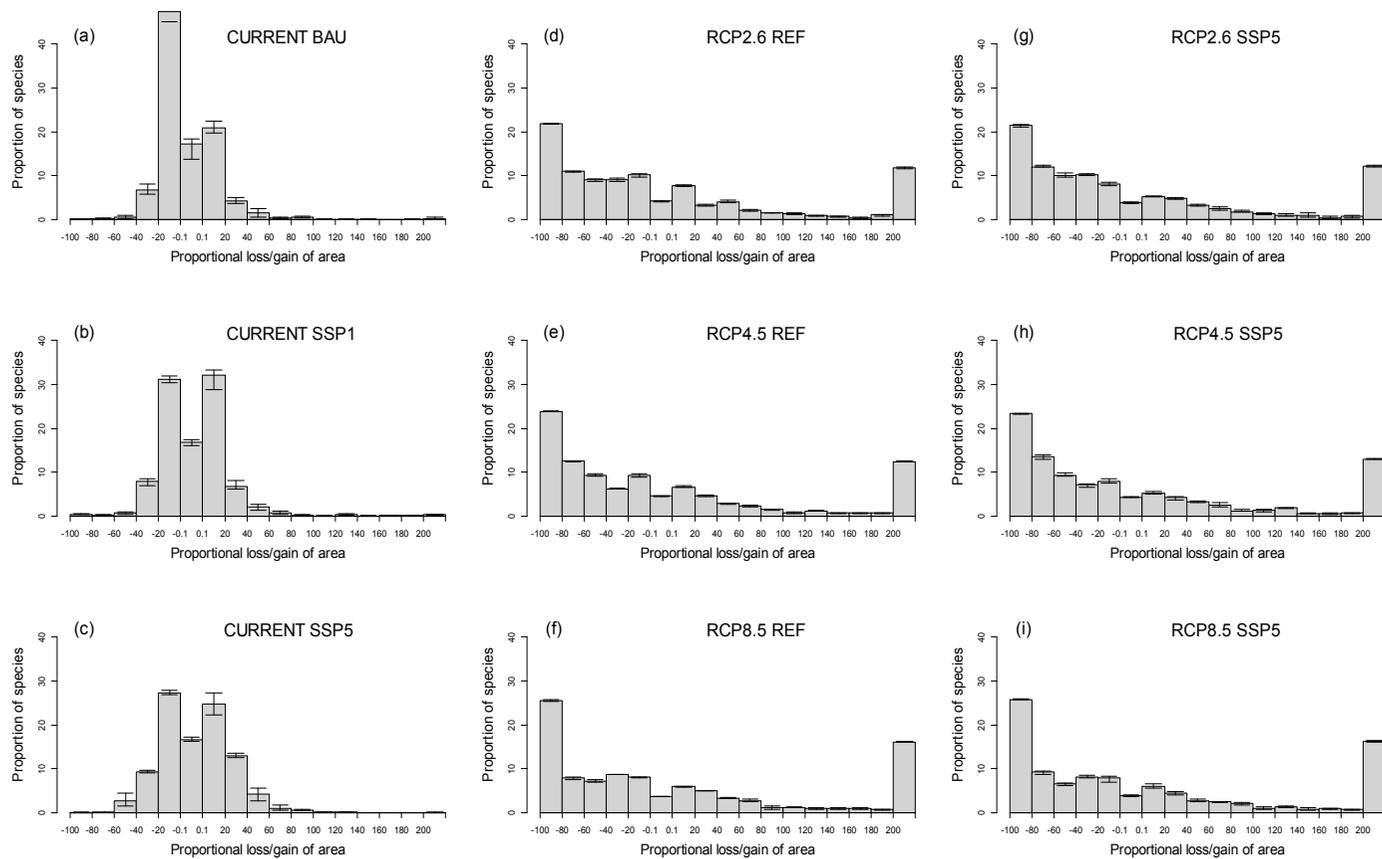
## FIGURES



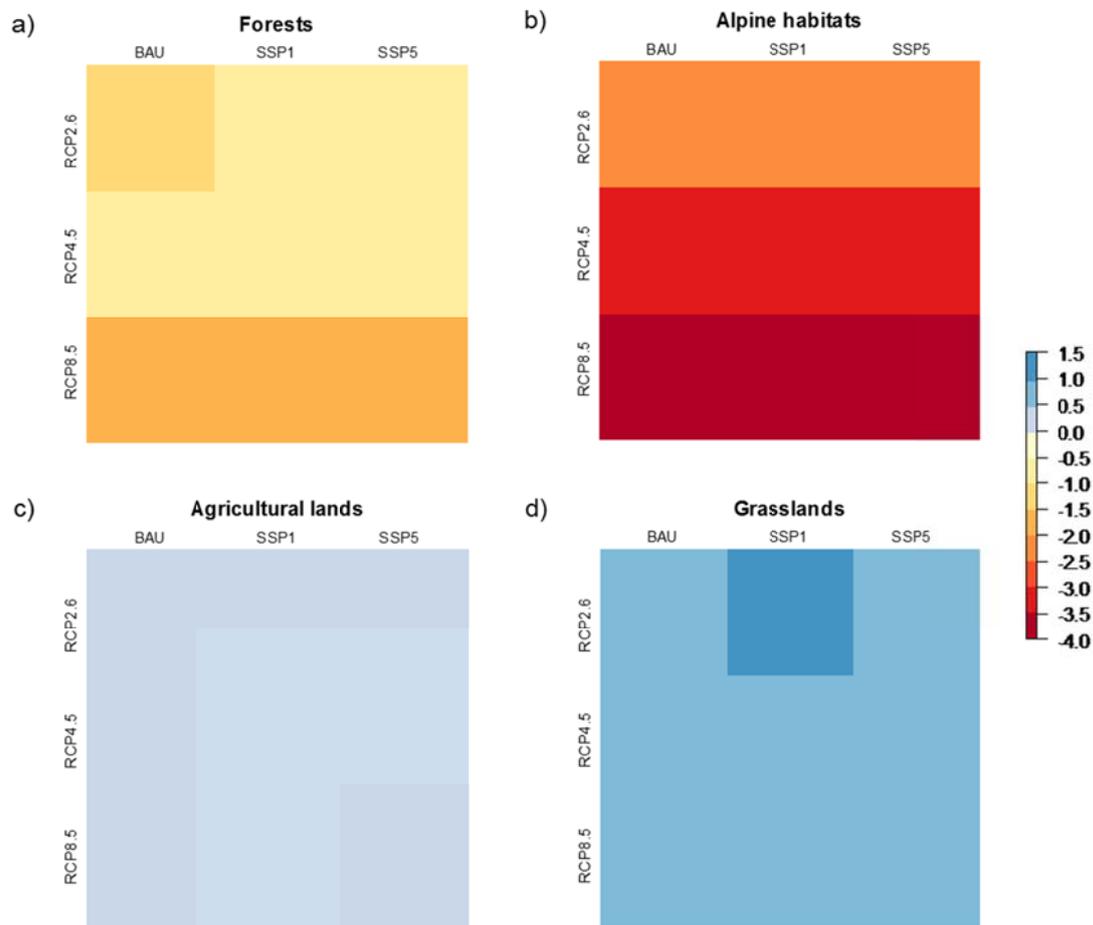
**Figure 1:** a) Map of study area with current land use summarized into four habitat groups. The raster overlaying the map represents cells (each 3 x 5' in size) of the floristic mapping grid of Austria; b) projected percentage changes of the area covered by these four habitat groups under different scenarios of land use (BAU, SSP1, SSP5) in comparison to their current extent. Barplots depict mean values for all five simulation runs for each scenario (combination), while whiskers depict the minimum and maximum changes from all five simulation runs.



**Figure 2:** Importance of predictor variables in models, evaluated separately for the three modelling techniques: **a)** Random Forests, **b)** Artificial Neuronal Networks and **c)** Gradient Boosting Machine. Each boxplot represents results for 832 species. Black lines within the boxes mark the median, box boundaries the upper and lower quartiles, and whiskers the 10th and 90th percentiles. The variables modelled and tested are: BIO6 (Min Temperature of the Coldest Month), BIO7 (Temperature Annual Range), BIO15 (Precipitation Seasonality), BIO18 (Precipitation of Warmest Quarter), LUC (Land-use classes), Substrate (presence/ absence calcareous) and Solar (solar radiation income).



**Figure 3:** Projected changes in the size of suitable ranges of 832 species in the study region. Changes are depicted for different combinations of land-use and climate change scenarios: **(a)-(c)** proportional loss/gain of suitable area under current climate ('CURRENT') but varying land-use scenarios, **(d)-(f)** under varying climate but current land use ('REF'), and **(h)-(i)** under varying climate and the SSP5 land-use scenario. Barplots depict mean values for all five simulation runs for each scenario (combination), while whiskers depict the minimum and maximum changes from all five simulation runs.



**Figure 4:** The amount of range change calculated separately for subsets of species specialized to the indicated habitats. Changes are depicted for the respective land-use and climate change scenario combinations and have been calculated as the natural logarithm of the ratio of the number of cells predicted to be suitable in the future and under current conditions, respectively. Colours represent average values for all species belonging to the specific habitat (Forests: 160 species, Alpine habitats: 147 species, Agricultural lands: 57 species, Grasslands: 165 species).

## TABLES

**Table 1:** The 22 land-use classes distinguished, the four broad habitat groups they have been assigned to, and the proportional area of each land-use class under current conditions or predicted (by the respective centroid simulation runs) under the three land-use scenarios BAU (business-as-usual), SSP1 (sustainability-oriented) and SSP5 (unconstrained economic growth).

Habitat group	Land-use class	CURRENT	BAU	SSP1	SSP5
Agricultural lands	Arable land fallow and low-input	0.41	0.51	0.59	0.6
Agricultural lands	Cereal crop	2.46	0.97	0.77	1.23
Agricultural lands	Cereal crop low-input	0.21	0.78	0.42	0.26
Agricultural lands	Energy crop	0.01	0.7	2.43	0.69
Agricultural lands	Misc. arable land	0.79	0.83	0.82	0.82
Agricultural lands	Non-cereal crop	2.21	1.62	0.35	3.1
Agricultural lands	Non-cereal crop low-input	0.19	1.36	1.35	0.33
Agricultural lands	Ruderal	2.53	2.53	2.53	2.53
Grasslands	Dry grassland	0.03	0.03	0.03	0.03
Grasslands	Extensive meadow (one- or two-cut)	2.33	3.19	3.35	1.91
Grasslands	Extensive pasture (max. 1.5 livestock units)	6.67	7.4	7.23	5.07
Grasslands	Intensive meadow (min. three-cut)	3.96	0.51	0.34	1.83
Grasslands	Intensive pasture (min. 1.5 livestock units)	4.6	0.45	0.25	0.94
Grasslands	Orchard meadow and fruit plantation	0.02	0.02	0.02	0.02
Grasslands	Riparian	1.02	1.02	1.02	1.02
Grasslands	Wetland	0.1	0.1	0.1	0.98
Forests	Broad-leaved forest	23.6	22.31	27.85	33.22
Forests	Conifer forest	41.7	49.24	44.24	38.55
Forests	Felling area	1.28	0.38	0.35	1.64
Alpine habitats	Alpine grassland	1.02	1.02	1.02	1.02
Alpine habitats	Rock and scree	3.51	3.51	3.51	3.51
Alpine habitats	Scrub & Shrub (incl. Krummholz)	1.39	1.5	1.45	1.58

**Table 2:** Results of a linear mixed-effects model relating the natural logarithm of the ratio of the number of cells predicted to be suitable to the 832 model species in the future and under current conditions, respectively, to climate change scenario, land-use change scenario, and their interaction. Lower AIC (Akaike Information Criterion) values indicate better models.  $R^2_m$  and  $R^2_c$  are the marginal and conditional  $R^2$ -values of the model.

Predictors	Estimate	Std. error	p-value	AIC	$R^2_m$	$R^2_c$
Climate change scenario* Land-use change scenario				257592	0.018	0.668
RCP2.6	-0.548	0.036	0			
RCP4.5	-0.644	0.036	0			
RCP8.5	-1.044	0.036	0			
BAU	-0.018	0.036	0.613			
SSP1	-0.002	0.036	0.945			
SSP5	0.008	0.036	0.823			
RCP2.6 : BAU	-0.024	0.050	0.631			
RCP4.5 : BAU	-0.022	0.050	0.660			
RCP8.5 : BAU	-0.046	0.050	0.357			
RCP2.6 : SSP1	0.002	0.050	0.971			
RCP4.5 : SSP1	0.001	0.050	0.985			
RCP8.5 : SSP1	-0.020	0.050	0.698			
RCP2.6 : SSP5	-0.004	0.050	0.930			
RCP4.5 : SSP5	-0.001	0.050	0.989			
RCP8.5 : SSP5	-0.020	0.050	0.687			
excluding						
Climate change scenario				261041	0.000	0.650
Land-use change scenario				257516	0.018	0.668
Climate change scenario : Land-use change scenario				257534	0.018	0.668

## SUPPORTING INFORMATION

### A socio-ecological model for predicting impacts of land use and climate change on regional plant diversity

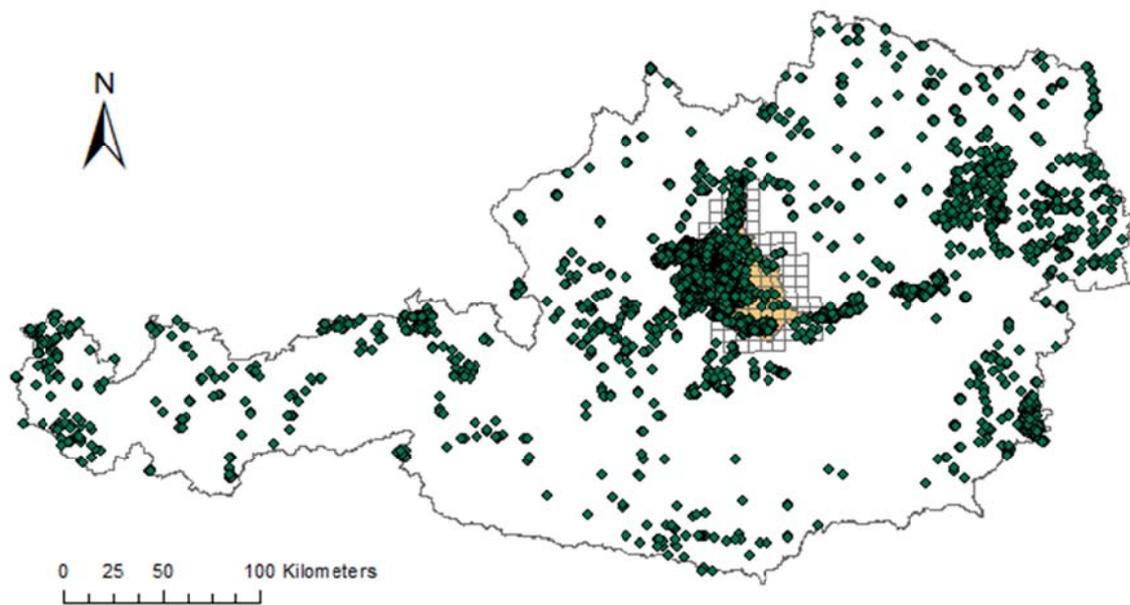
Iwona Dullinger, Johannes Wessely, Andreas Gattringer, Dietmar Moser, Christoph Plutzer, Wolfgang Willner, Claudine Egger, Veronika Gaube, Helmut Haberl, Andreas Mayer, Andreas Böhner, Christian Gilli, Kathrin Pascher, Franz Essi and Stefan Dullinger

