PUBLIZIERBARER ENDBERICHT

A) Projektdaten

Kurztitel:	RAG-Clim
Langtitel:	Climate effects on the recent range expansion of ragweed in Central Europe
Programm:	ACRP 3rd Call
Dauer:	28 months
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Projektübersicht

1A) Executive Summary, English

Common ragweed (*Ambrosia artemisiifolia* L.; Asteraceae) is an annual weed species which is native to North America but by now widespread in several other parts of the world including Europe. Due to its highly allergenic pollen, the species imposes a serious threat to human health (Taramarcaz *et al*. 2005). During the most recent decades, invasive spread in Central Europe has gained considerable momentum. The reasons behind this acceleration are not fully clear, but it is suggested that recent climatic trends have strongly contributed to the species' accelerated regional spread. Nevertheless, the recent invasion dynamics may also be attributed to other factors, such as changes in land use patterns, new or more efficient dispersal pathways provided by human activities, or lagged population effects where the invasion may have recently reached a critical threshold for explosive spread (Hobbs 2000, Lockwood *et al*. 2005, von der Lippe & Kowarik 2007). Our project aimed to disentangle these factors, and specifically to isolate the impact of historical climate change from that of other drivers.

We first collated data on the species and its environment: Historical ragweed invasion data were collected for eight Central European countries: Austria, Czech Republic, Germany, Hungary, Liechtenstein, Slovakia, Slovenia and Switzerland up to the year 2010. Environmental data included climate and human land use patterns. We further calculated connectivity measures along road- and railway infrastructure networks which may act as long-distance dispersal routes. Data describe the spatial pattern of these environmental features and their changes over time.

The second project phase was dedicated to the development of a novel, spatio-temporal invasion modelling framework. To disentangle the impact of different factors on an invasion, they need to become analysed jointly, but presently no invasion modelling tool provides such functionality. Our framework unifies concepts of several stand-alone modelling approaches (e.g. Kot *et al*. 1996, Elith *et al*. 2006, Muirhead *et al*. 2006, Smolik *et al*. 2010) and considers how well a location is suited for the species and its growth as well as its spread rates by means of various dispersal means. Our framework further acknowledged that data records may be incomplete and hence only part of the real invasion has been observed and documented at any point of time. Using this framework, we fitted various model variants to the historical invasion from the 19th century up to 2010 and compared their results.

In Central Europe the highest invasion levels are observed for the lowland areas east of the Alps, with Eastern Austria, Hungary and Slovenia particularly invaded. However, several areas outside the core invasion region have also become heavily invaded, for example in the Rhine Valley or Bavaria. Our model-based analysis confirmed the impact of climate on the invasion: throughout all model variants climate, and in particular temperature, plays an outstanding role both with respect to the invasion risk of individual sites, as well as to the rate of population expansion after colonization. Dispersal occurs by various means, but on average local, radial spread is the most important pathway. Overall, the invasion process was a combination of initial, accidental introduction at multiple locations followed by subsequent establishment, population growth, and spread into the vicinity.

Our model indicates that species' observations capture the true invasion progress in a very incomplete manner: by 2010 the most likely model suggests that the area infested is about twice as large as the documented spread pattern. Detection rates obviously vary among countries, with Hungary and Switzerland apparently well surveyed. Detection rates are further suggested to have varied over time with a marked increase during the most recent past. However, pronounced lags between establishment and detection of the species at a particular site seem to be the rule rather than the exception.

We conclude that the Common ragweed invasion is driven by many components, but that climate is of outstanding importance. Recent climate warming has already contributed to an accelerated invasion, and with temperatures on the rise the species' spread will gain further momentum. By the end of this century about one half of the study region may be climatically favorable to the species. For upcoming decades, we hence need both well-designed surveying schemes and effective management strategies.

1A) Executive Summary, Deutsch

Die Beifußambrosie (Ambrosia artemisiifolia L.; Asteraceae) ist ein ursprünglich aus Nordamerika stammendes, annuelles Unkraut. Verschleppt durch den Menschen tritt sie mittlerweile jedoch in vielen Teilen der Welt auf, auch in Mitteleuropa. Die Art produziert einen hochallergenen Pollen und verursacht dadurch erhebliche Folgekosten (Taramarcaz *et al*. 2005). In den letzten Jahrzehnten hat sich ihre mitteleuropäische Ausbreitungsdynamik erheblich beschleunigt. Die Gründe dafür sind nicht vollständig geklärt, doch da die Art wärmeliebend ist wird vermutet, dass der klimatische Trend seit den späten 80er Jahren dafür verantwortlich ist. Alternativ könnten allerdings auch i) veränderte Landnutzungsmuster; ii) neue bzw. effizientere Verbreitungswege der Samen bedingt durch menschliche Aktivitäten; oder iii) zeitverzögerte Populationseffekte, welche exponentielle Populationsexplosionen verursachen können (Hobbs 2000, Lockwood *et al*. 2005, von der Lippe & Kowarik 2007), für die rezente Ausbreitung von Ragweed verantwortlich sein. In unserem Projekt untersuchen wir diese Faktoren auf ihren jeweiligen Einfluss, und insbesondere versuchen wir, die Bedeutung des historischen Klimawandels relativ zu dem anderer Faktoren zu bewerten.

Wir sammelten historische wie rezente Verbreitungsdaten der Beifußambrosie für Österreich und die Nachbarländer Schweiz, Liechtenstein, Deutschland, die Tschechische Republik, Slowakei, Ungarn und Slowenien. Die Datenserie reicht zurück bis zum Invasionsbeginn im 19. Jahrhundert. Weiters erfassten die räumliche Verteilung und zeitliche Veränderung von Umweltbedingungen wie Temperatur und Niederschlag sowie menschliche Landnutzungsmuster. Wir errechneten außerdem ein Konnektivitätsmaß zwischen den Lokalitäten des Untersuchungsraums (gegliedert in regelmäßige Rasterzellen zu ca. 36 km^2), basierend auf Straßen- und Eisenbahnrouten, um mögliche selektive Ausbreitungswege der Ambrosie entlang dieser Netzwerke zu berücksichtigen.

In der zweiten Projektphase entwickelten wir neue Modellierungs- und Simulations-Software, um die räumlich-zeitliche Dynamik von biologischen Invasionen unter Berücksichtigung von multiplen Einflussfaktoren abzubilden und zu analysieren. Diese Eigenentwicklung war notwendig, da etablierte Modellierungsansätze (z.B. Kot *et al*. 1996, Elith *et al*. 2006, Muirhead *et al*. 2006, Smolik *et al*. 2010) nur ausgewählte Ausbreitungsfaktoren berücksichtigen, aber nicht ihr Zusammenspiel. Unser Modell untersucht unter anderem, wie sehr lokale Umweltbedingungen, Wachstums- und Ausbreitungsraten, sowie verschiedene Samenverbreitungswege die Invasion prägten. Wir berücksichtigen weiters, dass unser Wissen über die Artverbreitung unvollständig sein kann, d.h. die Ambrosie in Wirklichkeit noch weiter verbreitet sein könnte als die bekannte Funde dokumentieren. Wir nutzen unser Modell um durch die Analyse der Invasionsgeschichte verschiedene Hypothesen über die für die Verbreitung der Ambrosie entscheidenden Faktoren zu testen.

In Mitteleuropa sind die Tieflagen östlich der Alpen aktuell am dichtesten von der Ambrosia besiedelt, v.a. das östliche und nord-östliche Österreich, Ungarn, und Slowenien. Bedeutsame Vorkommen existieren jedoch auch außerhalb dieser Kernregion, etwa in föhngeprägten Alpentälern oder in lokalen klimatischen hot-spots in Deutschland, etwa in Rheinnähe.

Unsere Modellierungen haben den determinierenden Einfluss von Klima bestätigt: in allen von uns angepassten Modellvarianten leistete Klima, und insbesondere Temperatur, einen erheblichen Erklärungsbeitrag zum Invasionsmuster. Sowohl die Chancen einer erfolgreichen Besiedelung einer Region wie auch das anschließend zu erwartende Wachstum der Population und ihre lokale Ausbreitung werden durch die Temperaturverhältnisse entscheidend beeinflusst. Räumliche Ausbreitung kann über verschiedene Wege erfolgen, jedoch ist innerhalb unseres Arbeitsgebietes eine diffusionsartige radiale Expansion am bedeutsamsten. Straßen- und Eisenbahnnetzwerke sind somit als bevorzugte Migrationskorridore in Mitteleuropa von untergeordneter Bedeutung.

Unsere Modellierung suggeriert, dass die verfügbaren Beobachtungen der Art ihre tatsächliche Verbreitung nur lückenhaft widerspiegeln: im Jahr 2010 könnte die Ambrosie schon ein Fläche besiedeln, die annähernd doppelt so groß ist wie durch Beobachtungsdaten dokumentiert. Die meisten noch nicht entdeckten Populationen werden dabei in den klimatisch günstigsten Regionen vermutet, jedoch ergibt sich im Detail ein differenzierteres Bild. Die Verbreitung der Art dürfte in Ungarn und in der Schweiz relativ vollständig bekannt sein. In den anderen Ländern hingegen unterstellt unsere Modellierung eine relativ schlechte Dokumentation des tatsächlichen Verbreitungsmusters. In den letzten Jahren ist die Beobachtungsdichte gestiegen, aber erhebliche Verzögerungen zwischen neu etablierten Populationen und deren Entdeckung scheinen immer noch generell die Regel zu sein.

Unsere Ergebnisse lassen darauf schließen dass die Invasion der Beifußambrosie von verschiedenen Faktoren ko-determiniert wird, aber das Klima dabei die wichtigste Rolle spielt. Vergangene Klimaerwärmung hat die Invasion der Ambrosie bereits begünstigt, und die vorhergesagte Klimaerwärmung wird sie vermutlich weiter beschleunigen. Unter aktuellen Temperaturanstiegsprognosen wird zum Ende des Jahrhunderts circa die Hälfte des mitteleuropäischen Studiengebiets ein Klima zeigen, dass für die Art ideal ist. Um ökonomischen Auswirkungen der Ambrosieninvasion zu reduzieren brauchen wir in Zukunft verbesserte Monitoringkonzepte und effizientere Bekämpfungsmaßnahmen.

2 Hintergrund und Zielsetzung

Biological invasions are an essential component of global change (e.g. Sala *et al*. 2000). With the rise of global trade and transport, species become both deliberately and accidentally introduced to regions where they have not occurred previously. Although many of these species will neither reach a wide distribution in their novel range, nor have pronounced impacts, some cause considerable problems. Invasive species may impose threats to native biodiversity (e.g. Vilà *et al*. 2011), human health (Taramarcaz *et al*. 2005), or cause economic damage (e.g. Pimentel *et al*. 2005). Scientifically, however, they are of particular interest, as they allow for real-time investigations of spatio-temporal ecological processes driven by a multitude of determinants, including species traits, the environment, and human behaviour.

In Central Europe an invasion of high concern is the spread of Common ragweed (*Ambrosia artemisiifolia* L.; Asteraceae). Native to central North America (FNA 2006), this annual, wind-pollinated herb was first accidentally introduced to Europe in the 19th century (the first record dates from Germany in 1841) (Chauvel *et al*. 2006, Brandes & Nitzsche 2007, Essl *et al*. 2009), but spread and subsequent naturalization only started in the first decades of the 20th century. Range expansion gained momentum after World War II, and particularly during the last two decades. Occurrences are concentrated in warmer lowland areas and the species is primarily found in segetal and ruderal habitats shaped by humans. Medium and long-distance dispersal is primarily dependent on human activities, e.g. as seed contaminant, with soil or by agricultural machinery, or along roads (Buttenschøn *et al*. 2009, von der Lippe & Kowarik 2007).