#### **Additional methods.** Description of the agent-based model

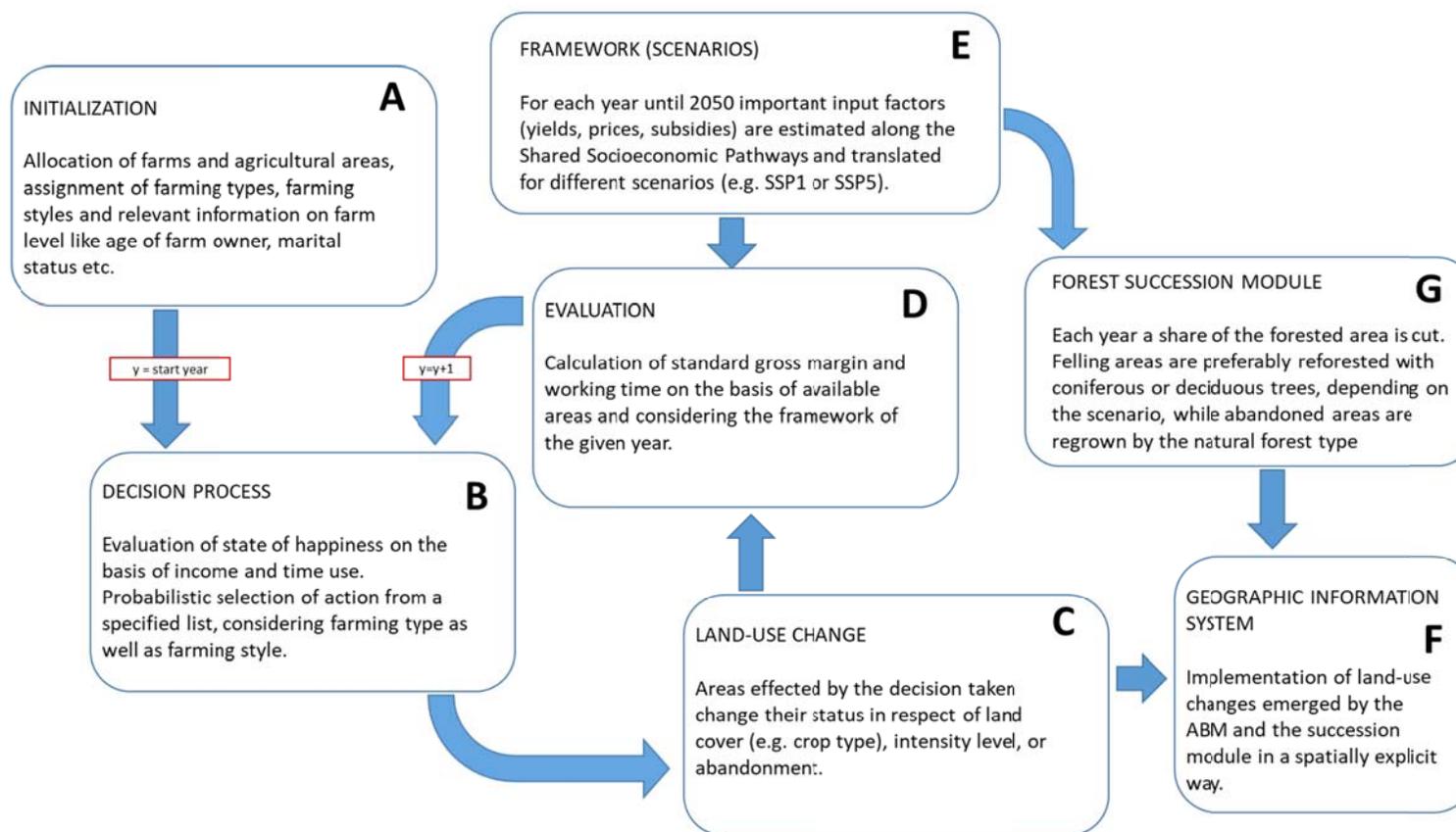
SECLAND is an agent-based model (ABM) simulating decisions of relevant actors on agricultural land over time. Due to its modular structure it is capable to handle a broad list of questions related to land use change.

Agent-based models rely on the design of agents, representing real-world actors and their interactions. These agents are not necessarily individuals, but also entities like companies, institutional and governance structures, or – as in the case of SECLAND – farms. Embedded in an environment, with which they interact, agents act goal-oriented (but not necessarily with an objective to optimize), autonomous and self-directed, with the ability to learn and adapt. In the SECLAND application run for this study, agents try to keep a satisfactory balance between workload (= invested time) and income. After an initialization process (Fig. S2 A), where each agricultural holding is assigned relevant information (e.g. farming type, farming style, age of farm owner), each farm evaluates its “happiness” on the basis of these criteria (Fig. S2 B). The outcome of this evaluation is affected by the farming style, which represents different value systems of land users (classified according to the typology of Schmitzberger et al. 2005), and determines the probability that farmers select particular options from a predefined set of actions (e.g. termination, intensification, extensification, change to other modes of land use). The list of possible actions and their associated probabilities was based on combining model assumptions (Table S3) with a stakeholder process including expert interviews, and additional literature data (e.g. Schmitzberger *et al.*, 2005). After an option has been selected, the land parcels belonging to a farm are affected by the respective consequences (Fig. S2 C). Abandoned patches (due to termination of the farm hold or reduction of its area) become part of the rental market where they are available for farms willing to expand. Agricultural areas that are not cultivated undergo a succession process, gradually transforming them into fallows and further into semi-natural and

natural habitat types (mostly forests). The consequences of the changes made in a specific year are the basis of the evaluation of the next year (Fig. S2 D). The configuration of each farm due to area, land use types and intensity level is linked with socio-economic input variables like standard gross margins, yields, prices and subsidies. These are external numbers that are prepared for each year, allowing a scenario framework by providing different input trends over time/future (Fig. S2 E). One important feature of SECLAND is its ability to link to a Geographic Information System (GIS) and hence to handle spatially explicit data (Fig. S2 F). For forested areas, a probabilistic felling model outside SECLAND was developed (Fig. S2 G), representing different felling strategies along the narratives of the scenario-framework (Fig. S2 E). The outcomes of Fig. S2 C and Fig. S2 G were combined using GIS-techniques to prepare the inputs for the SDM.



**Figure S1:** Distribution of the 12,498 vegetation plots across Austria. Plots clustered in and around the study area are mostly derived from Office of the State of Upper Austria (1993-2013).



**Figure S2:** The ABM "SECLAND" and its different components and steps.

**Table S1.** Information on vegetation plot data

The table lists for all vegetation plot databases, the number of plot records, age of the plots, accuracy of the coordinates and information on how land-use classes have been assigned to the plots.

<b>Database</b>	<b>Pascher <i>et al.</i> (2011)</b>	<b>Office of the State of Upper Austria (1993-2013)</b>	<b>Willner <i>et al.</i> (2012)</b>	<b>own records</b>
<b>Number of plots</b>	1786	3938	6619	155
<b>Year of sampling</b>	2007	1993-2013	1991-2014	2016
<b>Accuracy of geographical localisation</b>	c. 20 m	Plots were assigned to the centre of gravity of the biotope polygons they characterize. These polygons vary in size between 50 and 100,000 m <sup>2</sup>	< 250 m	< 10 m
<b>Assignment of land-use information (see Tab. 1) to plots</b>	Direct classification in the field	Direct classification in the field	Land use information was derived from available phytosociological classification of each plot	Direct classification in the field

**Table S2.** List of modelled species, information on model performance and habitat group assignment

The table lists for all species and each modelling technique the mean TSS over all replicates, the number of failed replicate runs, the number of replicates with TSS < 0.5 and the TSS value of the Ensemble Model. Additionally, information on habitat groups is given: species have been assigned to one of the four groups (forests, alpine habitats (*'alpine'*), agricultural lands (*'agriculture'*), grasslands) when having at least 75 % of their occurrences in vegetation plots assigned to this category.

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
Abies alba	0.773	0 / 0	0.774	0 / 0	0.764	0 / 0	0.85	forests
Acer campestre	0.825	0 / 0	0.808	0 / 0	0.784	0 / 0	0.887	forests
Acer platanoides	0.751	0 / 0	0.715	0 / 0	0.681	0 / 0	0.858	forests
Acer pseudoplatanus	0.765	0 / 0	0.746	0 / 0	0.742	0 / 0	0.797	forests
Achillea atrata	0.884	0 / 0	0.912	0 / 0	0.821	0 / 0	0.939	alpine
Achillea clavennae	0.849	0 / 0	0.858	0 / 0	0.84	0 / 0	0.915	alpine
Achillea clusiana	0.785	0 / 0	0.899	0 / 0	0.852	0 / 0	0.921	alpine
Achillea millefolium agg.	0.762	0 / 0	0.75	0 / 0	0.735	0 / 0	0.8	
Aconitum lycoctonum	0.751	0 / 0	0.73	0 / 0	0.712	0 / 0	0.865	forests
Aconitum napellus agg.	0.722	0 / 0	0.746	0 / 0	0.732	0 / 0	0.85	
Aconitum variegatum agg.	0.595	0 / 0	0.737	0 / 0	0.682	0 / 0	0.834	
Actaea spicata	0.687	0 / 0	0.708	0 / 0	0.66	0 / 0	0.849	forests
Adenostyles alliariae	0.722	0 / 0	0.763	0 / 0	0.687	0 / 0	0.882	
Adenostyles alpina	0.763	0 / 0	0.744	0 / 0	0.721	0 / 0	0.867	
Adoxa moschatellina	0.784	0 / 0	0.829	0 / 0	0.811	0 / 0	0.947	forests
Aegopodium podagraria	0.693	0 / 0	0.662	0 / 0	0.669	0 / 0	0.791	
Aethusa cynapium	0.503	0 / 0	0.79	0 / 0	0.582	0 / 0	0.914	agriculture
Agrimonia eupatoria	0.767	0 / 0	0.62	0 / 0	0.61	0 / 0	0.887	
Agrostis alpina	0.846	0 / 0	0.898	0 / 0	0.874	0 / 0	0.93	alpine
Agrostis canina	0.752	0 / 0	0.775	0 / 0	0.78	1 / 0	0.853	grasslands
Agrostis capillaris	0.647	0 / 0	0.596	0 / 0	0.533	0 / 1	0.832	
Agrostis rupestris	0.822	0 / 0	0.863	0 / 0	0.858	0 / 0	0.938	alpine
Agrostis stolonifera	0.624	0 / 0	0.578	0 / 0	0.542	0 / 1	0.857	
Ajuga reptans	0.628	0 / 0	0.538	0 / 0	0.532	0 / 0	0.767	
Alliaria petiolata	0.815	0 / 0	0.829	0 / 0	0.687	0 / 0	0.926	forests
Allium ursinum	0.555	0 / 0	0.738	0 / 0	0.655	0 / 0	0.88	forests
Allium victorialis	0.924	0 / 0	0.936	0 / 0	0.935	0 / 0	0.981	alpine
Alnus glutinosa	0.695	0 / 0	0.659	0 / 0	0.687	0 / 0	0.811	
Alnus incana	0.705	0 / 0	0.613	0 / 0	0.587	0 / 0	0.818	
Alopecurus pratensis	0.842	0 / 0	0.759	0 / 0	0.748	0 / 0	0.888	
Amaranthus retroflexus	0.878	0 / 0	0.91	0 / 0	0.877	0 / 0	0.955	agriculture
Amelanchier ovalis	0.688	0 / 0	0.763	0 / 0	0.689	1 / 0	0.872	forests
Anagallis arvensis	0.769	0 / 0	0.877	0 / 0	0.749	0 / 0	0.934	agriculture
Andromeda polifolia	0.734	0 / 0	0.871	0 / 0	0.855	0 / 0	0.892	grasslands
Androsace chamaejasme	0.903	0 / 0	0.936	0 / 0	0.877	0 / 0	0.967	alpine
Anemonastrum narcissiflorum	0.875	0 / 0	0.886	0 / 0	0.855	0 / 0	0.947	alpine

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
Anemone nemorosa	0.679	0 / 0	0.616	0 / 0	0.58	0 / 0	0.789	
Angelica sylvestris	0.579	0 / 0	0.569	0 / 0	0.558	0 / 0	0.761	
Antennaria dioica	NA	0 / 3	0.576	0 / 0	0.634	1 / 1	0.837	
Anthemis arvensis	0.944	0 / 0	0.831	0 / 0	0.836	0 / 0	0.949	agriculture
Anthericum ramosum	0.664	0 / 0	0.661	0 / 0	0.679	0 / 0	0.855	
Anthoxanthum alpinum	0.86	0 / 0	0.893	0 / 0	0.878	0 / 0	0.926	alpine
Anthoxanthum odoratum	0.766	0 / 0	0.681	0 / 0	0.693	0 / 0	0.79	grasslands
Anthriscus nitidus	0.715	0 / 1	0.732	0 / 0	0.715	2 / 0	0.863	forests
Anthriscus sylvestris s. str.	0.675	0 / 0	0.658	0 / 0	0.563	0 / 0	0.852	
Anthyllis vulneraria subsp. alpicola	0.865	0 / 0	0.878	0 / 0	0.824	0 / 0	0.934	alpine
Anthyllis vulneraria	0.854	0 / 0	0.851	0 / 0	0.869	0 / 0	0.924	grasslands
Apera spica-venti	0.843	0 / 0	0.826	0 / 0	0.794	0 / 0	0.94	agriculture
Aphanes arvensis	0.873	0 / 0	0.876	0 / 0	0.714	0 / 0	0.967	agriculture
Aposeris foetida	0.685	0 / 0	0.708	0 / 0	0.673	0 / 0	0.908	forests
Aquilegia atrata	0.69	0 / 0	0.696	0 / 0	0.627	0 / 0	0.841	
Arabidopsis arenosa	0.629	0 / 0	0.63	0 / 0	0.57	0 / 0	0.832	
Arabidopsis thaliana	0.915	0 / 0	0.814	0 / 0	0.753	0 / 0	0.931	
Arabis alpina subsp. alpina	0.682	0 / 0	0.755	0 / 0	0.746	0 / 0	0.891	
Arabis ciliata	0.553	0 / 0	0.662	0 / 0	0.568	0 / 2	0.89	
Arabis hirsuta s. str.	0.668	0 / 0	0.77	0 / 0	0.72	0 / 0	0.927	grasslands
Arabis pumila agg.	0.822	0 / 0	0.837	0 / 0	0.805	0 / 0	0.925	alpine
Arctium lappa	0.672	0 / 0	0.672	0 / 0	0.566	0 / 1	0.893	
Arctostaphylos alpinus	0.798	0 / 0	0.872	0 / 0	0.775	0 / 0	0.943	alpine
Arenaria ciliata s. str.	0.823	0 / 0	0.919	0 / 0	0.888	0 / 0	0.945	alpine
Arenaria serpyllifolia s. str.	0.778	0 / 0	0.737	0 / 0	0.752	0 / 0	0.891	
Armeria alpina s. str.	0.92	0 / 0	0.916	0 / 0	0.86	0 / 0	0.96	alpine
Arnica montana	0.795	0 / 0	0.831	0 / 0	0.791	0 / 0	0.905	
Arrhenatherum elatius	0.774	0 / 0	0.717	0 / 0	0.706	0 / 0	0.806	
Aruncus dioicus	0.664	0 / 0	0.681	0 / 0	0.681	0 / 0	0.832	forests
Asarum europaeum	0.71	0 / 0	0.72	0 / 0	0.707	0 / 0	0.82	forests
Asperula cynanchica s. str.	0.806	0 / 0	0.829	0 / 0	0.768	0 / 0	0.947	grasslands
Asplenium ruta-muraria	0.697	0 / 0	0.654	0 / 0	0.687	0 / 0	0.86	
Asplenium scolopendrium	0.612	0 / 1	0.768	0 / 0	0.572	2 / 0	0.861	forests
Asplenium trichomanes	0.69	0 / 0	0.657	0 / 0	0.65	0 / 0	0.846	forests
Asplenium viride	0.711	0 / 0	0.751	0 / 0	0.75	0 / 0	0.852	
Aster alpinus	0.708	0 / 0	0.864	0 / 0	0.627	0 / 1	0.958	alpine
Astragalus glycyphyllos	0.613	0 / 0	0.546	0 / 1	NA	1 / 2	0.91	
Astrantia major	0.691	0 / 0	0.674	0 / 0	0.647	0 / 0	0.781	
Athamanta cretensis	0.873	0 / 0	0.873	0 / 0	0.805	0 / 0	0.949	alpine
Athyrium filix-femina	0.689	0 / 0	0.688	0 / 0	0.66	0 / 0	0.813	forests
Atropa belladonna	0.719	0 / 0	0.78	0 / 0	0.723	1 / 0	0.854	forests