Common ragweed is of high public health concern as it produces the most allergenic pollen of any plant species occurring in Europe (Jäger 2000, Taramarcaz *et al*. 2005, Wopfner *et al*. 2005). Moreover, the species expands the allergy season considerably because it starts flowering only in (late) summer. Jäger (2006) estimated the annual allergy costs of ragweed in Austria to 90 million € in 2005. Since then the species has expanded its range considerably.

Climate is a key driver behind ragweed's current spatial distribution (Dullinger *et al*. 2009, Essl *et al*. 2009), and the recent invasion's rapid expansion correlates well with records of climate warming. However, biological invasions are inherently complex processes and thus alternative explanations are also plausible: altered human land use patterns, traffic and trade increase and thus more efficient dispersal pathways, lagged population effects, and, finally, an over-proportional increase in records due to higher attention paid to the species may have equally, or additionally, shaped the (observed) invasion pattern.

A thorough analysis of the interplay between these possible invasion drivers requires that all are considered in combination. Presently however, no tool is capable for conducting such an integrative analysis: established models may relate species occurrences to prevailing environmental conditions, describe spread as function of local growth, propagule production and dispersal in a homogeneous environment, or investigate spread along selective corridors. Each of these modelling approaches has its particular strengths, but they largely ignore aspects central to the other approaches; yet for the Common ragweed invasion each of them may be essential. Moreover it is unclear in how far our perception of the invasion is co-determined by imperfect detection: at a large spatial scale species detections are mostly accidental, and it is unknown how many established populations are actually still undetected. Surveying schemes vary further over space and time and thus may themselves induce distinct data patterns. An integrative analysis of biological invasions must hence acknowledge on the one hand that the invasion may be driven by a multitude of ecological processes, while concurrently our perception of the invasion process is incomplete and blurred.

In our project we aim to disentangle the network of ragweed invasion drivers and human observation issues to identify the key factors behind the invasion pattern.

As a first working step, the invasion history of ragweed shall be reconstructed from first observations of the species in the early 19^{th} century up to the present day (2010). Secondly, a novel invasion modelling framework shall be developed that accommodates the need to investigate Common ragweed spread from an integrative perspective. It thus unifies aspects of established modelling approaches. Third, the potentially imperfect observation of the invasion shall be explicitly acknowledged. The framework will be extended in a manner that assumes that our data stem from an incomplete observation process, with species detections lagged or yet outstanding and thus indicate areas as yet uncolonized by Common ragweed although possibly already invaded. Moreover, the extension shall allow for inferences on the detection process *per se* as well as on the likely realized invasion state. Finally, as a fourth objective, all pieces will be put together to analyse the dynamics of the common ragweed invasion. Thereby we specifically, we ask the following research questions: i) Which invasion drivers have co-determined the invasion and how do their effects relate to each other? ii) What is the role of climate with respect to establishment rates of uninvaded sites, and to growth and propagule production rates at invaded locations? iii) How does the effect of climate change compare to changes in human land use patterns over time? iv) Is the observation of the invasion process likely to be incomplete, and if yes, what is the most likely invasion state reached by now?

3 Projektinhalt und Ergebnis(se)

Our project bridges macro-ecology with quantitative analyses. It thus covers collection of species and environmental data, the calculation of explanatory variables, development of a new analytical approach and its application, and conclusions drawn from a number of results.

Work package 1: species data

In the first work package (WP 1) we collated historical data on the Common ragweed (Fig. 1) invasion for eight Central European countries: Austria, Czech Republic, Germany, Hungary, Liechtenstein, Slovakia, Slovenia and Switzerland. Data were collected by querying existing databases, herbaria records and local experts. Records were associated with a geo-referenced coordinate and a recording date. A total of 12,017 entries were obtained (Tab. 1). Most records stem from recent years: Only 443 records are from up to 1970, and 961 from up to 1980. The invasion gained considerable momentum afterwards: 1,911 records are available from up to 1990, 2,697 from up to 2000, 4,899 from up to 2005, and finally, 12,017 by 2010 (Fig. 2).

All records were mapped to a study lattice system of 5’ × 3’ geographical minutes (~ 36 km^2); the total study region was comprised of 22,472 lattice system cells. Data record varies considerable across countries; most records were available for Austria and Hungary (Tab. 1).

Tab. 1. The number of Common ragweed records until 2010 for the eight study region countries, number of study lattice cells per country, and the number of invaded cells by 2010 as stated by records.

country	***records***	***lattice system cells***	***cells invaded by 2010***
Austria	5,430	2,442	549 (22.5 %)
Czech Republic	434	2,437	130 (5.3 %)
Germany	1,266	11,436	639 (5.6 %)
Hungary	3,407	2,749	1,825 (66.4 %)
Liechenstein	0	5	0 (0 %)
Slovakia	414	1,490	141 (9.5 %)
Slovenia	423	631	189 (29.3 %)
Switzerland	643	1,282	148 (11.5 %)
study system (all)	12,017	22,472	3,621 (16.1 %)

Fig. 1. Ragweed populations at a railway station in eastern Austria (left) and a ragweed plant ad the edge of a field © F. Essl

All data records together flagged 3,621 lattice system cells as colonized by 2010 (Tab. 1). Although most records stem from the warmer lowland areas east of the Alps, the species also occurs in alpine valleys and cooler, more oceanic climates towards the North (Fig. 3).

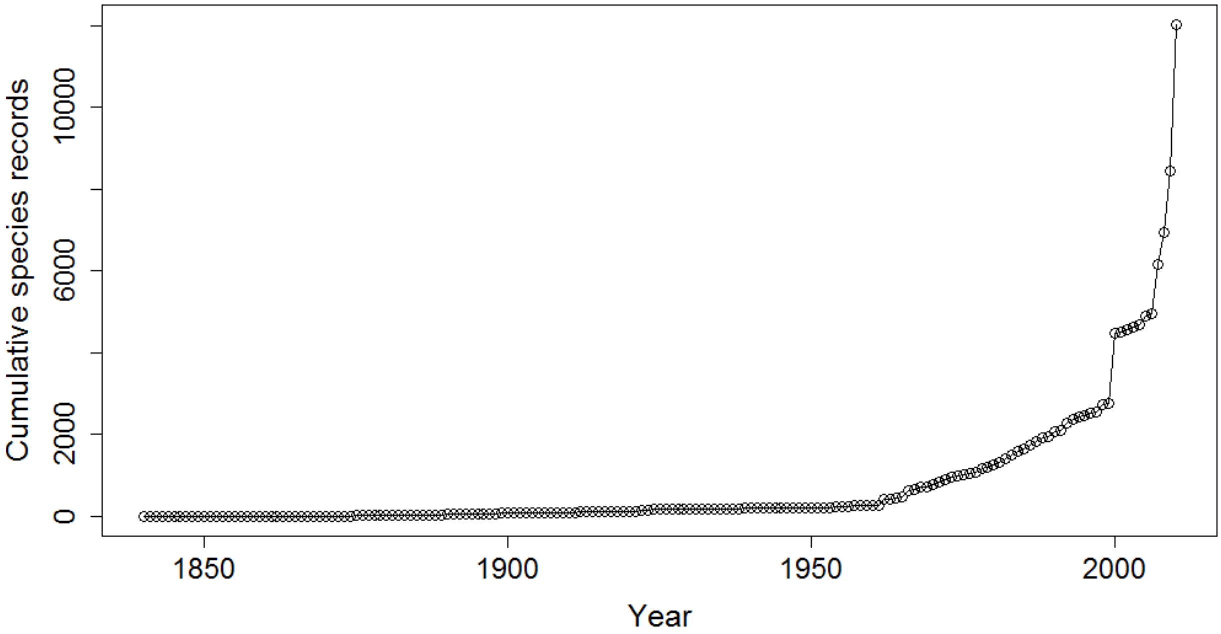

Fig. 2. Cumulative number of Common ragweed records from 1841 (first data record) up to 2010 obtained for Central Europe.

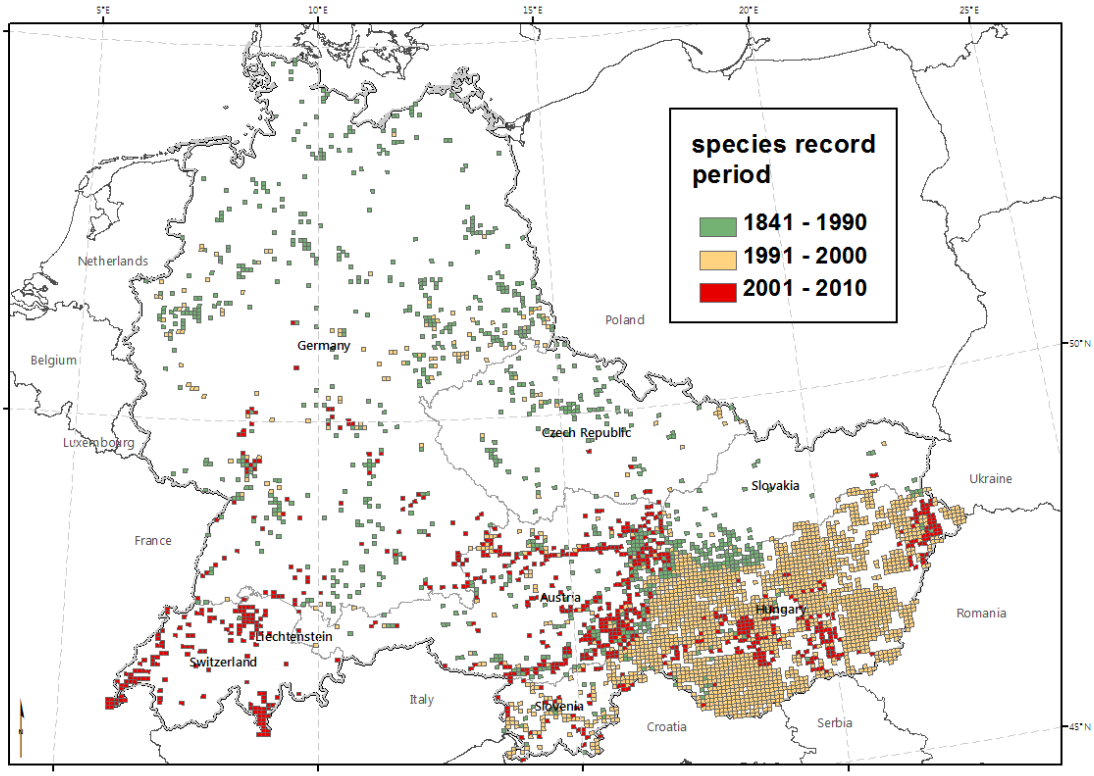

Fig. 3. Common ragweed occurrence in the Central European study region. Species records are shown for three different data periods at a resolution of 5' × 3' geographical minutes.

Work package 2: environmental data

In work package 2 we compiled a number of variables for each lattice system cell to characterize the local environment: temperature and precipitation data were collected on a monthly basis and pooled for the spring germination season. Land use variables stated urban, rural and grassland area, respectively, and rural, urban and total human population size, respectively. As original spatial resolution of data varied, we matched them to the study lattice system through statistical scaling approaches (e.g. Zimmermann *et al*. 2007, Randin *et al*. 2009).

Variables showed considerable variation over time but type of variation ranged from long-term, gradual trends to high inter-annual variability. For example, temperature shows both a long-term inter-annual variability around a relatively constant value but with a marked rise since about 1990 (Fig. 4). Crop land area, on the other hand, varied markedly both in space and time (Fig. 5).

Work package 3: dispersal networks

In work package 3 we collected network data on roads and railways and calculated pairwise connectivity measures between cells by a so-called cost-distance functions: the possible routes along a network graph become weighted by a measure of travel cost, and then the least-expensive path along this network is calculated. Thereby a combined measure of distance and connection type is derived. Cost-distances were calculated separately for roads and railway networks. Roads were weighted according to their type – motorways, primary and secondary roads, with the former imposing the least cost and the latter the highest.

We further incorporated averaged economy data (Bolt & Zanden 2013) as proxies of relative traffic intensity over the study timeframe.