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
<i>Avena fatua</i>	0.938	0 / 0	0.885	0 / 0	0.88	0 / 0	0.945	agriculture
<i>Avenella flexuosa</i>	0.659	0 / 0	0.596	0 / 0	0.59	0 / 0	0.861	
<i>Avenula versicolor</i>	0.805	0 / 0	0.939	0 / 0	0.909	0 / 0	0.973	alpine
<i>Ballota nigra</i>	0.932	0 / 0	0.886	0 / 0	0.869	0 / 0	0.958	
<i>Bartsia alpina</i>	0.798	0 / 0	0.833	0 / 0	0.848	0 / 0	0.884	alpine
<i>Bellidiastrum michellii</i>	0.62	0 / 0	0.646	0 / 0	0.63	0 / 0	0.796	
<i>Bellis perennis</i>	0.764	0 / 0	0.746	0 / 0	0.688	0 / 0	0.884	grasslands
<i>Berberis vulgaris</i>	0.642	0 / 0	0.696	0 / 0	0.688	0 / 0	0.822	
<i>Betonica alopeucuros</i>	0.703	0 / 0	0.73	0 / 0	0.695	0 / 0	0.871	
<i>Betonica officinalis</i>	0.756	0 / 0	0.751	0 / 0	0.714	0 / 0	0.831	grasslands
<i>Betula pendula</i>	0.536	0 / 0	0.536	0 / 0	0.556	0 / 0	0.737	forests
<i>Betula pubescens</i>	0.605	0 / 1	0.826	0 / 0	0.624	0 / 0	0.899	grasslands
<i>Biscutella laevigata</i>	0.891	0 / 0	0.884	0 / 0	0.873	0 / 0	0.919	alpine
<i>Blechnum spicant</i>	0.696	0 / 0	0.71	0 / 0	0.699	0 / 0	0.85	forests
<i>Botrychium lunaria</i>	0.732	0 / 0	0.867	0 / 0	0.814	0 / 0	0.955	alpine
<i>Brachypodium pinnatum</i>	0.709	0 / 0	0.653	0 / 0	0.623	0 / 0	0.809	
<i>Brachypodium sylvaticum</i>	0.705	0 / 0	0.73	0 / 0	0.714	0 / 0	0.838	forests
<i>Briza media</i>	0.72	0 / 0	0.711	0 / 0	0.725	0 / 0	0.797	grasslands
<i>Bromus benekenii</i>	0.693	0 / 0	0.687	0 / 0	0.718	0 / 0	0.858	forests
<i>Bromus erectus</i>	0.913	0 / 0	0.87	0 / 0	0.861	0 / 0	0.919	grasslands
<i>Bromus hordeaceus</i>	0.768	0 / 0	0.725	0 / 0	0.703	0 / 0	0.86	
<i>Bromus sterilis</i>	0.959	0 / 0	0.895	0 / 0	0.886	0 / 0	0.951	agriculture
<i>Bromus tectorum</i>	0.955	0 / 0	0.925	0 / 0	0.88	0 / 0	0.963	agriculture
<i>Buphthalmum salicifolium</i>	0.709	0 / 0	0.69	0 / 0	0.686	0 / 0	0.823	
<i>Calamagrostis canescens</i>	0.946	0 / 0	0.942	0 / 0	0.968	0 / 0	0.989	grasslands
<i>Calamagrostis epigejos</i>	0.514	0 / 1	NA	0 / 3	NA	0 / 3	0.922	
<i>Calamagrostis varia</i>	0.732	0 / 0	0.742	0 / 0	0.736	0 / 0	0.795	forests
<i>Calamagrostis villosa</i>	0.646	0 / 1	0.738	0 / 0	0.533	0 / 2	0.851	
<i>Calluna vulgaris</i>	0.695	0 / 0	0.722	0 / 0	0.698	0 / 0	0.769	grasslands
<i>Caltha palustris</i>	0.528	0 / 0	0.523	0 / 1	0.554	0 / 1	0.777	
<i>Calystegia sepium s. str.</i>	0.707	0 / 0	0.752	0 / 0	0.69	0 / 0	0.884	
<i>Camelina microcarpa</i>	0.931	0 / 0	0.919	0 / 0	0.9	0 / 0	0.962	agriculture
<i>Campanula alpina</i>	0.904	0 / 0	0.927	0 / 0	0.898	0 / 0	0.952	alpine
<i>Campanula barbata</i>	0.852	0 / 0	0.883	0 / 0	0.845	0 / 0	0.976	alpine
<i>Campanula cespitosa</i>	0.63	0 / 0	0.681	0 / 0	0.568	0 / 0	0.894	
<i>Campanula cochleariifolia</i>	0.71	0 / 0	0.745	0 / 0	0.734	0 / 0	0.868	
<i>Campanula patula</i>	0.771	0 / 0	0.776	0 / 0	0.761	0 / 0	0.854	grasslands
<i>Campanula persicifolia</i>	0.653	0 / 0	0.703	0 / 0	0.664	0 / 0	0.835	
<i>Campanula pulla</i>	0.848	0 / 0	0.87	0 / 0	0.852	0 / 0	0.932	alpine
<i>Campanula rapunculoides</i>	0.602	0 / 0	0.631	0 / 0	0.596	0 / 1	0.851	
<i>Campanula rotundifolia</i>	0.634	0 / 0	0.588	0 / 0	0.582	0 / 0	0.832	
<i>Campanula scheuchzeri</i>	0.779	0 / 0	0.787	0 / 0	0.795	0 / 0	0.849	alpine
<i>Campanula trachelium</i>	0.668	0 / 0	0.631	0 / 0	0.624	0 / 0	0.818	forests
<i>Capsella bursa- pastoris</i>	0.816	0 / 0	0.825	0 / 0	0.812	0 / 0	0.898	agriculture
<i>Cardamine amara</i>	0.588	0 / 0	0.598	0 / 0	0.52	0 / 1	0.806	

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
Cardamine bulbifera	0.713	0 / 0	0.752	0 / 0	0.676	0 / 0	0.877	forests
Cardamine enneaphylos	0.782	0 / 0	0.796	0 / 0	0.815	0 / 0	0.863	forests
Cardamine flexuosa	0.505	0 / 1	0.703	1 / 1	0.546	0 / 0	0.816	forests
Cardamine impatiens	0.595	0 / 0	0.744	0 / 0	0.702	0 / 0	0.822	forests
Cardamine pratensis agg.	0.754	0 / 0	0.684	0 / 0	0.681	1 / 0	0.844	grasslands
Cardamine trifolia	0.787	0 / 0	0.781	0 / 0	0.784	0 / 0	0.861	forests
Carduus acanthoides	0.907	0 / 0	0.884	0 / 0	0.873	0 / 0	0.94	agriculture
Carduus defloratus s. lat.	0.715	0 / 0	0.708	0 / 0	0.728	0 / 0	0.824	
Carex acuta	0.79	0 / 0	0.87	0 / 0	0.853	0 / 0	0.94	grasslands
Carex acutiformis	0.743	0 / 0	0.755	0 / 0	0.714	0 / 0	0.875	
Carex alba	0.807	0 / 0	0.788	0 / 0	0.781	0 / 0	0.832	forests
Carex atrata	0.857	0 / 0	0.868	0 / 0	0.823	0 / 0	0.942	alpine
Carex brachystachys	0.697	0 / 1	0.723	0 / 0	0.722	0 / 1	0.874	forests
Carex brizoides	0.791	0 / 0	0.763	0 / 0	0.7	0 / 0	0.855	
Carex canescens	0.596	0 / 1	0.776	0 / 0	0.606	1 / 0	0.86	grasslands
Carex capillaris	0.838	0 / 0	0.84	0 / 0	0.846	0 / 0	0.916	alpine
Carex caryophyllea	0.784	0 / 0	0.83	0 / 0	0.848	0 / 0	0.894	grasslands
Carex curvula	0.927	0 / 0	0.918	0 / 0	0.912	0 / 0	0.967	alpine
Carex davalliana	0.882	0 / 0	0.807	1 / 0	0.814	0 / 0	0.861	grasslands
Carex digitata	0.66	0 / 0	0.621	0 / 0	0.628	0 / 0	0.854	forests
Carex echinata	0.733	0 / 0	0.796	0 / 0	0.797	0 / 0	0.836	grasslands
Carex elata	0.854	0 / 0	0.881	0 / 0	0.87	0 / 0	0.918	grasslands
Carex ferruginea	0.749	0 / 0	0.787	0 / 0	0.743	0 / 0	0.879	
Carex firma	0.845	0 / 0	0.875	0 / 0	0.846	0 / 0	0.92	alpine
Carex flacca	0.623	0 / 0	0.552	0 / 0	0.556	0 / 0	0.758	
Carex flava agg.	0.644	0 / 0	0.706	0 / 0	0.703	0 / 0	0.796	grasslands
Carex fuliginosa	0.89	0 / 0	0.906	0 / 0	0.908	0 / 0	0.953	alpine
Carex hirta	0.628	0 / 0	0.642	0 / 0	0.516	0 / 0	0.823	
Carex hostiana	0.792	0 / 0	0.821	0 / 0	0.82	0 / 0	0.88	grasslands
Carex humilis	0.653	0 / 0	0.692	0 / 0	0.66	0 / 0	0.892	
Carex leporina	0.51	0 / 2	0.646	0 / 1	NA	1 / 2	0.788	
Carex limosa	0.675	0 / 0	0.848	0 / 0	0.8	0 / 0	0.896	grasslands
Carex montana	0.671	0 / 0	0.655	0 / 0	0.618	0 / 0	0.867	
Carex mucronata	0.714	0 / 0	0.75	0 / 0	0.738	0 / 0	0.897	alpine
Carex muricata agg.	0.611	0 / 0	0.638	0 / 0	0.51	0 / 0	0.826	
Carex nigra	0.762	0 / 0	0.778	0 / 0	0.762	0 / 0	0.836	grasslands
Carex ornithopoda	0.573	0 / 0	0.623	0 / 0	0.668	1 / 0	0.847	
Carex pallescens	0.702	0 / 0	0.665	0 / 0	0.611	0 / 0	0.808	grasslands
Carex panicea	0.764	0 / 0	0.752	0 / 0	0.73	0 / 0	0.827	grasslands
Carex paniculata	0.664	0 / 0	0.664	0 / 0	0.578	0 / 0	0.836	grasslands
Carex parviflora	0.653	0 / 0	0.844	0 / 0	0.788	0 / 0	0.958	alpine
Carex pauciflora	0.822	0 / 0	0.872	0 / 0	0.883	0 / 0	0.908	grasslands
Carex pendula	0.689	0 / 0	0.713	0 / 0	0.687	0 / 0	0.856	forests
Carex pilosa	0.815	0 / 0	0.851	0 / 0	0.774	0 / 0	0.912	forests
Carex pilulifera	0.614	0 / 0	0.691	0 / 0	0.678	0 / 1	0.871	
Carex praecox	0.941	0 / 0	0.928	0 / 0	0.917	0 / 0	0.973	grasslands
Carex pulicaris	0.822	0 / 0	0.854	0 / 0	0.8	0 / 0	0.94	grasslands
Carex remota	0.549	0 / 0	0.663	0 / 0	0.603	0 / 1	0.838	forests
Carex rostrata	0.836	0 / 0	0.847	0 / 0	0.829	0 / 0	0.866	grasslands
Carex sempervirens	0.807	0 / 0	0.843	0 / 0	0.829	0 / 0	0.893	alpine
Carex sylvatica	0.694	0 / 0	0.65	0 / 0	0.658	0 / 0	0.806	forests
Carex tomentosa	0.697	0 / 0	0.675	0 / 0	0.644	0 / 0	0.905	grasslands
Carex umbrosa	0.557	0 / 2	0.691	0 / 0	0.621	1 / 1	0.818	
Carex vesicaria	0.666	0 / 0	0.761	0 / 0	0.734	0 / 0	0.93	grasslands
Carex vulpina agg.	0.625	0 / 0	0.708	0 / 0	0.679	0 / 0	0.927	grasslands
Carlina acaulis	0.786	0 / 0	0.787	0 / 0	0.721	0 / 0	0.884	

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<i>Carpinus betulus</i>	0.766	0 / 0	0.707	0 / 0	0.747	0 / 0	0.842	forests
<i>Carum carvi</i>	0.714	0 / 0	0.728	0 / 0	0.7	0 / 0	0.878	grasslands
<i>Castanea sativa</i>	NA	3 / 0	NA	3 / 0	NA	3 / 0	NA	
<i>Centaurea jacea</i>	0.787	0 / 0	0.758	0 / 0	0.755	0 / 0	0.834	grasslands
<i>Centaurea scabiosa</i>	0.786	0 / 0	0.735	0 / 0	0.725	0 / 0	0.863	grasslands
<i>Centaurea stoebe</i>	0.789	0 / 0	0.841	0 / 0	0.757	0 / 0	0.967	grasslands
<i>Cephalanthera damasonium</i>	0.546	0 / 1	0.739	0 / 0	0.624	1 / 0	0.812	forests
<i>Cephalanthera longifolia</i>	0.539	0 / 0	0.615	0 / 0	0.649	1 / 1	0.861	forests
<i>Cerastium alpinum</i> agg.	0.927	0 / 0	0.941	0 / 0	0.835	1 / 0	0.987	alpine
<i>Cerastium arvense</i> s. lat.	0.805	0 / 0	0.822	0 / 0	0.796	0 / 0	0.873	
<i>Cerastium carinthiacum</i>	0.869	0 / 0	0.925	0 / 0	0.845	0 / 0	0.932	alpine
<i>Cerastium holosteoides</i>	0.773	0 / 0	0.738	0 / 0	0.736	0 / 0	0.824	
<i>Chaerophyllum aureum</i>	0.7	0 / 0	0.698	0 / 0	0.626	0 / 0	0.887	
<i>Chaerophyllum hirsutum</i> s. str.	0.661	0 / 0	0.626	0 / 0	0.638	0 / 0	0.793	
<i>Chaerophyllum villarsii</i>	0.566	0 / 1	0.699	0 / 0	0.548	0 / 1	0.825	
<i>Chamaecytisus supinus</i>	0.699	0 / 0	0.705	0 / 0	0.72	0 / 0	0.958	
<i>Chelidonium majus</i>	0.655	0 / 0	0.552	0 / 0	0.553	1 / 0	0.897	
<i>Chenopodium album</i> agg.	0.881	0 / 0	0.874	0 / 0	0.866	0 / 0	0.925	agriculture
<i>Chenopodium hybridum</i>	0.913	0 / 0	0.91	0 / 0	0.815	0 / 0	0.952	agriculture
<i>Chenopodium polyspermum</i>	0.921	0 / 0	0.745	0 / 0	0.708	0 / 0	0.974	agriculture
<i>Chrysosplenium alternifolium</i>	0.633	0 / 0	0.737	0 / 0	0.632	0 / 0	0.83	forests
<i>Cichorium intybus</i>	0.837	0 / 0	0.814	0 / 0	0.703	0 / 0	0.97	agriculture
<i>Circaea lutetiana</i>	0.683	0 / 0	0.733	0 / 0	0.713	0 / 0	0.827	forests
<i>Cirsium arvense</i>	0.626	0 / 0	0.592	0 / 0	0.558	0 / 0	0.803	
<i>Cirsium erisithales</i>	0.693	0 / 0	0.67	0 / 0	0.661	0 / 0	0.841	forests
<i>Cirsium oleraceum</i>	0.616	0 / 0	0.604	0 / 0	0.557	0 / 0	0.78	
<i>Cirsium palustre</i>	0.526	0 / 0	0.581	0 / 0	0.53	0 / 0	0.769	
<i>Cirsium pannonicum</i>	0.871	0 / 0	0.917	0 / 0	0.78	0 / 0	0.955	grasslands
<i>Cirsium rivulare</i>	0.714	0 / 0	0.801	0 / 0	0.796	1 / 0	0.919	grasslands
<i>Cirsium vulgare</i>	0.618	0 / 0	0.605	0 / 1	NA	1 / 2	0.933	
<i>Clematis alpina</i>	0.842	0 / 0	0.864	0 / 0	0.668	0 / 0	0.913	forests
<i>Clematis vitalba</i>	0.694	0 / 0	0.659	0 / 0	0.686	0 / 0	0.799	forests
<i>Clinopodium alpinum</i>	0.729	0 / 0	0.768	0 / 0	0.788	0 / 0	0.889	
<i>Clinopodium vulgare</i>	0.602	0 / 0	0.551	0 / 0	0.551	0 / 0	0.799	
<i>Coeloglossum viride</i>	0.73	0 / 0	0.795	0 / 0	0.699	0 / 0	0.87	alpine
<i>Colchicum autumnale</i>	0.722	0 / 0	0.716	0 / 0	0.713	0 / 0	0.847	grasslands
<i>Comarum palustre</i>	0.584	0 / 0	0.802	0 / 0	0.777	0 / 0	0.897	grasslands
<i>Consolida regalis</i>	0.932	0 / 0	0.917	0 / 0	0.911	0 / 0	0.966	agriculture
<i>Convallaria majalis</i>	0.73	0 / 0	0.721	0 / 0	0.698	0 / 0	0.869	forests
<i>Convolvulus arvensis</i>	0.859	0 / 0	0.846	0 / 0	0.821	0 / 0	0.885	agriculture
<i>Cornus mas</i>	0.771	0 / 0	0.806	0 / 0	0.728	0 / 0	0.921	forests
<i>Cornus sanguinea</i>	0.709	0 / 0	0.702	0 / 0	0.699	0 / 0	0.814	
<i>Corydalis solida</i>	0.837	0 / 0	0.946	0 / 0	0.771	0 / 0	0.975	forests
<i>Corylus avellana</i>	0.743	0 / 0	0.706	0 / 0	0.707	0 / 0	0.802	forests