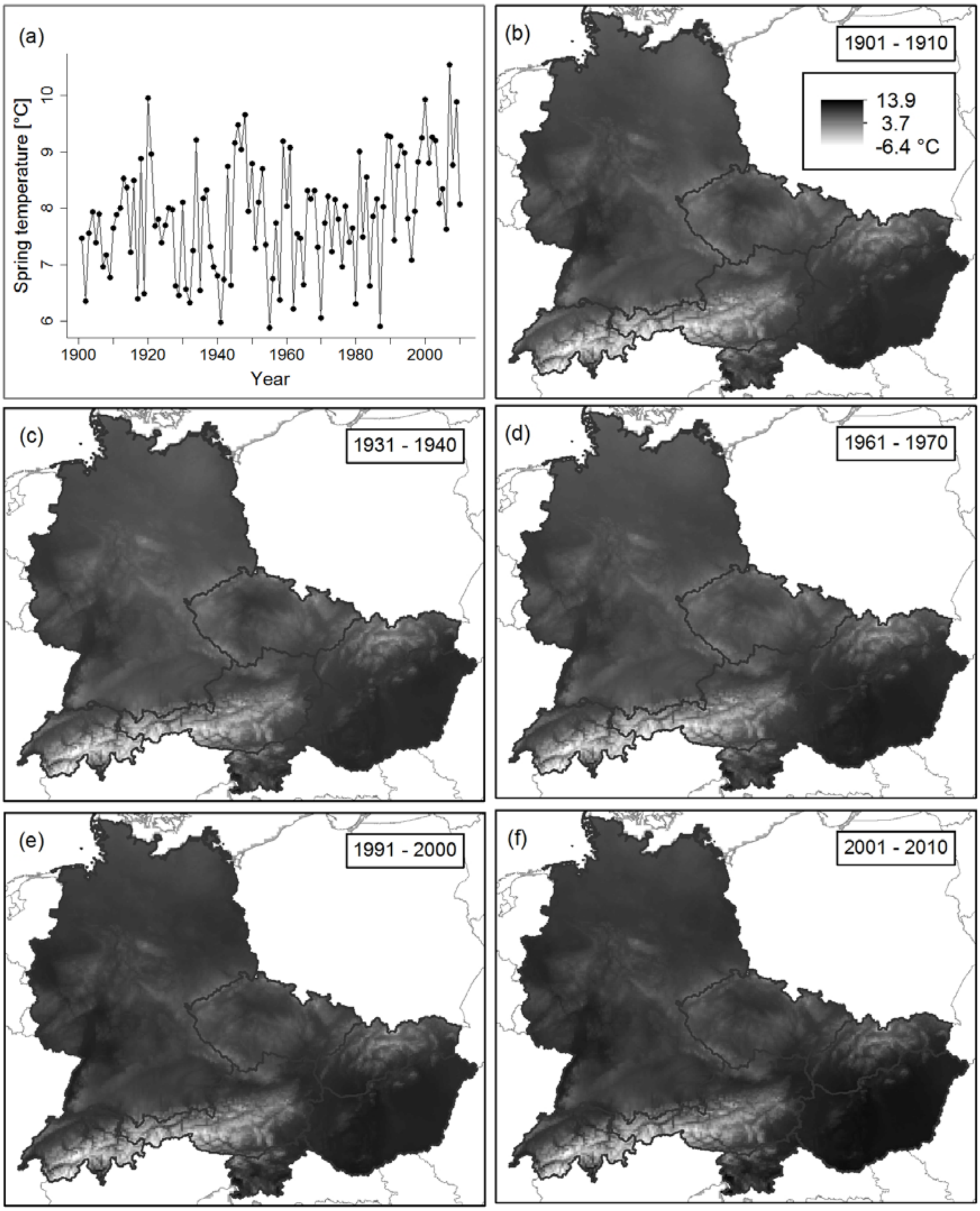

Fig. 4. Annual time series of spring temperature (1900 – 2010), averaged across the study area (upper left panel), and spatial variation of this variable (at a resolution of 3 x 5 geographical minutes) averaged over five different time periods.