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
<i>Crataegus laevigata</i>	0.675	0 / 0	0.749	0 / 0	0.726	0 / 0	0.848	
<i>Crataegus monogyna</i>	0.663	0 / 0	0.632	0 / 0	0.622	0 / 0	0.794	
<i>Crepis aurea</i>	0.809	0 / 0	0.797	0 / 0	0.748	0 / 0	0.88	
<i>Crepis biennis</i>	0.804	0 / 0	0.74	0 / 0	0.75	0 / 0	0.877	grasslands
<i>Crepis mollis</i>	0.532	0 / 0	0.628	0 / 0	0.536	1 / 0	0.905	grasslands
<i>Crepis paludosa</i>	0.612	0 / 0	0.63	0 / 0	0.56	0 / 0	0.805	
<i>Cruciata glabra</i>	0.946	0 / 0	0.919	0 / 0	0.787	0 / 0	0.969	forests
<i>Cruciata laevipes</i>	0.697	0 / 0	0.672	0 / 0	0.627	0 / 0	0.831	
<i>Cuscuta epithimum</i>	0.562	0 / 1	0.779	0 / 0	0.591	0 / 1	0.855	grasslands
<i>Cyanus montanus</i>	0.64	0 / 0	0.714	1 / 0	0.633	0 / 0	0.865	forests
<i>Cyanus segetum</i>	0.923	0 / 0	0.88	0 / 0	0.862	0 / 0	0.964	agriculture
<i>Cyclamen purpurascens</i>	0.754	0 / 0	0.746	0 / 0	0.748	0 / 0	0.831	forests
<i>Cynosurus cristatus</i>	0.795	0 / 0	0.8	0 / 0	0.823	0 / 0	0.878	grasslands
<i>Cystopteris alpina</i>	0.811	0 / 0	0.908	0 / 0	0.754	0 / 0	0.972	alpine
<i>Cystopteris fragilis</i> s. str.	0.743	0 / 0	0.784	0 / 0	0.674	0 / 0	0.887	
<i>Dactylis glomerata</i>	0.68	0 / 0	0.637	0 / 0	0.637	0 / 0	0.78	
<i>Dactylis polygama</i>	0.934	0 / 0	0.919	0 / 0	0.921	0 / 0	0.971	forests
<i>Dactylorhiza incarnata</i>	0.506	0 / 2	0.687	0 / 0	0.607	0 / 0	0.819	grasslands
<i>Dactylorhiza maculata</i> s. lat.	0.615	0 / 0	0.646	0 / 0	0.582	0 / 0	0.822	
<i>Dactylorhiza majalis</i>	0.769	0 / 0	0.758	0 / 0	0.741	0 / 0	0.831	grasslands
<i>Danthonia decumbens</i>	0.719	0 / 0	0.769	0 / 0	0.71	0 / 0	0.88	grasslands
<i>Daphne laureola</i>	0.756	0 / 0	0.802	0 / 0	0.796	0 / 0	0.928	forests
<i>Daphne mezereum</i>	0.724	0 / 0	0.715	0 / 0	0.675	0 / 0	0.81	forests
<i>Daucus carota</i>	0.707	0 / 0	0.706	0 / 0	0.694	1 / 0	0.86	
<i>Deschampsia cespitosa</i>	0.563	0 / 0	NA	0 / 3	NA	0 / 3	0.874	
<i>Descurainia sophia</i>	0.948	0 / 0	0.921	0 / 0	0.906	0 / 0	0.966	agriculture
<i>Dianthus alpinus</i>	0.957	0 / 0	0.926	0 / 0	0.931	0 / 0	0.96	alpine
<i>Dianthus carthusianorum</i> agg.	0.803	0 / 0	0.793	0 / 0	0.728	0 / 0	0.918	grasslands
<i>Digitalis grandiflora</i>	0.72	0 / 0	0.702	0 / 0	0.665	0 / 0	0.831	forests
<i>Doronicum austriacum</i>	0.588	0 / 0	0.688	0 / 0	0.723	0 / 0	0.897	forests
<i>Doronicum clusii</i> agg.	0.876	0 / 0	0.93	0 / 0	0.885	0 / 0	0.94	alpine
<i>Dorycnium germanicum</i>	0.836	0 / 0	0.682	0 / 0	0.784	0 / 0	0.992	grasslands
<i>Drosera rotundifolia</i>	0.71	0 / 0	0.821	0 / 0	0.804	0 / 0	0.87	grasslands
<i>Dryas octopetala</i>	0.888	0 / 0	0.907	0 / 0	0.893	0 / 0	0.941	alpine
<i>Dryopteris affinis</i> s. lat.	0.642	0 / 0	0.684	0 / 0	0.67	0 / 0	0.848	forests
<i>Dryopteris carthusiana</i> s. str.	0.527	0 / 0	0.647	0 / 0	0.618	0 / 0	0.786	forests
<i>Dryopteris dilatata</i>	0.68	0 / 0	0.757	0 / 0	0.685	0 / 0	0.854	forests
<i>Dryopteris filix-mas</i> agg.	0.756	0 / 0	0.843	0 / 0	0.66	0 / 0	0.937	forests
<i>Dryopteris filix-mas</i> s. str.	0.667	0 / 0	0.715	0 / 0	0.714	0 / 0	0.814	forests
<i>Echinochloa crus-galli</i>	0.912	0 / 0	0.86	0 / 0	0.868	0 / 0	0.959	agriculture
<i>Echium vulgare</i>	0.706	0 / 0	0.789	0 / 0	0.607	0 / 0	0.942	
<i>Eleocharis palustris</i> agg.	0.587	0 / 1	0.794	0 / 0	0.632	0 / 0	0.892	grasslands
<i>Elymus caninus</i>	0.664	0 / 0	0.738	0 / 0	0.65	0 / 1	0.957	

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<i>Elymus repens</i>	0.814	0 / 0	0.791	0 / 0	0.777	0 / 0	0.868	
<i>Empetrum nigrum</i> agg.	0.67	0 / 1	0.821	0 / 0	0.737	1 / 0	0.915	
<i>Epilobium</i> <i>hirsutum</i>	0.51	0 / 2	0.584	0 / 2	NA	0 / 3	0.711	
<i>Epilobium</i> <i>montanum</i>	0.588	0 / 0	0.573	0 / 0	0.547	0 / 0	0.808	forests
<i>Epilobium</i> <i>palustre</i>	0.634	0 / 1	0.726	0 / 0	0.667	1 / 0	0.857	grasslands
<i>Epilobium</i> <i>parviflorum</i>	0.553	0 / 2	0.544	0 / 1	NA	1 / 2	0.763	
<i>Epipactis</i> <i>atrorubens</i>	0.72	0 / 0	0.788	0 / 0	0.689	0 / 0	0.84	
<i>Epipactis</i> <i>helleborine</i> s. lat.	0.648	0 / 0	0.674	0 / 0	0.617	0 / 0	0.826	forests
<i>Epipactis palustris</i>	0.755	0 / 0	0.789	0 / 0	0.793	0 / 0	0.862	grasslands
<i>Equisetum</i> <i>arvense</i>	0.612	0 / 0	0.608	0 / 0	0.577	0 / 0	0.785	
<i>Equisetum</i> <i>fluviatile</i>	0.693	0 / 0	0.78	0 / 0	0.81	0 / 0	0.875	grasslands
<i>Equisetum</i> <i>palustre</i>	0.771	0 / 0	0.762	0 / 0	0.741	0 / 0	0.812	grasslands
<i>Equisetum</i> <i>sylvaticum</i>	0.645	0 / 0	0.676	0 / 0	0.667	0 / 0	0.851	
<i>Equisetum</i> <i>telmateia</i>	0.752	0 / 0	0.674	0 / 0	0.675	0 / 0	0.854	
<i>Erica carnea</i>	0.681	0 / 0	0.672	0 / 0	0.658	0 / 0	0.856	
<i>Erigeron annuus</i>	0.827	0 / 0	0.754	0 / 0	0.601	0 / 0	0.877	
<i>Erigeron</i> <i>canadensis</i>	0.835	0 / 0	0.772	0 / 0	0.736	0 / 0	0.912	agriculture
<i>Eriophorum</i> <i>angustifolium</i>	0.761	0 / 0	0.835	0 / 0	0.831	0 / 0	0.841	grasslands
<i>Eriophorum</i> <i>latifolium</i>	0.833	0 / 0	0.825	0 / 0	0.814	0 / 0	0.875	grasslands
<i>Eriophorum</i> <i>vaginatum</i>	0.809	0 / 0	0.852	0 / 0	0.839	0 / 0	0.873	grasslands
<i>Erodium</i> <i>cicutarium</i> s. str.	0.844	0 / 0	0.748	0 / 0	0.73	0 / 0	0.938	agriculture
<i>Eryngium</i> <i>campestre</i>	0.904	0 / 0	0.87	0 / 0	0.789	0 / 0	0.957	
<i>Euonymus</i> <i>europaeus</i>	0.767	0 / 0	0.663	0 / 0	0.689	0 / 0	0.839	
<i>Euonymus</i> <i>latifolius</i>	0.664	0 / 0	0.744	0 / 0	0.592	2 / 0	0.887	forests
<i>Eupatorium</i> <i>cannabinum</i>	0.675	0 / 0	0.656	0 / 0	0.674	0 / 0	0.782	forests
<i>Euphorbia</i> <i>amygdaloides</i>	0.71	0 / 0	0.702	0 / 0	0.662	0 / 0	0.834	forests
<i>Euphorbia</i> <i>austriaca</i>	0.694	0 / 0	0.713	0 / 0	0.546	0 / 1	0.895	
<i>Euphorbia</i> <i>cyparissias</i>	0.636	0 / 0	0.62	0 / 0	0.566	0 / 0	0.846	
<i>Euphorbia dulcis</i>	0.669	0 / 0	0.785	0 / 0	0.605	0 / 0	0.842	forests
<i>Euphorbia esula</i> s. str.	0.675	0 / 0	0.622	0 / 0	0.562	0 / 0	0.874	
<i>Euphorbia</i> <i>helioscopia</i>	0.895	0 / 0	0.825	0 / 0	0.635	0 / 0	0.922	agriculture
<i>Euphorbia</i> <i>verrucosa</i>	0.588	0 / 1	0.586	0 / 0	0.516	0 / 0	0.878	grasslands
<i>Euphrasia minima</i> agg.	0.875	0 / 0	0.862	0 / 0	0.863	0 / 0	0.93	alpine
<i>Euphrasia</i> <i>officinalis</i> agg.	0.666	0 / 0	0.69	0 / 0	0.647	0 / 0	0.776	
<i>Euphrasia</i> <i>salisburgensis</i> s. str.	0.824	0 / 0	0.848	0 / 0	0.799	0 / 0	0.904	alpine
<i>Fagus sylvatica</i>	0.841	0 / 0	0.834	0 / 0	0.828	0 / 0	0.866	forests
<i>Falcaria vulgaris</i>	0.897	0 / 0	0.858	0 / 0	0.852	0 / 0	0.939	
<i>Fallopia</i> <i>convolvulus</i>	0.9	0 / 0	0.89	0 / 0	0.837	0 / 0	0.92	agriculture

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
Fallopia dumetorum	0.862	0 / 0	0.925	0 / 0	0.87	0 / 0	0.989	forests
Festuca amethystina	0.758	0 / 0	0.814	0 / 0	0.666	0 / 0	0.935	
Festuca arundinacea	0.792	0 / 0	0.72	0 / 0	0.643	0 / 0	0.919	
Festuca gigantea	0.621	0 / 0	0.676	0 / 0	0.691	0 / 0	0.809	forests
Festuca heterophylla	0.788	0 / 0	0.908	0 / 0	0.886	0 / 0	0.966	forests
Festuca norica	0.906	0 / 0	0.909	0 / 0	0.894	0 / 0	0.98	alpine
Festuca picturata	0.913	0 / 0	0.911	0 / 0	0.776	0 / 0	0.978	alpine
Festuca pratensis s. str.	0.858	0 / 0	0.801	0 / 0	0.787	0 / 0	0.856	grasslands
Festuca pseudodura	0.98	0 / 0	0.945	0 / 0	0.939	0 / 0	0.983	alpine
Festuca pumila	0.909	0 / 0	0.907	1 / 0	0.903	0 / 0	0.941	alpine
Festuca rubra agg.	0.673	0 / 0	0.64	0 / 0	0.662	0 / 0	0.792	
Festuca rupicaprina	0.888	0 / 0	0.876	0 / 0	0.767	0 / 0	0.935	alpine
Festuca rupicola	0.828	0 / 0	0.845	0 / 0	0.794	0 / 0	0.918	grasslands
Festuca versicolor	0.894	0 / 0	0.88	0 / 0	0.853	0 / 0	0.94	alpine
Ficaria verna agg.	0.649	0 / 0	0.656	0 / 0	0.601	0 / 0	0.864	
Filipendula ulmaria	0.769	0 / 0	0.682	0 / 0	0.664	0 / 0	0.822	
Filipendula vulgaris	0.87	0 / 0	0.878	0 / 0	0.86	0 / 0	0.939	grasslands
Fragaria moschata	0.602	0 / 1	0.556	0 / 0	0.563	1 / 0	0.864	
Fragaria vesca	0.664	0 / 0	0.627	0 / 0	0.638	0 / 0	0.801	
Fragaria viridis	0.771	0 / 0	0.792	0 / 0	0.712	0 / 0	0.899	
Frangula alnus	0.609	0 / 0	0.619	1 / 0	0.575	0 / 0	0.773	
Fraxinus excelsior	0.763	0 / 0	0.733	0 / 0	0.739	0 / 0	0.81	forests
Galeobdolon flavidum	0.555	0 / 0	0.759	0 / 0	0.694	1 / 0	0.882	
Galeobdolon montanum	0.717	0 / 0	0.706	0 / 0	0.691	0 / 0	0.854	forests
Galeopsis pubescens	0.759	0 / 0	0.724	0 / 0	0.66	0 / 0	0.895	forests
Galeopsis speciosa	0.602	0 / 0	0.626	0 / 0	0.631	0 / 0	0.791	forests
Galeopsis tetrahit	0.646	0 / 0	0.619	0 / 0	0.656	0 / 1	0.877	
Galium anisophyllum	0.798	0 / 0	0.781	0 / 0	0.81	0 / 0	0.861	alpine
Galium aparine s. str.	0.858	0 / 0	0.852	0 / 0	0.849	0 / 0	0.872	
Galium boreale s. str.	0.791	0 / 0	0.804	0 / 0	0.754	0 / 0	0.879	grasslands
Galium elongatum	0.971	0 / 0	0.973	0 / 0	0.973	0 / 0	0.993	grasslands
Galium lucidum s. str.	0.638	0 / 0	0.683	0 / 0	0.616	0 / 0	0.878	
Galium mollugo agg.	0.647	0 / 0	0.613	0 / 0	0.626	0 / 0	0.775	
Galium noricum	0.841	0 / 0	0.883	0 / 0	0.853	0 / 0	0.931	alpine
Galium odoratum	0.749	0 / 0	0.763	0 / 0	0.759	0 / 0	0.848	forests
Galium palustre agg.	0.804	0 / 0	0.906	0 / 0	0.903	0 / 0	0.972	grasslands
Galium palustre s. str.	0.656	0 / 0	0.679	0 / 0	0.683	0 / 0	0.815	grasslands
Galium pumilum	0.816	0 / 0	0.823	0 / 0	0.745	0 / 0	0.933	grasslands
Galium rotundifolium	0.708	0 / 0	0.708	0 / 0	0.677	0 / 0	0.868	forests
Galium sylvaticum	0.724	0 / 0	0.738	0 / 0	0.73	0 / 0	0.853	forests
Galium uliginosum	0.645	0 / 0	0.739	0 / 0	0.742	0 / 0	0.814	grasslands
Galium verum s. str.	0.825	0 / 0	0.779	0 / 0	0.729	0 / 0	0.852	grasslands
Gentiana acaulis	0.9	0 / 0	0.942	0 / 0	0.935	0 / 0	0.972	alpine
Gentiana asclepiadea	0.63	0 / 0	0.57	0 / 0	0.58	0 / 0	0.803	