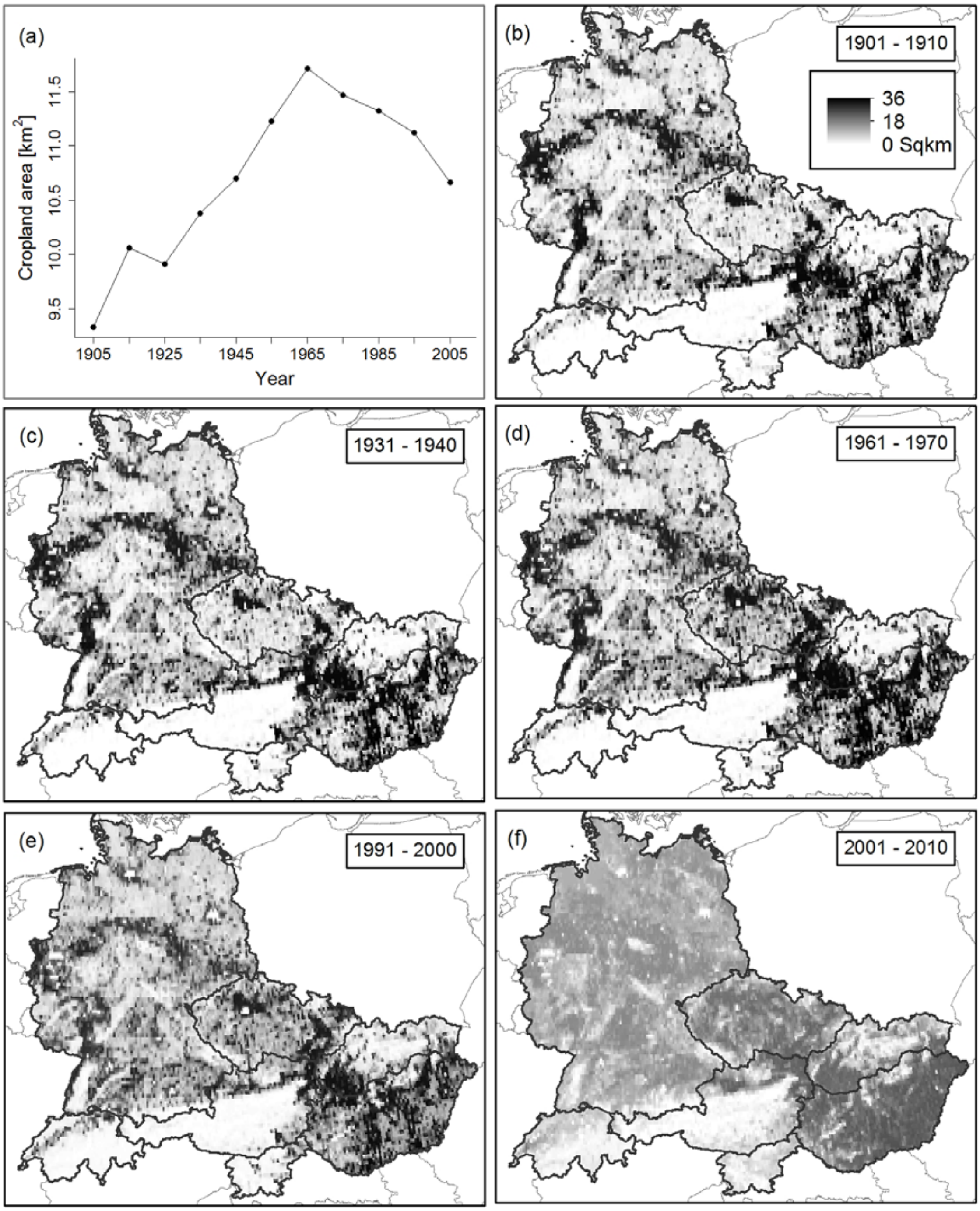

Fig. 5. Change of average cropland area per 3 x 5' (~ 36 km²) cell between 1905 and 2010 (upper left panel), and spatial variation of this variable averaged over five different time periods.

Work package 4: modelling framework

Work package 4 designed and implemented the analytical tool for modelling the invasion, building on earlier research in this field by project members. The model framework is capable of integrating many different invasion drivers while it retains, conceptually, compatibility to established modelling approaches. This eases comparison to alternative quantitative approaches. The framework investigates stepwise the sequence of invasion (= first observed colonization by ragweed) events in the lattice system and relates them to supposed invasion drivers like local environmental conditions ("habitat suitability") and change therein, local population growth, and (seed) dispersal (Fig. 6). The data collected in WPs 2 and 3 enter the framework as time-series covering more than a century.

Our modelling follows the idea that the factors to be investigated impact the invasion, but neither the magnitude of their effect nor the way how their effect changes with increasing levels of the respective factor (e.g. rising temperature, decreasing precipitation, accelerating local population growth) is known. In our model, these factors are hence associated with initially unknown parameters (= weighting) which are then estimated based on the available data of the invasion process and the concurrent time series of environmental conditions. Conclusions are finally based on these parameter estimates.

More specifically, the framework was used to specify several model variants which represent different ideas of which factors have actually driven the invasion process. All models included environmental conditions and, gradually, added spatially implicit invasion sources (= propagule with spatially unspecified source location), population growth within lattice cells and seed production at invaded locations, radial dispersal and network-driven dispersal along road and railways.

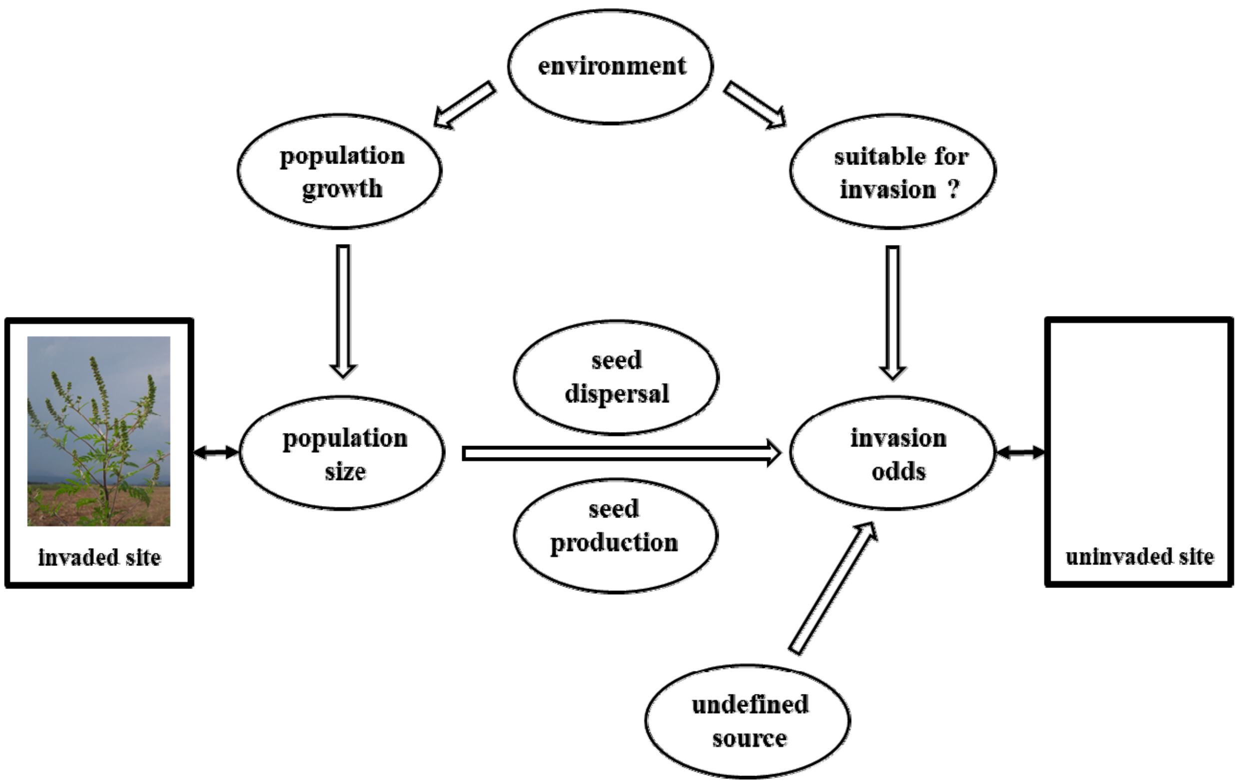

Fig. 6. Conceptual representation of the factors driving invasions, and their interplay, and corresponding framework modules used in modelling the spread of Common ragweed.