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
<i>Gentiana bavarica</i> s. str.	0.754	0 / 0	0.886	0 / 0	0.761	0 / 0	0.925	alpine
<i>Gentiana clusii</i>	0.8	0 / 0	0.859	0 / 0	0.88	0 / 0	0.904	alpine
<i>Gentiana nivalis</i>	0.718	0 / 0	0.89	0 / 0	0.813	1 / 0	0.934	alpine
<i>Gentiana orbicularis</i>	0.834	0 / 0	0.909	0 / 0	0.533	0 / 0	0.922	alpine
<i>Gentiana pannonica</i>	0.775	0 / 0	0.815	0 / 0	0.7	0 / 0	0.918	
<i>Gentiana pneumonanthe</i>	0.854	0 / 0	0.907	0 / 0	0.867	0 / 0	0.968	grasslands
<i>Gentiana pumila</i>	0.886	0 / 0	0.892	0 / 0	0.839	0 / 0	0.952	alpine
<i>Gentiana verna</i> s. str.	0.677	0 / 0	0.784	0 / 0	0.788	0 / 0	0.874	alpine
<i>Gentianella aspera</i>	0.516	0 / 1	0.644	0 / 0	0.523	0 / 1	0.858	
<i>Gentianella austriaca</i>	0.958	0 / 0	0.941	0 / 0	0.813	0 / 0	0.967	alpine
<i>Gentianella germanica</i> s. lat.	0.813	0 / 0	0.856	0 / 0	0.861	0 / 0	0.937	alpine
<i>Gentianopsis ciliata</i>	0.503	0 / 2	0.653	0 / 0	0.519	1 / 1	0.81	
<i>Geranium dissectum</i>	0.714	0 / 0	0.538	0 / 0	0.725	0 / 0	0.871	agriculture
<i>Geranium phaeum</i>	0.7	0 / 0	0.705	0 / 0	0.696	0 / 0	0.874	
<i>Geranium pusillum</i>	0.862	0 / 0	0.77	0 / 0	0.785	0 / 0	0.902	agriculture
<i>Geranium robertianum</i> s. str.	0.67	0 / 0	0.643	0 / 0	0.623	0 / 0	0.822	forests
<i>Geranium sylvaticum</i>	0.683	0 / 0	0.613	0 / 0	0.604	0 / 0	0.847	
<i>Geum montanum</i>	0.87	0 / 0	0.885	0 / 0	0.849	0 / 0	0.928	alpine
<i>Geum rivale</i>	0.579	0 / 0	0.533	0 / 0	0.503	1 / 0	0.805	
<i>Geum urbanum</i>	0.726	0 / 0	0.706	0 / 0	0.71	0 / 0	0.81	
<i>Glechoma hederacea</i>	0.72	0 / 0	0.669	0 / 0	0.653	0 / 0	0.834	
<i>Globularia cordifolia</i>	0.78	0 / 0	0.708	0 / 0	0.714	1 / 0	0.908	
<i>Globularia nudicaulis</i>	0.554	0 / 0	0.532	0 / 0	NA	1 / 2	0.858	
<i>Glyceria fluitans</i> agg.	NA	0 / 3	0.566	0 / 2	0.583	1 / 1	0.647	
<i>Gymnadenia conopsea</i> s. lat.	0.65	0 / 0	0.662	0 / 0	0.664	0 / 0	0.816	
<i>Gymnocarpium dryopteris</i>	0.716	0 / 0	0.775	0 / 0	0.744	0 / 0	0.876	forests
<i>Gymnocarpium robertianum</i>	0.745	0 / 0	0.779	0 / 0	0.763	0 / 0	0.851	forests
<i>Hedera helix</i>	0.767	0 / 0	0.767	0 / 0	0.754	0 / 0	0.841	forests
<i>Hedysarum hedysaroides</i>	0.891	0 / 0	0.898	0 / 0	0.908	0 / 0	0.941	alpine
<i>Helianthemum alpestre</i> s. str.	0.868	0 / 0	0.901	0 / 0	0.905	0 / 0	0.942	alpine
<i>Helianthemum nummularium</i> s. lat.	0.781	0 / 0	0.774	0 / 0	0.755	0 / 0	0.853	
<i>Helianthus annuus</i>	0.87	0 / 0	0.862	0 / 0	0.78	0 / 0	0.943	agriculture
<i>Helictotrichon parlatorei</i>	0.867	0 / 0	0.881	0 / 0	0.814	0 / 0	0.967	alpine
<i>Heliosperma alpestre</i>	0.85	0 / 0	0.827	0 / 0	0.823	0 / 0	0.924	alpine
<i>Heliosperma pusillum</i> s. lat.	0.748	0 / 0	0.822	0 / 0	0.755	0 / 0	0.894	alpine
<i>Helleborus niger</i>	0.755	0 / 0	0.748	0 / 0	0.749	0 / 0	0.841	forests
<i>Hepatica nobilis</i>	0.701	0 / 0	0.718	0 / 0	0.688	0 / 0	0.831	forests
<i>Heracleum austriacum</i>	0.705	0 / 0	0.711	0 / 0	0.7	0 / 0	0.869	
<i>Heracleum sphondylium</i>	0.628	0 / 0	0.554	0 / 0	0.535	0 / 0	0.78	

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Hieracium alpinum s. lat.	0.796	0 / 0	0.849	0 / 0	0.812	0 / 0	0.937	alpine
Hieracium bauhini	0.584	0 / 0	0.837	0 / 0	0.863	1 / 1	0.938	grasslands
Hieracium bifidum	0.609	0 / 0	0.577	0 / 0	0.572	0 / 1	0.834	
Hieracium lachenalii	0.543	0 / 1	0.593	0 / 0	0.6	0 / 1	0.858	
Hieracium lactucella	0.529	0 / 2	0.688	0 / 0	0.632	1 / 1	0.854	grasslands
Hieracium murorum	0.632	0 / 0	0.616	0 / 0	0.606	0 / 0	0.786	forests
Hieracium pilosella	0.79	0 / 0	0.791	0 / 0	0.774	0 / 0	0.895	
Hieracium racemosum	0.803	0 / 0	0.847	0 / 0	0.811	0 / 0	0.974	forests
Hieracium villosum	0.806	0 / 0	0.861	0 / 0	0.851	0 / 0	0.942	alpine
Hippocrepis comosa	0.835	0 / 0	0.805	0 / 0	0.781	0 / 0	0.909	
Hippocrepis emerus	0.582	0 / 0	0.704	0 / 0	0.606	0 / 0	0.883	forests
Holcus lanatus	0.803	0 / 0	0.783	0 / 0	0.733	0 / 0	0.853	grasslands
Holcus mollis	0.61	0 / 0	0.613	0 / 0	0.56	2 / 0	0.891	
Holosteum umbellatum	0.827	0 / 0	0.794	0 / 0	0.632	0 / 0	0.955	
Homalotrichon pubescens	0.849	0 / 0	0.829	0 / 0	0.819	0 / 0	0.888	grasslands
Homogyne alpina	0.64	0 / 0	0.686	0 / 0	0.687	0 / 0	0.804	
Homogyne discolor	0.88	0 / 0	0.885	0 / 0	0.838	0 / 0	0.919	alpine
Hordelymus europaeus	0.712	0 / 0	0.711	0 / 0	0.754	0 / 0	0.886	forests
Hornungia alpina s. lat.	0.889	0 / 0	0.937	0 / 0	0.941	0 / 0	0.956	alpine
Humulus lupulus	0.772	0 / 0	0.76	0 / 0	0.71	0 / 0	0.878	
Huperzia selago	0.599	0 / 0	0.617	0 / 0	0.659	1 / 0	0.844	
Hylotelephium telephium agg.	0.595	0 / 1	0.542	0 / 0	NA	1 / 2	0.865	
Hypericum hirsutum	0.555	0 / 0	0.635	0 / 0	0.559	0 / 0	0.813	forests
Hypericum maculatum s. str.	0.672	0 / 0	0.642	0 / 0	0.675	0 / 0	0.801	
Hypericum perforatum	0.51	0 / 1	0.5	0 / 1	NA	0 / 3	0.883	
Hypericum tetrapterum	NA	0 / 3	0.519	0 / 1	NA	0 / 3	0.713	
Hypochaeris radicata	0.801	0 / 0	0.773	0 / 0	0.782	0 / 0	0.912	grasslands
Hypochaeris uniflora	0.968	0 / 0	0.966	0 / 0	0.952	0 / 0	0.995	alpine
Impatiens glandulifera	0.796	0 / 0	0.757	0 / 0	0.638	1 / 0	0.936	forests
Impatiens noli-tangere	0.669	0 / 0	0.666	0 / 0	0.662	1 / 0	0.807	forests
Impatiens parviflora	0.652	0 / 0	0.642	0 / 0	0.624	0 / 0	0.829	
Inula britannica	0.832	0 / 0	0.932	0 / 0	0.916	0 / 0	0.981	grasslands
Inula conyzae	NA	0 / 3	0.566	0 / 1	0.581	0 / 2	0.797	
Inula salicina	0.769	0 / 0	0.767	0 / 0	0.769	0 / 0	0.901	grasslands
Iris pseudacorus	0.877	0 / 0	0.916	0 / 0	0.882	0 / 0	0.945	
Juglans regia	0.675	0 / 0	0.589	0 / 0	0.53	0 / 0	0.848	
Juncus alpinoarticulatus	0.846	0 / 0	0.873	0 / 0	0.861	0 / 0	0.893	grasslands
Juncus articulatus	0.612	0 / 0	0.714	0 / 0	0.578	0 / 0	0.82	grasslands
Juncus effusus	0.613	0 / 0	0.563	0 / 0	0.536	0 / 0	0.769	
Juncus filiformis	0.648	0 / 0	0.756	0 / 0	0.708	0 / 0	0.856	grasslands
Juncus inflexus	0.667	0 / 0	0.709	0 / 0	0.644	0 / 0	0.839	grasslands
Juncus jacquinii	0.858	0 / 0	0.929	0 / 0	0.932	0 / 0	0.959	alpine
Juncus monanthos	0.778	0 / 0	0.833	0 / 0	0.861	0 / 0	0.919	alpine
Juncus trifidus	0.948	0 / 0	0.925	0 / 0	0.908	0 / 0	0.967	alpine

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
Juniperus communis	NA	0 / 3	NA	0 / 3	NA	0 / 3	NA	
Kernera saxatilis	0.574	0 / 0	0.703	0 / 0	0.567	1 / 0	0.886	
Knautia arvensis s. str.	0.811	0 / 0	0.725	0 / 0	0.753	1 / 0	0.861	grasslands
Knautia drymeia s. lat.	0.822	0 / 0	0.87	0 / 0	0.83	0 / 0	0.934	
Knautia maxima	0.641	0 / 0	0.615	0 / 0	0.615	0 / 0	0.799	
Koeleria macrantha	0.991	0 / 0	0.994	0 / 0	0.993	0 / 0	0.994	grasslands
Koeleria pyramidata	0.786	0 / 0	0.843	0 / 0	0.827	0 / 0	0.928	grasslands
Lactuca muralis	0.703	0 / 0	0.721	0 / 0	0.701	0 / 0	0.832	forests
Lactuca serriola	0.848	0 / 0	0.812	0 / 0	0.762	0 / 0	0.927	agriculture
Lamium amplexicaule	0.961	0 / 0	0.876	0 / 0	0.868	0 / 0	0.953	agriculture
Lamium maculatum	0.699	0 / 0	0.653	0 / 0	0.635	0 / 0	0.809	
Lamium purpureum	0.814	0 / 0	0.744	0 / 0	0.768	0 / 0	0.891	agriculture
Lapsana communis	0.755	0 / 0	0.823	0 / 0	0.601	0 / 0	0.875	
Larix decidua	0.753	0 / 0	0.742	0 / 0	0.745	0 / 0	0.824	forests
Laserpitium latifolium	0.646	0 / 0	0.703	0 / 0	0.649	0 / 0	0.82	
Lathyrus pratensis	0.736	0 / 0	0.67	0 / 0	0.677	0 / 0	0.79	grasslands
Lathyrus tuberosus	0.884	0 / 0	0.914	0 / 0	0.809	1 / 0	0.954	agriculture
Lathyrus vernus	0.799	0 / 0	0.906	0 / 0	0.912	0 / 0	0.972	forests
Leontodon hispidus	0.671	0 / 0	0.632	0 / 0	0.603	0 / 0	0.767	
Leontodon incanus	0.581	0 / 1	0.675	0 / 0	0.584	0 / 0	0.833	
Lepidium draba	0.957	0 / 0	0.849	0 / 0	0.505	0 / 0	0.959	agriculture
Leucanthemopsis alpina	0.836	0 / 0	0.966	0 / 0	0.932	0 / 0	0.981	alpine
Leucanthemum atratum s. str.	0.88	0 / 0	0.871	0 / 0	0.815	0 / 0	0.92	alpine
Leucanthemum irtutianum	0.809	0 / 0	0.766	0 / 0	0.78	0 / 0	0.884	grasslands
Leucanthemum vulgare agg.	0.766	0 / 0	0.753	0 / 0	0.693	0 / 0	0.887	grasslands
Leucanthemum vulgare s. str.	0.845	0 / 0	0.824	0 / 0	0.785	0 / 0	0.885	grasslands
Ligustrum vulgare	0.749	0 / 0	0.727	0 / 0	0.735	0 / 0	0.836	
Lilium martagon	0.617	0 / 0	0.682	0 / 0	0.636	0 / 0	0.816	
Linaria alpina	0.895	0 / 0	0.896	0 / 0	0.813	1 / 0	0.954	alpine
Linum alpinum	0.776	0 / 0	0.798	0 / 0	0.604	0 / 0	0.925	alpine
Linum catharticum	0.66	0 / 0	0.652	0 / 0	0.646	0 / 0	0.776	grasslands
Listera ovata	0.519	0 / 0	0.523	0 / 0	0.53	0 / 1	0.792	
Loiseleuria procumbens	0.828	0 / 0	0.82	0 / 0	0.825	0 / 0	0.948	alpine
Lolium multiflorum	0.959	0 / 0	0.894	0 / 0	0.874	0 / 0	0.941	
Lolium perenne	0.83	0 / 0	0.79	0 / 0	0.771	0 / 0	0.857	
Lonicera alpigena	0.714	0 / 0	0.739	0 / 0	0.696	0 / 0	0.86	forests
Lonicera nigra	0.546	0 / 0	0.682	0 / 0	0.655	0 / 0	0.881	forests
Lonicera xylosteum	0.766	0 / 0	0.732	0 / 0	0.73	0 / 0	0.828	forests
Lotus corniculatus s. str.	0.702	0 / 0	0.617	0 / 0	0.612	0 / 0	0.772	
Lunaria rediviva	0.569	0 / 0	0.628	0 / 0	0.583	1 / 0	0.873	forests
Luzula alpinopilosa	0.886	0 / 0	0.972	0 / 0	0.91	0 / 0	0.984	alpine
Luzula campestris agg.	0.666	0 / 0	0.697	0 / 0	0.574	0 / 0	0.824	grasslands
Luzula glabrata	0.899	0 / 0	0.926	0 / 0	0.851	0 / 0	0.949	alpine
Luzula luzulina	0.647	0 / 0	0.76	0 / 0	0.632	1 / 0	0.924	
Luzula luzuloides	0.669	0 / 0	0.658	0 / 0	0.599	0 / 0	0.806	forests

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
<i>Luzula multiflora</i> s. lat.	0.695	0 / 0	0.693	0 / 0	0.641	0 / 0	0.798	
<i>Luzula pilosa</i>	0.618	0 / 0	0.61	0 / 0	0.58	0 / 0	0.827	forests
<i>Luzula spicata</i>	0.887	0 / 0	0.967	0 / 0	0.947	0 / 0	0.953	alpine
<i>Luzula sylvatica</i> s. lat.	0.688	0 / 0	0.737	0 / 0	0.756	0 / 0	0.819	
<i>Lychnis flos-cuculi</i>	0.745	0 / 0	0.707	0 / 0	0.652	0 / 0	0.802	grasslands
<i>Lycopodium annotinum</i>	0.747	0 / 0	0.807	0 / 0	0.775	0 / 0	0.877	
<i>Lycopus europaeus</i>	0.616	0 / 0	0.669	0 / 0	0.616	0 / 0	0.854	
<i>Lysimachia nemorum</i>	0.655	0 / 0	0.564	1 / 0	0.615	0 / 0	0.812	
<i>Lysimachia nummularia</i>	0.637	0 / 0	0.627	0 / 0	0.628	0 / 0	0.815	
<i>Lysimachia vulgaris</i>	0.774	0 / 0	0.728	0 / 0	0.71	0 / 0	0.858	grasslands
<i>Lythrum salicaria</i>	0.74	0 / 0	0.703	0 / 0	0.719	0 / 0	0.861	grasslands
<i>Maianthemum bifolium</i>	0.682	0 / 0	0.683	0 / 0	0.703	0 / 0	0.824	forests
<i>Malus domestica</i>	0.554	0 / 2	NA	0 / 3	NA	0 / 3	0.72	
<i>Matricaria chamomilla</i>	0.953	0 / 0	0.955	0 / 0	0.893	0 / 0	0.976	agriculture
<i>Matricaria discoidea</i>	0.812	0 / 0	0.749	0 / 0	0.728	0 / 0	0.906	
<i>Medicago falcata</i>	0.788	0 / 0	0.79	0 / 0	0.709	0 / 0	0.919	grasslands
<i>Medicago lupulina</i>	0.793	0 / 0	0.782	0 / 0	0.68	0 / 0	0.827	
<i>Medicago sativa</i> agg.	0.824	0 / 0	0.8	0 / 0	0.707	0 / 0	0.895	
<i>Melampyrum pratense</i>	NA	0 / 3	0.582	0 / 0	0.595	0 / 0	0.711	
<i>Melampyrum sylvaticum</i> s. str.	0.698	0 / 0	0.689	0 / 0	0.702	0 / 0	0.829	
<i>Melica nutans</i>	0.642	0 / 0	0.66	0 / 0	0.657	0 / 0	0.818	forests
<i>Melittis melissophyllum</i>	0.895	0 / 0	0.844	0 / 0	0.842	0 / 0	0.938	forests
<i>Mentha aquatica</i>	0.773	0 / 0	0.761	0 / 0	0.784	0 / 0	0.887	grasslands
<i>Mentha arvensis</i>	0.626	0 / 0	0.671	0 / 0	0.646	0 / 0	0.835	grasslands
<i>Mentha longifolia</i>	0.612	0 / 0	0.561	0 / 0	0.529	0 / 1	0.781	
<i>Menyanthes trifoliata</i>	0.805	0 / 0	0.844	0 / 0	0.853	0 / 0	0.873	grasslands
<i>Mercurialis annua</i>	0.968	0 / 0	0.845	0 / 0	0.773	0 / 0	0.98	agriculture
<i>Mercurialis perennis</i> s. str.	0.729	0 / 0	0.728	0 / 0	0.738	0 / 0	0.823	forests
<i>Meum athamanticum</i>	0.804	0 / 0	0.823	0 / 0	0.768	0 / 0	0.959	alpine
<i>Microthlaspi perfoliatum</i>	0.926	0 / 0	0.845	0 / 0	0.707	0 / 0	0.951	
<i>Milium effusum</i>	0.704	0 / 0	0.725	0 / 0	0.662	0 / 0	0.859	forests
<i>Minuartia austriaca</i>	0.865	0 / 0	0.873	0 / 0	0.839	1 / 0	0.972	alpine
<i>Minuartia gerardii</i>	0.798	0 / 0	0.862	0 / 0	0.839	0 / 0	0.921	alpine
<i>Minuartia sedoides</i>	0.905	0 / 0	0.902	0 / 0	0.903	0 / 0	0.949	alpine
<i>Moehringia ciliata</i>	0.829	0 / 0	0.83	0 / 0	0.818	0 / 0	0.963	alpine
<i>Moehringia muscosa</i>	0.717	0 / 0	0.784	0 / 0	0.765	1 / 0	0.873	forests
<i>Moehringia trinervia</i>	0.611	0 / 2	0.547	0 / 0	0.631	0 / 1	0.799	forests
<i>Molinia arundinacea</i>	NA	0 / 3	0.569	0 / 1	0.565	0 / 2	0.685	
<i>Molinia caerulea</i> agg.	0.547	0 / 0	0.525	0 / 1	0.506	0 / 2	0.887	
<i>Molinia caerulea</i>	0.712	0 / 0	0.661	0 / 0	0.668	0 / 0	0.795	grasslands
<i>Mutellina adonidifolia</i>	0.853	0 / 0	0.868	0 / 0	0.853	0 / 0	0.921	alpine
<i>Myosotis alpestris</i>	0.849	0 / 0	0.873	0 / 0	0.866	0 / 0	0.909	alpine
<i>Myosotis arvensis</i>	0.784	0 / 0	0.763	0 / 0	0.742	0 / 0	0.869	agriculture
<i>Myosotis palustris</i> agg.	0.587	0 / 0	0.501	0 / 0	0.563	0 / 2	0.791	

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
<i>Myosotis sylvatica</i> s. str.	0.677	0 / 0	0.625	0 / 0	0.585	0 / 0	0.832	
<i>Narcissus radiiflorus</i>	0.795	0 / 0	0.811	0 / 0	0.722	0 / 0	0.941	grasslands
<i>Nardus stricta</i>	0.642	0 / 0	0.626	0 / 0	0.634	0 / 0	0.772	
<i>Neottia nidus-avis</i>	0.674	0 / 0	0.781	0 / 0	0.769	0 / 0	0.855	forests
<i>Nigritella nigra</i> agg.	0.695	0 / 0	0.834	0 / 0	0.73	0 / 0	0.928	alpine
<i>Noccaea crantzii</i>	0.851	0 / 0	0.886	0 / 0	0.886	0 / 0	0.929	alpine
<i>Onobrychis viciifolia</i> agg.	0.864	0 / 0	0.79	0 / 0	0.691	0 / 0	0.943	grasslands
<i>Ononis spinosa</i>	0.696	0 / 0	0.759	0 / 0	0.671	0 / 0	0.894	grasslands
<i>Orchis mascula</i> s. lat.	0.764	0 / 0	0.72	0 / 0	0.679	0 / 0	0.86	grasslands
<i>Oreochloa disticha</i>	0.942	0 / 0	0.859	0 / 0	0.894	0 / 0	0.978	alpine
<i>Origanum vulgare</i> s. str.	0.654	0 / 0	0.591	0 / 0	0.602	0 / 0	0.789	
<i>Oxalis acetosella</i>	0.762	0 / 0	0.764	0 / 0	0.767	0 / 0	0.836	forests
<i>Oxytropis campestris</i>	0.865	0 / 0	0.921	0 / 0	0.935	0 / 0	0.967	alpine
<i>Oxytropis montana</i> agg.	0.746	0 / 0	0.7	0 / 0	0.689	0 / 0	0.936	alpine
<i>Pachypleurum mutellinoides</i>	0.907	0 / 0	0.868	0 / 0	0.87	0 / 0	0.977	alpine
<i>Papaver rhoeas</i>	0.904	0 / 0	0.908	0 / 0	0.905	0 / 0	0.934	agriculture
<i>Paris quadrifolia</i>	0.696	0 / 0	0.708	0 / 0	0.712	0 / 0	0.825	forests
<i>Parnassia palustris</i>	0.707	0 / 0	0.697	0 / 0	0.645	0 / 0	0.803	
<i>Pastinaca sativa</i>	0.774	0 / 0	0.719	0 / 0	0.669	0 / 0	0.87	
<i>Pedicularis foliosa</i>	0.935	0 / 0	0.961	0 / 0	0.919	0 / 0	0.981	alpine
<i>Pedicularis palustris</i>	0.708	0 / 0	0.851	0 / 0	0.75	1 / 0	0.899	grasslands
<i>Pedicularis rostratocapitata</i>	0.884	0 / 0	0.91	0 / 0	0.905	0 / 0	0.941	alpine
<i>Pedicularis verticillata</i>	0.817	0 / 0	0.874	0 / 0	0.868	0 / 0	0.922	alpine
<i>Persicaria amphibia</i>	0.782	0 / 0	0.764	0 / 0	0.806	0 / 0	0.962	grasslands
<i>Persicaria bistorta</i>	0.679	0 / 1	0.586	0 / 0	0.539	2 / 0	0.837	
<i>Persicaria hydropiper</i>	0.532	0 / 0	0.566	0 / 0	0.589	0 / 1	0.858	
<i>Persicaria lapathifolia</i>	0.826	0 / 0	0.786	0 / 0	0.657	0 / 0	0.942	agriculture
<i>Persicaria maculosa</i>	0.896	0 / 0	0.896	0 / 0	0.74	0 / 0	0.943	agriculture
<i>Persicaria vivipara</i>	0.876	0 / 0	0.868	0 / 0	0.86	0 / 0	0.912	alpine
<i>Petasites albus</i>	0.691	0 / 0	0.698	0 / 0	0.692	0 / 0	0.834	forests
<i>Petasites hybridus</i>	0.613	0 / 0	0.575	0 / 0	0.616	0 / 0	0.823	
<i>Petasites paradoxus</i>	0.61	0 / 0	0.743	0 / 0	0.653	0 / 0	0.849	
<i>Peucedanum oreoselinum</i>	0.719	0 / 0	0.745	0 / 0	0.614	0 / 0	0.925	
<i>Peucedanum ostruthium</i>	0.744	0 / 0	0.747	0 / 0	0.706	0 / 0	0.892	
<i>Peucedanum palustre</i>	0.725	0 / 0	0.853	0 / 0	0.842	0 / 0	0.929	grasslands
<i>Phacelia tanacetifolia</i>	0.845	0 / 0	0.858	0 / 0	0.805	0 / 0	0.914	agriculture
<i>Phalaris arundinacea</i>	0.807	0 / 0	0.81	0 / 0	0.742	0 / 0	0.897	
<i>Phegopteris connectilis</i>	0.628	0 / 0	0.776	0 / 0	0.646	1 / 0	0.875	forests
<i>Phleum alpinum</i> agg.	0.752	0 / 0	0.833	0 / 0	0.769	0 / 0	0.906	
<i>Phleum hirsutum</i>	0.737	0 / 0	0.804	0 / 0	0.699	0 / 0	0.932	alpine
<i>Phleum phleoides</i>	0.769	0 / 0	0.967	0 / 0	0.787	0 / 0	0.987	grasslands
<i>Phleum pratense</i>	0.717	0 / 0	0.611	0 / 0	0.533	0 / 1	0.844	

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
Phragmites australis	0.793	0 / 0	0.701	0 / 0	0.68	0 / 0	0.841	grasslands
Phyteuma confusum	0.858	0 / 0	0.92	0 / 0	0.68	1 / 0	0.949	alpine
Phyteuma globulariifolium	0.989	0 / 0	0.956	0 / 0	0.982	0 / 0	0.985	alpine
Phyteuma orbiculare	0.746	0 / 0	0.751	0 / 0	0.703	0 / 0	0.809	
Phyteuma spicatum	0.72	0 / 0	0.709	0 / 0	0.689	0 / 0	0.83	forests
Picea abies	0.783	0 / 0	0.761	0 / 0	0.761	0 / 0	0.85	forests
Picris hieracioides s. lat.	0.846	0 / 0	0.822	0 / 0	0.683	0 / 0	0.923	
Pimpinella major	0.545	0 / 0	0.522	0 / 0	0.541	0 / 0	0.796	
Pimpinella saxifraga agg.	0.744	0 / 0	0.673	0 / 0	0.668	0 / 0	0.844	
Pinguicula alpina	0.665	0 / 0	0.701	0 / 0	0.684	0 / 0	0.867	
Pinguicula vulgaris	0.716	0 / 0	0.791	0 / 0	0.804	2 / 0	0.867	grasslands
Pinus mugo s. str.	0.653	0 / 0	0.749	0 / 0	0.704	0 / 0	0.812	
Pinus sylvestris	0.608	0 / 0	0.642	0 / 0	0.594	0 / 0	0.789	forests
Pisum sativum	0.867	0 / 0	0.849	0 / 0	0.75	0 / 0	0.937	agriculture
Plantago lanceolata	0.814	0 / 0	0.757	0 / 0	0.756	0 / 0	0.841	grasslands
Plantago major s. lat.	0.709	0 / 0	0.583	0 / 0	0.561	0 / 0	0.81	
Plantago media	0.81	0 / 0	0.796	0 / 0	0.768	1 / 0	0.876	grasslands
Platanthera bifolia	NA	0 / 3	0.511	0 / 0	NA	1 / 2	0.731	
Poa alpina	0.86	0 / 0	0.863	0 / 0	0.853	0 / 0	0.898	alpine
Poa angustifolia	0.813	0 / 0	0.786	0 / 0	0.776	0 / 0	0.885	
Poa annua	0.803	0 / 0	0.768	0 / 0	0.721	0 / 0	0.875	
Poa compressa	0.836	0 / 0	0.74	0 / 0	0.607	0 / 0	0.918	
Poa minor	0.898	0 / 0	0.926	0 / 0	0.904	0 / 0	0.98	alpine
Poa nemoralis	0.732	0 / 0	0.679	0 / 0	0.659	0 / 0	0.829	forests
Poa palustris	0.692	0 / 0	0.743	0 / 0	0.69	1 / 0	0.859	
Poa pratensis agg.	0.955	0 / 0	0.949	0 / 0	0.902	0 / 0	0.971	grasslands
Poa pratensis	0.724	0 / 0	0.699	0 / 0	0.685	0 / 0	0.806	
Poa trivialis subsp. trivialis	0.707	0 / 0	0.63	0 / 0	0.641	0 / 0	0.799	
Polygala amara	0.666	0 / 0	0.62	0 / 0	0.666	1 / 0	0.878	
Polygala amarella	0.789	0 / 0	0.834	0 / 0	0.744	0 / 0	0.895	grasslands
Polygala chamaebuxus	0.644	0 / 0	0.666	0 / 0	0.674	0 / 1	0.811	
Polygala comosa	0.695	0 / 0	0.794	0 / 0	0.705	0 / 0	0.889	grasslands
Polygala vulgaris	0.783	0 / 0	0.876	0 / 0	0.845	0 / 0	0.904	grasslands
Polygonatum multiflorum	0.762	0 / 0	0.742	0 / 0	0.732	0 / 0	0.833	forests
Polygonatum odoratum	0.692	0 / 0	0.669	0 / 0	0.635	0 / 0	0.835	
Polygonatum verticillatum	0.732	0 / 0	0.757	0 / 0	0.78	0 / 0	0.846	forests
Polygonum aviculare s. lat.	0.889	0 / 0	0.844	0 / 0	0.821	0 / 0	0.909	agriculture
Polypodium vulgare s. str.	0.558	0 / 1	0.588	0 / 0	0.595	1 / 0	0.802	forests
Polystichum aculeatum s. str.	0.751	0 / 0	0.766	0 / 0	0.773	0 / 0	0.859	forests
Polystichum lonchitis	0.668	0 / 0	0.748	0 / 0	0.73	0 / 0	0.876	
Populus tremula	0.568	0 / 0	0.614	0 / 0	0.549	0 / 1	0.816	
Potentilla anserina	0.742	0 / 0	0.718	0 / 0	0.589	1 / 0	0.894	
Potentilla aurea	0.905	0 / 0	0.892	0 / 0	0.898	0 / 0	0.923	alpine
Potentilla clusiana	0.827	0 / 0	0.866	0 / 0	0.814	0 / 0	0.933	alpine
Potentilla crantzii	0.881	0 / 0	0.876	0 / 0	0.805	0 / 0	0.938	alpine
Potentilla erecta	0.69	0 / 0	0.681	0 / 0	0.668	0 / 0	0.775	grasslands
Potentilla reptans	0.825	0 / 0	0.75	0 / 0	0.739	0 / 0	0.89	grasslands
Potentilla sterilis	0.594	0 / 0	0.703	0 / 0	0.586	0 / 1	0.862	