Next we extended the framework to acknowledge imperfect observation of the invasion process: here, it is assumed that the true invasion remained hidden to us and that data records comprise only a snapshot. Detections may be delayed, that is the species may have become established much earlier than it was observed, and sites already invaded may not show up at all in the data up to 2010.

Detection uncertainty is implemented through a hierarchical model structure in which one layer represents the invasion itself, and a second layer represents observation. Our species records arise from both processes acting in concert, but with our approach we aim to disentangle their effects on the time series of the data (= the observed invasion process). Similar to the invasion itself the detection process is assumed to have a spatio-temporally varied intensity. We modelled detection rates dependent on country, time period, and human population size.

Work package 5: modelling fittings

Models became fitted in work package 5. Results show that environmental conditions have a pronounced effect on the invasion, particularly temperature. Contrasting models however also showed that the more potential invasion drivers are integrated jointly in the analysis, the more the apparent importance of each single one decreases. The role of changing human land use patterns and disturbance regimes seems minor while local population growth and seed production of established populations are important but themselves strongly dependent on climatic conditions. In models that assume data to represent the real invasion without error and delay, dispersal appears mainly diffusive, but relatively far-reaching. Dispersal among corridors of accelerated spread, i.e. roads and railways is contributing to a lesser degree and foremost during the most recent decades. Once detection uncertainty is accounted for diffusive spread appears much more restricted to short annual distances. At the same time, the rare establishment of remote invasion foci is attributed to “random” events from unknown propagule sources. In general, however, the most recent wave of invasion seems to be mainly driven by short-distance migration from established (and quickly growing) populations.

In the hierarchical model, environmental variables plays a less pronounced role for determining geographical spread patterns, but they are nevertheless important (Tab. 2). Temperature, in particular, retains its role as a major determinant, supplemented by precipitation. Detection efficiency is estimated to have varied considerable across countries. Hungary and Switzerland have high and relatively immediate observation rates while in Germany and the Czech Republic observations lag considerably behind colonizations. For Austria, detection rates appear intermediate. With the establishment of floristic mapping schemes around 1970 detection rates improved. Human population size is a significant driver of detection rates and thus populations near urban centres are more likely to be detected than those in remote areas.

Estimates of the current real invasion state suggest that about twice as many cells are actually already invaded by 2010 than is documented by available data. The bulk of these cells are located in the climatically highly suitable regions east of the Alps and, to a lesser degree, in climate hot-spots throughout the study system.

Tab. 2. Qualitative comparison among models demonstrating the contribution of environmental variability as whole, and temperature in particular, to explaining the historic Common ragweed invasion pattern

Model setup	***environmental invasion filter***	***temperature dominance***
EnvVar + spatially undefined source	+++	+++
EnvVar + spatially undefined source with time trend	+++	+++
EnvVar + invaded sites + spatially undefined source	++	+++
EnvVar + invaded sites + spatially undefined source with time trend	++	+++
EnvVar + invaded sites with population dynamics + spatially undefined source with time trend	++	+++
EnvVar + invaded sites with pop. dynamics + spatially undefined source with time trend + dispersal along infrastructure networks	++	+++
Full hierarchical model acknowledging detection uncertainty	+(+)	+(+)

4 Schlussfolgerungen und Empfehlungen

With respect to the common ragweed invasion we conclude that the invasion has multiple facets. At the macro-scale the invasion has a strong spatial relationship to climate both with respect to (initial) invasion risk and population growth after first colonization. The bulk of the invasion occurs in warmer lowland areas east of the Alps, yet a considerable range of records from Alpine valleys and more oceanic and/or northern parts of the study region shows that these regions have a substantial invasion risk, too (Fig. 3). The invasion is clearly established over the whole of Central Europe and thus, even if hot-spots are distinguishable, pollen impact is certainly wide-spread.

Previous common ragweed invasion modelling has shown that climate strongly determines the invasion pattern, but no dynamic modelling approach has been used so far. The reason probably is that established modelling approaches are not supporting a both dynamic and integrative analysis of the invasion. The framework developed within our project has shown that an integrative modelling approach to biological invasions is useful. In reality, invasions are co-driven by the spatial pattern of environment conditions, the temporal change of these patterns, the growth of local populations and the consequently rising seed production and the spatial dispersal of these seeds. Our results and the comparisons among models have shown that acknowledging the interplay of these processes in modelling allows for a more comprehensive understanding of their relative effects.

With respect to invasion drivers, we identified climate as most important environmental determinant. Recently rising temperatures have clearly contributed to the accelerated spread, and so is future climate projected to trigger further waves of invasion.

Our modelling framework allowed for comparing a number of models with varying assumptions but also commonalities. We found that for a number of parameters, including climate, the variability in their parameter estimates among models was more pronounced than parameter uncertainty within single model setups as they necessarily arise from statistical constraints. Therefore not problems of input data or differences among the statistical model fitting routines dominate residual uncertainty, but the underlying assumptions about the factors and processes driving invasions which guide the design and setup of individual models. This is an important finding for invasion modelling as established modelling approaches normally do not allow much variation of inherent model assumptions, and thus this residual uncertainty remains undetected. With respect to climate, its outstanding impact on the invasion dynamics of ragweed in Central Europe is beyond question, but quantification of its impact has to be done carefully.

Macro-ecological invasion analyses frequently rely on species records from the field, but many records stem from accidental sightings. This is the usual case given that large areas cannot be completely surveyed, and even less so can surveys be repeated within short time intervals. We have hence always been aware that even the large number of records that we have compiled in this project will only represent part of the real invasion process. This motivated our attempt to integrate detection issues into the modelling framework to obtain an estimate of the likely realized invasion status. We point out, however, that computing requirements are very high and even under modern-day hardware still impose a challenge; fortunately forthcoming technology will certainly relax this situation.

The estimate of the realized invasion state is, naturally, an inference based on model assumptions and no model can ever reconstruct the realized invasion state with certainty. However, a figure of about twice as many cells already invaded than what is known appears realistic in qualitative terms and has been fully within the estimate suggested by experts from field experience.

Our models clearly suggest that Common ragweed is already more abundant and more widely distributed than documented by the data. At this stage, complete eradication appears unfeasible, but control efforts can still reduce negative impacts considerably (Richter *et al*. 2013). Currently, various projects specifically target control optimization of ragweed on both national and EU-scales. Management efforts, including estimated costs and efficiency, however rely on knowing the already realized spread pattern, and our modelling contributes to this knowledge.

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B) Projektdetails

5 Methodik

Work package 1: species data

Historical data on the common ragweed invasion were obtained for eight Central European countries (Austria, Czech Republic, Germany, Hungary, Liechtenstein, Slovakia, Slovenia and Switzerland) by querying existing databases, herbaria records and local experts. Records were associated with a geo-referenced coordinate and a recording date. Furthermore, if individual records stated specific supplementary information (e.g. estimate of population size or micro-habitat conditions) these were also logged. All data were entered into a standardized database and mapped to a study lattice system of 5’ × 3’ geographical minutes (~ 36 km^2).

Work package 2: environmental data

For each lattice system cell a number of environmental covariates were collected:

Temperature and precipitation data were collected on a monthly basis from the CRU (CRU TS 1.2, Mitchell *et al*. 2004) and E-OBS 5.0 (E-OBS 5.0, Haylock *et al*. 2008) data sets for the years 1901–2010 and subsequently pooled to annual, cell-wise spring (March–May) values; we used the mean of the first two decades of the 20th century as proxy for 19th century climate for which comparable data were not available.

Land use variables of urban, rural and grassland area and rural, urban and total human population size, respectively, were obtained from the HYDE 3.1 data set version 3.1 (HYDE 3.1, Goldewijk *et al*. 2011) stating data at 10-year intervals; to retain consistency with climate measures for landscape variables we too held the period 1800–1900 constant by using the (cell-wise) values of the first decade of the 20th century. Original spatial resolution of data varied, but all data were re-sampled to the resolution of our study lattice system using a statistical scaling approach (Zimmermann *et al*. 2007, Randin *et al*. 2009).

For each cell we further collected data on total length of motorways, primary and secondary roads, respectively, and railways. These data were based on Open-Street-Map (OpenStreetMap) and are resolved only on a spatial basis; we thus assumed the same (cell-wise) constant value for all study period years.

Work package 3: dispersal networks

Detailed roads and railways network data were based on Open-Street-Map (OpenStreetMap) and used to calculate an anisotropic connectivity measure (Bossenbroek *et al*. 2001, 2007) between cells: roads were classified as primary, secondary or motorways and assigned cost values of 10, 5 and 1, respectively; for railways a single category was used throughout. For each cell, cost-distances of roads and railways, respectively, were calculated to every cell within a surrounding of 15 cells. Calculations were performed using the Cost Distance algorithm of ArcGis 10.1. Derived cost-distance measures ranged from 1 to 2,024 for roads, and from 1 to 486 for railways, respectively.

Historical traffic data for roads and railways could not be reliably obtained. We used Central European trading intensity (Bolt & Zanden 2013) as proxy for traffic intensity. We first interpolated country-wise data for the whole study time frame based on data anchor points, and subsequently pooled, weighted by country area, to a single time series.

Work package 4 + 5: modelling framework, model fittings

Based on previous research (a DOC-project of the Austrian Academy of Sciences) we developed a novel modelling framework. Based on a lattice system the response variable is invasion times of cells. Parameter fitting occurs through a Bayesian paradigm with Markov chain Monte Carlo (MCMC) (Gelman *et al*. 2004). The framework is constructed on a modular basis where modules act as building blocks to smoothly construct models of varying complexity. Framework modules integrated into the analysis consist of: local establishment chance dependent on environmental variables; local growth; seed production; dispersal by geographic distance and along road and railway structures, respectively; and a generic, spatially unspecified background seed source. Temporal variability enters at various stages, e.g. through the environment itself and the system-wide invasion state.

The hierarchical model adds detection aspects by attaching an observation stage to the invasion. First a cell becomes invaded, and then the local population detected. The hierarchical model uses data augmentation parameters to represent, and then infer on, the realized yet unobserved invasion state. Detection rates that translate invasion into records are assumed to be themselves unknown and to be inferred; they were modelled to vary by study country, time period, and human population size.

Albeit powerful, framework fitting consumed vast computing resources and required the use of system-heterogeneous programming for efficient parallelization. Besides the Bayesian approach we further provided maximum-likelihood estimation capability.

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6 Arbeits- und Zeitplan

Phase 1: Data collection

In the first project phase we collected historical Common ragweed invasion data (WP 1), environmental data (WP 2) and road and railway network data for the Central European study region. These data were the basis of all modelling and analyses.

Phase 2: Framework development

During the second stage we developed the modelling framework and implementated it into a computing environment.

Phase 3: Model fittings

Once implemented we used the framework to parameterize models. Early model output provided hints for technical adaptations required.

Phase 4: Comparative analyses

Fitted models were compared and the results used for conclusions on the probable impact of climate on ragweed invasion dynamics.

7 Publikationen und Disseminierungsaktivitäten

Essl, F., Dullinger, S., Kleinbauer, I., Leitner, M., Mang, T., Moser, D., Richter, R. & Vogl, G. (2011) Aktuelle Verbreitung, Einwanderungsgeschichte und Szenarien des weiteren Ausbreitungsverlaufs in Österreich. Paper presented at AGES ragweed symposium; 2011 Nov 25; Vienna, Austria.

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