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
Potentilla verna agg.	0.943	0 / 0	0.898	0 / 0	0.885	0 / 0	0.958	grasslands
Prenanthes purpurea	0.742	0 / 0	0.739	0 / 0	0.735	0 / 0	0.855	forests
Primula auricula	0.848	0 / 0	0.889	0 / 0	0.867	0 / 0	0.932	alpine
Primula clusiana	0.861	0 / 0	0.881	0 / 0	0.883	0 / 0	0.931	alpine
Primula elatior s. str.	0.619	0 / 0	0.627	0 / 0	0.617	0 / 0	0.795	
Primula farinosa	0.835	0 / 0	0.851	0 / 0	0.818	0 / 0	0.891	grasslands
Primula minima	0.91	0 / 0	0.933	0 / 0	0.964	0 / 0	0.972	alpine
Primula veris subsp. veris	0.794	0 / 0	0.783	0 / 0	0.773	0 / 0	0.891	grasslands
Primula vulgaris	0.929	0 / 0	0.896	0 / 0	0.848	0 / 0	0.965	forests
Prunella grandiflora	0.741	0 / 0	0.814	0 / 0	0.75	0 / 0	0.917	grasslands
Prunella vulgaris	0.65	0 / 0	0.597	0 / 0	0.568	0 / 1	0.775	grasslands
Prunus avium	0.753	0 / 0	0.713	0 / 0	0.684	0 / 0	0.825	
Prunus padus	0.754	0 / 0	0.766	0 / 0	0.683	0 / 0	0.877	
Pteridium aquilinum	0.672	0 / 0	0.71	0 / 0	0.679	0 / 0	0.82	forests
Pulmonaria kernerii	0.653	0 / 1	0.574	0 / 0	0.539	0 / 1	0.845	forests
Pulmonaria officinalis s. str.	0.664	0 / 0	0.687	0 / 0	0.689	0 / 0	0.824	forests
Pulsatilla alpina s. lat.	0.798	0 / 0	0.861	0 / 0	0.726	0 / 0	0.953	alpine
Pyrus pyraeaster	0.732	0 / 0	0.776	0 / 0	0.78	0 / 0	0.942	forests
Quercus petraea s. lat.	0.929	0 / 0	0.921	0 / 0	0.89	0 / 0	0.959	forests
Quercus robur	0.676	0 / 0	0.663	0 / 0	0.61	0 / 0	0.787	
Ranunculus aconitifolius s. str.	NA	0 / 3	0.515	0 / 0	NA	0 / 3	0.79	
Ranunculus acris s. lat.	0.72	0 / 0	0.685	0 / 0	0.629	0 / 0	0.784	grasslands
Ranunculus alpestris	0.894	0 / 0	0.903	0 / 0	0.885	0 / 0	0.928	alpine
Ranunculus auricomus agg.	0.821	0 / 0	0.797	0 / 0	0.735	1 / 0	0.926	
Ranunculus bulbosus	0.859	0 / 0	0.844	0 / 0	0.821	0 / 0	0.926	grasslands
Ranunculus hybridus	0.7	0 / 0	0.859	0 / 0	0.69	0 / 0	0.924	alpine
Ranunculus lanuginosus	0.649	0 / 0	0.698	0 / 0	0.692	0 / 0	0.835	forests
Ranunculus montanus agg.	0.86	0 / 0	0.839	0 / 0	0.83	0 / 0	0.859	alpine
Ranunculus nemorosus	0.681	0 / 0	0.619	0 / 0	0.645	0 / 0	0.793	
Ranunculus polyanthemus s. str.	0.886	0 / 0	0.76	0 / 0	0.819	0 / 0	0.969	grasslands
Ranunculus repens	0.66	0 / 0	0.626	0 / 0	0.578	0 / 0	0.809	
Reseda lutea	0.842	0 / 0	0.928	0 / 0	0.865	0 / 0	0.943	agriculture
Rhamnus cathartica	0.657	0 / 0	0.699	0 / 0	0.537	1 / 0	0.835	
Rhinanthus alectorolophus s. lat.	0.796	0 / 0	0.798	0 / 0	0.807	0 / 0	0.919	grasslands
Rhinanthus glacialis	0.764	0 / 0	0.814	0 / 0	0.761	0 / 0	0.895	
Rhinanthus minor	0.774	0 / 0	0.769	0 / 0	0.702	0 / 0	0.877	grasslands
Rhododendron hirsutum	0.748	0 / 0	0.732	0 / 0	0.741	0 / 0	0.859	
Rhodothamnus chamaecistus	0.768	0 / 0	0.828	0 / 0	0.693	0 / 0	0.902	alpine
Rhynchospora alba	0.887	0 / 0	0.912	0 / 0	0.927	0 / 0	0.951	grasslands
Robinia pseudacacia	0.76	0 / 0	0.781	0 / 0	0.764	0 / 0	0.911	

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
Rosa arvensis	0.67	0 / 0	0.714	0 / 0	0.661	0 / 0	0.853	
Rosa canina agg.	0.693	0 / 0	0.618	0 / 0	0.601	0 / 0	0.811	
Rosa pendulina	0.605	0 / 0	0.66	0 / 0	0.654	0 / 0	0.849	
Rubus caesius	0.714	0 / 0	0.664	0 / 0	0.666	0 / 0	0.815	
Rubus fruticosus agg.	0.673	0 / 0	0.645	0 / 0	0.631	0 / 0	0.787	forests
Rubus idaeus	0.63	0 / 0	0.618	0 / 0	0.612	0 / 0	0.786	forests
Rubus saxatilis	0.708	0 / 0	0.742	0 / 0	0.724	0 / 0	0.854	
Rumex acetosa	0.823	0 / 0	0.788	0 / 0	0.771	0 / 0	0.875	grasslands
Rumex alpestris	0.872	0 / 0	0.823	0 / 0	0.822	0 / 0	0.916	
Rumex crispus	0.649	0 / 0	0.706	0 / 0	0.739	0 / 0	0.867	
Rumex obtusifolius	0.765	0 / 0	0.627	0 / 0	0.554	0 / 0	0.817	
Rumex scutatus	0.744	0 / 0	0.812	0 / 0	0.78	1 / 0	0.94	alpine
Salix alba	0.701	0 / 0	0.751	0 / 0	0.736	0 / 0	0.893	forests
Salix alpina	0.831	0 / 0	0.854	0 / 0	0.79	0 / 0	0.936	alpine
Salix appendiculata s. str.	0.645	0 / 0	0.662	0 / 0	0.649	0 / 0	0.849	
Salix caprea	0.559	0 / 1	0.581	0 / 0	0.52	0 / 2	0.76	
Salix cinerea s. str.	0.579	0 / 0	0.742	0 / 0	0.578	2 / 0	0.873	
Salix eleagnos	0.639	0 / 0	0.756	0 / 0	0.712	0 / 0	0.886	
Salix fragilis s. str.	0.756	0 / 0	0.857	0 / 0	0.853	1 / 0	0.925	forests
Salix myrsinifolia	0.746	0 / 0	0.744	0 / 0	0.618	0 / 1	0.923	
Salix purpurea	0.646	0 / 0	0.648	0 / 0	0.539	0 / 0	0.841	
Salix repens	0.593	0 / 2	0.759	0 / 0	0.697	0 / 0	0.87	grasslands
Salix reticulata	0.874	0 / 0	0.886	0 / 0	0.872	0 / 0	0.937	alpine
Salix retusa s. str.	0.885	0 / 0	0.897	0 / 0	0.887	0 / 0	0.938	alpine
Salix serpyllifolia	0.919	0 / 0	0.912	0 / 0	0.915	0 / 0	0.963	alpine
Salvia glutinosa	0.744	0 / 0	0.721	0 / 0	0.7	0 / 0	0.817	forests
Salvia pratensis	0.902	0 / 0	0.849	0 / 0	0.835	0 / 0	0.936	grasslands
Salvia verticillata	0.817	0 / 0	0.831	0 / 0	0.802	0 / 0	0.91	grasslands
Sambucus ebulus	NA	0 / 3	0.545	0 / 1	NA	2 / 1	0.737	forests
Sambucus nigra	0.696	0 / 0	0.638	0 / 0	0.645	0 / 0	0.792	forests
Sambucus racemosa	0.678	0 / 0	0.701	0 / 0	0.572	1 / 0	0.849	forests
Sanguisorba minor	0.906	0 / 0	0.855	0 / 0	0.804	0 / 0	0.939	grasslands
Sanguisorba officinalis	0.842	0 / 0	0.825	0 / 0	0.785	0 / 0	0.898	grasslands
Sanicula europaea	0.714	0 / 0	0.723	0 / 0	0.715	0 / 0	0.852	forests
Saponaria pumila	0.979	0 / 0	0.983	0 / 0	0.86	0 / 0	0.991	alpine
Saxifraga aizoides	0.792	0 / 0	0.789	0 / 0	0.772	0 / 0	0.896	alpine
Saxifraga androsacea	0.889	0 / 0	0.897	0 / 0	0.786	0 / 0	0.932	alpine
Saxifraga bryoides	0.864	0 / 0	0.934	0 / 0	0.871	0 / 0	0.986	alpine
Saxifraga caesia	0.864	0 / 0	0.888	0 / 0	0.852	0 / 0	0.936	alpine
Saxifraga moschata	0.851	0 / 0	0.923	0 / 0	0.883	0 / 0	0.958	alpine
Saxifraga oppositifolia s. str.	0.901	0 / 0	0.968	0 / 0	0.884	0 / 0	0.979	alpine
Saxifraga paniculata	0.813	0 / 0	0.843	0 / 0	0.81	0 / 0	0.901	alpine
Saxifraga rotundifolia	0.766	0 / 0	0.783	0 / 0	0.732	0 / 0	0.889	
Saxifraga sedoides	0.927	0 / 0	0.953	0 / 0	0.94	0 / 0	0.979	alpine
Saxifraga stellaris	0.785	0 / 0	0.825	0 / 0	0.797	0 / 0	0.91	alpine
Scabiosa columbaria s. str.	0.749	0 / 0	0.762	0 / 0	0.703	0 / 0	0.906	grasslands
Scabiosa lucida	0.777	0 / 0	0.798	0 / 0	0.751	0 / 0	0.859	
Scabiosa ochroleuca	0.848	0 / 0	0.841	0 / 0	0.824	0 / 0	0.957	grasslands
Scheuchzeria palustris	0.748	0 / 0	0.862	0 / 0	0.829	0 / 0	0.925	grasslands

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
Schoenus ferrugineus	0.915	0 / 0	0.903	0 / 0	0.895	0 / 0	0.941	grasslands
Scirpus sylvaticus	0.687	0 / 0	0.6	0 / 0	0.529	1 / 0	0.823	
Scorzonera humilis	0.508	0 / 0	0.704	0 / 0	0.683	0 / 0	0.87	grasslands
Scorzoneroides autumnalis	0.768	0 / 0	0.723	0 / 0	0.676	0 / 0	0.93	
Scorzoneroides helvetica	0.918	0 / 0	0.881	0 / 0	0.883	0 / 0	0.946	alpine
Scrophularia nodosa	0.586	0 / 0	0.575	0 / 0	0.531	0 / 0	0.804	
Securigera varia	0.804	0 / 0	0.829	0 / 0	0.754	0 / 0	0.925	
Sedum album	0.69	0 / 0	0.618	0 / 0	0.6	0 / 1	0.895	
Sedum atratum	0.776	0 / 0	0.832	0 / 0	0.795	0 / 0	0.913	alpine
Sedum sexangulare	0.798	0 / 0	0.826	0 / 0	0.7	0 / 0	0.929	grasslands
Selaginella selaginoides	0.842	0 / 0	0.823	0 / 0	0.802	0 / 0	0.875	alpine
Selinum carvifolia	0.772	0 / 0	0.82	0 / 0	0.776	0 / 0	0.932	grasslands
Senecio abrotanifolius	0.748	0 / 0	0.718	0 / 0	0.688	1 / 0	0.897	
Senecio incanus subsp. carniolicus	0.939	0 / 0	0.95	0 / 0	0.948	0 / 0	0.982	alpine
Senecio jacobaea	0.807	0 / 0	0.869	0 / 0	0.867	0 / 0	0.946	grasslands
Senecio nemorensis agg.	0.726	0 / 0	0.697	0 / 0	0.699	0 / 0	0.81	forests
Senecio subalpinus	0.818	0 / 0	0.81	0 / 0	0.701	0 / 0	0.92	
Senecio vulgaris	0.545	0 / 0	0.611	0 / 0	0.533	0 / 0	0.895	
Serratula tinctoria	0.918	0 / 0	0.912	0 / 0	0.906	0 / 0	0.959	grasslands
Sesleria caerulea s. str.	0.677	0 / 0	0.64	0 / 0	0.636	0 / 0	0.808	
Sesleria ovata	0.941	0 / 0	0.917	0 / 0	0.902	0 / 0	0.969	alpine
Setaria pumila	0.858	0 / 0	0.89	0 / 0	0.801	0 / 0	0.964	agriculture
Silene acaulis s. lat.	0.921	0 / 0	0.923	0 / 0	0.912	0 / 0	0.938	alpine
Silene dioica	0.587	0 / 0	0.548	0 / 0	0.532	0 / 1	0.818	
Silene latifolia	0.871	0 / 0	0.856	0 / 0	0.782	0 / 0	0.932	agriculture
Silene nutans s. lat	0.713	0 / 0	0.696	0 / 0	0.698	0 / 0	0.901	
Silene vulgaris	0.693	0 / 0	0.602	0 / 0	0.558	0 / 0	0.824	
Sinapis alba	0.919	0 / 0	0.883	0 / 0	0.812	0 / 0	0.963	agriculture
Sinapis arvensis	0.84	0 / 0	0.744	0 / 0	0.745	0 / 0	0.896	agriculture
Solanum dulcamara	0.614	0 / 0	0.666	0 / 0	0.685	1 / 0	0.832	
Solanum nigrum	0.828	0 / 1	0.653	0 / 0	0.599	0 / 0	0.92	agriculture
Solanum tuberosum	0.931	0 / 0	0.892	0 / 0	0.739	0 / 0	0.96	agriculture
Soldanella alpina	0.869	0 / 0	0.875	0 / 0	0.853	0 / 0	0.899	alpine
Soldanella austriaca	0.816	0 / 0	0.862	0 / 0	0.83	0 / 0	0.945	alpine
Soldanella pusilla	0.77	0 / 0	0.891	0 / 0	0.812	0 / 0	0.938	alpine
Solidago gigantea	0.742	0 / 0	0.779	0 / 0	0.744	0 / 0	0.893	
Solidago virgaurea	0.652	0 / 0	0.625	0 / 0	0.585	0 / 0	0.776	
Sonchus arvensis	0.673	0 / 0	0.77	0 / 0	0.513	0 / 0	0.942	agriculture
Sonchus asper	0.697	0 / 0	0.609	0 / 0	0.616	0 / 1	0.904	agriculture
Sonchus oleraceus	0.661	0 / 1	0.654	0 / 0	0.56	0 / 2	0.858	
Sorbus aria	0.7	0 / 0	0.689	0 / 0	0.704	0 / 0	0.81	forests
Sorbus aucuparia	0.683	0 / 0	0.704	0 / 0	0.709	0 / 0	0.82	forests
Sorbus torminalis	0.939	0 / 0	0.962	0 / 0	0.919	0 / 0	0.98	forests
Stachys alpina	0.542	0 / 2	0.513	0 / 0	NA	1 / 2	0.774	
Stachys recta subsp. recta	0.839	0 / 0	0.704	0 / 0	0.744	0 / 0	0.938	grasslands
Stachys sylvatica	0.692	0 / 0	0.705	0 / 0	0.69	0 / 0	0.787	forests
Stellaria graminea	0.74	0 / 0	0.76	0 / 0	0.706	1 / 0	0.889	grasslands
Stellaria holostea	0.904	0 / 0	0.937	0 / 0	0.93	0 / 0	0.963	forests
Stellaria media agg.	0.791	0 / 0	0.788	0 / 0	0.767	0 / 0	0.829	

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
<i>Stellaria nemorum</i> s. str.	0.703	0 / 0	0.74	0 / 0	0.722	0 / 0	0.906	forests
<i>Succisa pratensis</i>	0.811	0 / 0	0.782	0 / 0	0.782	0 / 0	0.872	grasslands
<i>Symphytotrichum</i> <i>lanceolatum</i>	0.902	0 / 0	0.953	0 / 0	0.929	0 / 0	0.979	grasslands
<i>Symphytum</i> <i>officinale</i> s. str.	0.786	0 / 0	0.75	0 / 0	0.675	0 / 0	0.871	
<i>Symphytum</i> <i>tuberosum</i> s. lat.	0.678	0 / 0	0.776	0 / 0	0.715	0 / 0	0.856	forests
<i>Tanacetum</i> <i>corymbosum</i> subsp. <i>corymbosum</i>	0.868	0 / 0	0.916	0 / 0	0.844	0 / 0	0.942	forests
<i>Taraxacum</i> sect. <i>Ruderalia</i>	0.708	0 / 0	0.678	0 / 0	0.665	0 / 0	0.764	
<i>Taxus baccata</i>	0.66	0 / 0	0.785	0 / 0	0.719	0 / 0	0.857	forests
<i>Teucrium</i> <i>chamaedrys</i>	0.759	0 / 0	0.683	0 / 0	0.729	0 / 0	0.855	
<i>Teucrium</i> <i>montanum</i>	0.738	0 / 0	0.878	0 / 0	0.698	0 / 0	0.932	
<i>Thalictrum</i> <i>aquilegifolium</i>	0.613	0 / 1	0.626	0 / 0	0.502	0 / 1	0.806	
<i>Thalictrum minus</i> s. lat.	0.85	0 / 0	0.779	0 / 0	0.732	0 / 0	0.913	
<i>Thelypteris</i> <i>limbosperma</i>	0.723	0 / 0	0.696	0 / 0	0.655	0 / 0	0.851	forests
<i>Thesium alpinum</i>	0.678	0 / 0	0.741	0 / 0	0.697	0 / 0	0.85	alpine
<i>Thlaspi arvense</i>	0.851	0 / 0	0.824	0 / 0	0.77	0 / 0	0.912	agriculture
<i>Thymus praecox</i> agg.	0.786	0 / 0	0.802	0 / 0	0.78	0 / 0	0.88	alpine
<i>Thymus</i> <i>pulegioides</i>	0.716	0 / 0	0.732	0 / 0	0.712	0 / 0	0.863	grasslands
<i>Tilia cordata</i>	0.758	0 / 0	0.786	0 / 0	0.78	0 / 0	0.86	forests
<i>Tilia platyphyllos</i>	0.777	0 / 0	0.807	0 / 0	0.807	0 / 0	0.87	forests
<i>Tofieldia</i> <i>calyculata</i>	0.601	0 / 0	0.635	0 / 0	0.623	0 / 0	0.758	
<i>Tragopogon</i> <i>dubius</i>	0.952	0 / 0	0.893	0 / 0	0.931	0 / 0	0.966	
<i>Tragopogon</i> <i>orientalis</i>	0.875	0 / 0	0.82	0 / 0	0.77	0 / 0	0.881	grasslands
<i>Traunsteinera</i> <i>globosa</i>	0.698	0 / 0	0.884	0 / 0	0.647	2 / 0	0.953	
<i>Trichophorum</i> <i>alpinum</i>	0.516	0 / 0	0.83	0 / 0	0.805	0 / 0	0.886	grasslands
<i>Trichophorum</i> <i>cespitosum</i>	0.808	0 / 0	0.868	0 / 0	0.842	0 / 0	0.902	grasslands
<i>Trifolium badium</i>	0.585	0 / 0	0.743	0 / 0	0.512	0 / 0	0.857	alpine
<i>Trifolium</i> <i>campestre</i>	0.78	0 / 0	0.804	0 / 0	0.647	0 / 0	0.919	
<i>Trifolium dubium</i>	0.661	0 / 0	0.777	0 / 0	0.619	0 / 0	0.891	grasslands
<i>Trifolium</i> <i>hybridum</i>	0.675	0 / 0	0.724	0 / 0	0.6	0 / 1	0.902	
<i>Trifolium medium</i>	0.722	0 / 0	0.642	0 / 0	0.554	0 / 0	0.861	grasslands
<i>Trifolium</i> <i>montanum</i>	0.783	0 / 0	0.839	0 / 0	0.83	0 / 0	0.896	grasslands
<i>Trifolium pratense</i>	0.741	0 / 0	0.662	0 / 0	0.664	0 / 0	0.796	
<i>Trifolium repens</i>	0.797	0 / 0	0.769	0 / 0	0.731	0 / 0	0.825	
<i>Tripleurospermum</i> <i>inodorum</i>	0.904	0 / 0	0.876	0 / 0	0.866	0 / 0	0.935	agriculture
<i>Trisetum alpestre</i>	0.849	0 / 0	0.847	0 / 0	0.767	0 / 0	0.921	alpine
<i>Trisetum</i> <i>flavescens</i>	0.839	0 / 0	0.797	0 / 0	0.773	0 / 0	0.863	grasslands
<i>Trollius</i> <i>europaeus</i>	0.644	0 / 0	0.583	0 / 0	0.618	0 / 0	0.776	
<i>Tussilago farfara</i>	0.539	0 / 0	NA	0 / 3	NA	0 / 3	0.934	
<i>Ulmus glabra</i>	0.744	0 / 0	0.741	0 / 0	0.752	0 / 0	0.852	forests
<i>Ulmus minor</i>	0.83	0 / 0	0.716	0 / 0	0.719	0 / 0	0.94	forests
<i>Urtica dioica</i>	0.624	0 / 0	0.551	0 / 0	0.565	0 / 0	0.766	
<i>Vaccinium</i> <i>gaultherioides</i>	0.783	0 / 0	0.834	0 / 0	0.85	0 / 0	0.921	alpine

Species	RF: mean TSS	RF: failed / TSS < 05	GBM: mean TSS	GBM: failed / TSS < 05	ANN: mean TSS	ANN: failed / TSS < 05	Ensemble Model: TSS	Habitat group
Vaccinium myrtillus	0.552	0 / 0	0.551	0 / 0	0.549	0 / 0	0.708	
Vaccinium oxycoccus s. str.	0.818	0 / 0	0.855	0 / 0	0.813	0 / 0	0.895	grasslands
Vaccinium uliginosum s. str.	0.754	0 / 0	0.842	0 / 0	0.792	0 / 0	0.881	grasslands
Vaccinium vitis-idaea	0.631	0 / 0	0.63	0 / 0	0.632	0 / 0	0.751	
Valeriana celtica subsp. norica	0.95	0 / 0	0.952	0 / 0	0.88	0 / 0	0.977	alpine
Valeriana dioica	0.725	0 / 0	0.679	0 / 0	0.632	0 / 0	0.794	grasslands
Valeriana elongata	0.887	0 / 0	0.91	0 / 0	0.91	0 / 0	0.958	alpine
Valeriana montana	0.729	0 / 0	0.765	0 / 0	0.666	0 / 0	0.875	
Valeriana officinalis s. lat.	0.57	0 / 0	0.607	0 / 0	0.587	0 / 0	0.803	
Valeriana saxatilis	0.636	0 / 0	0.713	0 / 0	0.727	0 / 0	0.843	
Valeriana tripteris	0.713	0 / 0	0.733	0 / 0	0.7	0 / 0	0.866	forests
Valerianella locusta	0.823	0 / 0	0.8	0 / 0	0.54	0 / 1	0.964	
Veratrum album s. lat.	0.61	0 / 0	0.582	0 / 0	0.553	0 / 0	0.793	
Veronica alpina	0.859	0 / 0	0.875	0 / 0	0.814	0 / 0	0.917	alpine
Veronica aphylla	0.695	0 / 0	0.881	0 / 0	0.777	0 / 0	0.91	alpine
Veronica arvensis	0.832	0 / 0	0.783	0 / 0	0.741	0 / 0	0.876	
Veronica beccabunga	0.538	0 / 1	0.548	0 / 0	NA	1 / 1	0.814	
Veronica chamaedrys agg.	0.884	0 / 0	0.892	0 / 0	0.881	0 / 0	0.976	grasslands
Veronica chamaedrys s. str.	0.686	0 / 0	0.643	0 / 0	0.632	0 / 0	0.819	
Veronica hederifolia agg.	0.855	0 / 0	0.835	0 / 0	0.812	1 / 0	0.93	agriculture
Veronica montana	0.529	0 / 0	0.732	0 / 0	0.652	0 / 0	0.86	forests
Veronica officinalis	0.617	0 / 0	0.64	0 / 0	0.627	0 / 0	0.828	
Veronica persica	0.916	0 / 0	0.873	0 / 0	0.877	0 / 0	0.921	agriculture
Veronica polita	0.931	0 / 0	0.917	0 / 0	0.882	1 / 0	0.956	agriculture
Veronica serpyllifolia	0.726	0 / 0	0.754	0 / 0	0.709	0 / 0	0.846	
Viburnum lantana	0.666	0 / 0	0.673	0 / 0	0.663	0 / 0	0.845	forests
Viburnum opulus	0.741	0 / 0	0.75	0 / 0	0.729	0 / 0	0.829	
Vicia angustifolia	0.84	0 / 0	0.74	0 / 0	0.692	0 / 0	0.935	
Vicia cracca s. strictiss.	0.663	0 / 0	0.609	0 / 0	0.564	0 / 0	0.809	grasslands
Vicia hirsuta	0.764	0 / 0	0.672	0 / 0	0.73	0 / 0	0.897	
Vicia sepium	0.711	0 / 0	0.634	0 / 0	0.514	0 / 0	0.842	
Vicia tenuifolia	0.548	0 / 1	0.628	0 / 1	NA	1 / 1	0.851	
Vicia tetrasperma s. str.	0.663	0 / 0	0.645	0 / 0	0.636	0 / 0	0.906	
Vinca minor	0.706	0 / 0	0.685	0 / 0	0.617	0 / 0	0.89	forests
Vincetoxicum hirsutaria	0.674	0 / 0	0.689	0 / 0	0.656	0 / 0	0.845	
Viola alba	0.973	0 / 0	0.991	0 / 0	0.932	0 / 0	0.978	forests
Viola arvensis	0.924	0 / 0	0.876	0 / 0	0.874	0 / 0	0.92	agriculture
Viola biflora	0.796	0 / 0	0.763	0 / 0	0.73	0 / 0	0.861	alpine
Viola canina	0.553	0 / 0	0.61	0 / 0	0.598	1 / 0	0.888	grasslands
Viola hirta	0.753	0 / 0	0.709	0 / 0	0.662	0 / 0	0.867	
Viola mirabilis	0.716	0 / 0	0.732	0 / 0	0.747	0 / 0	0.921	forests
Viola palustris	0.755	0 / 0	0.807	0 / 0	0.797	0 / 0	0.842	grasslands
Viola reichenbachiana	0.705	0 / 0	0.701	0 / 0	0.671	0 / 0	0.826	forests
Viola riviniana	0.683	0 / 0	0.736	0 / 0	0.709	1 / 0	0.873	forests
Willemetia stipitata	0.775	0 / 0	0.791	0 / 0	0.792	0 / 0	0.846	grasslands

**Table S3.** Information on the agent-based model and its assumptions

The following table lists, for all scenarios, the assumptions underlying the ABM with regard to yields, prices, subsidies, income, working hours, workload, extreme events and the national parks' decision concerning alpine pastures.

SCENARIOS	BAU	SSP1	SSP5
<b>Yields on crop- and grassland<sup>1,2</sup></b>	15-20 % increase	15-20 % increase	20-30 % increase
<b>Agricultureural product prices</b>	index adjusted	increase for low input products and energy plants	index adjusted
<b>Agricultureural subsidies</b>	index adjusted	increase for low input products and energy plants by year 2020	strong decrease by year 2020; no subsidies any more by year 2026
<b>Variable costs</b>	index adjusted	index adjusted	moderate increase
<b>Non-agricultureural income</b>	index adjusted	medium increase	minor increase in peri-urban areas, minor decrease in rural areas
<b>Agricultureural working hours per ha or livestock</b>	constant	constant	minor decrease
<b>Maximum of accepted work load</b>	constant	lower	constant
<b>Minimum of required agricultureural income</b>	index adjusted	minor increase	strong increase
<b>Extreme events</b>	low probability of occurrence, only few sub regions <sup>3</sup> affected; moderate reduction of standard output	very low probability of occurrence, only one affected sub region <sup>3</sup> , minor reduction of standard output	high probability of occurrence, more affected sub regions <sup>3</sup> ; strong reduction of standard output
<b>National park</b>	National parks lease every vacant alpine pasture	National parks lease every vacant alpine pasture	National parks stop leasing alpine pastures

<sup>1</sup> Erb KH, Lauk C, Kastner T, Mayer A, Theurl MC, Haberl H (2016) Exploring the biophysical option space for feeding the world without deforestation. *Nature Communications*, 7.

<sup>2</sup> Mitter H, Schönhart M, Meyer I et al. (2015) Agriculture. In: *Economic Evaluation of Climate Change Impacts: Development of a Cross-Sectoral Framework and Results for Austria*. (eds Steininger K, König M, Bednar-Friedl B, Kranzl L, Loibl W, Prettenhaler F), Vienna, Springer.

<sup>3</sup> n = 27

**Table S4:** The minimum (*min*), maximum (*max*), mean values (*mean*) and the standard deviation (*sd*) of the four bioclimatic variables used as predictors in the SDMs: minimum temperature of the coldest month (*BIO6*, unit: °C), temperature annual range (*BIO7*, unit: °C), precipitation seasonality (*BIO15*, unit: percent), precipitation of the warmest quarter (*BIO18*, unit: millimetres). Values are for the study region as depicted in Fig. 1a and were calculated for a) current climate and for the three future climate scenarios considered: b) RCP2.6, c) RCP4.5 and d) for RCP8.5.

<b>a) CURRENT</b>	<i>BIO6</i>	<i>BIO7</i>	<i>BIO15</i>	<i>BIO18</i>
<i>min</i>	-12.2	23.1	17	273
<i>max</i>	-4.5	30.6	37	717
<i>mean</i>	-7.3	28.8	25.4	462.5
<i>sd</i>	1.5	1.2	4.1	73.1

<b>b) RCP2.6</b>	<i>BIO6</i>	<i>BIO7</i>	<i>BIO15</i>	<i>BIO18</i>
<i>min</i>	-10.6	23	20	258
<i>max</i>	-2	29.7	38	769
<i>mean</i>	-4.9	27.8	26.5	481.9
<i>sd</i>	1.5	1.2	3.3	85

<b>c) RCP4.5</b>	<i>BIO6</i>	<i>BIO7</i>	<i>BIO15</i>	<i>BIO18</i>
<i>min</i>	-10.3	23.6	20	263
<i>max</i>	-0.9	29.5	37	732
<i>mean</i>	-4.4	27.9	26.3	462.9
<i>sd</i>	1.7	1	3.4	74.6

<b>d) RCP8.5</b>	<i>BIO6</i>	<i>BIO7</i>	<i>BIO15</i>	<i>BIO18</i>
<i>min</i>	-7.6	21	16	271
<i>max</i>	-9	29.5	32	724
<i>mean</i>	-3.5	27.1	22.1	449.2
<i>sd</i>	1.1	1.5	3.2	71

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## Abstract in German

Klimawandel, Landnutzungswandel und der Austausch von nichtheimischen Arten bedrohen die Biodiversität in verschiedener Weise und interagieren häufig miteinander. Diese Interaktionen führen zu großen Unsicherheiten in Vorhersagen der zukünftigen Änderungen der Biodiversität. In meiner Doktorarbeit untersuche ich die potentiellen Reaktionen von Pflanzenverbreitungsmustern auf diese drei Komponenten des Globalen Wandels im 21. Jahrhundert auf unterschiedlichen räumlich-zeitlichen Ebenen mit Hilfe von Artenverbreitungsmodellen. Zuerst eruiere ich die Effekte des Klimawandels auf das Einbürgerungs- und Hybridisierungspotenzial von gebietsfremden Gartenpflanzen in Europa für die zweite Hälfte des 21. Jahrhunderts, unter Berücksichtigung aktueller Landnutzungsmuster. Anschließend untersuche ich die gemeinsamen Effekte von Klima- und Landnutzungswandel auf die zukünftige Verbreitung von Arten. Ich beginne mit einem Überblick über die Herausforderungen, die sich bei der Integration von Landnutzung in Modellen von Artenverbreitung und -vielfalt stellen. Des Weiteren erforsche ich die gemeinsamen Effekte dieser beiden Faktoren auf einen regionalen Pool von Arten in Österreich für die Mitte des 21. Jahrhunderts.

Die Ergebnisse zeigen, dass sich Hotspots des Einbürgerungsrisikos von gebietsfremden Arten unter Klimawandel deutlich vergrößern. Dadurch wird auch das Risiko negativer Auswirkungen, die durch eine Massenvermehrung dieser Arten entstehen könnten, größer. Allerdings liefern meine Modelle keinen Hinweis darauf, dass der Risiko der Hybridisierung zwischen gebietsfremden und nativen Arten steigen wird.

Für eine bessere Integration des Faktors Landnutzung in Modelle der Artenverbreitung und -vielfalt sind folgende Schritte notwendig: eine angemessene Darstellung der Komplexität von Landnutzungs-Biodiversitäts-Beziehungen sowie eine Verbesserung der Datenverfügbarkeit. Für die in Mitteleuropa (Österreich) liegende Untersuchungsregion und den berücksichtigten Zeithorizont deutet mein Artenverbreitungsmodell darauf hin, dass der Klimawandel eine große Rolle für die zukünftige Verbreitung der Arten spielen wird, während der Landnutzungswandel nur geringe Auswirkungen hat. Dennoch ist die Integration von Landnutzungsszenarien in Biodiversitätsvorhersagen wichtig, da die relativen Auswirkungen von Klimawandel und Landnutzungswandel von Region zu Region variieren können.

Zusammen genommen zeigen meine Resultate, dass die Kombination verschiedener Komponenten des Globalen Wandels Voraussetzung für realitätsnähere Vorhersagen über die zukünftige Verbreitung von Arten, und damit für effektives vorausschauendes Management von Biodiversität ist.

## Publication Record

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