


RESEARCH ARTICLE

Simulating the spread and establishment of alien species along aquatic and terrestrial transport networks: A multi-pathway and high-resolution approach

Maurizio Bagnara¹ | Larissa Nowak^{1,2}  | Hans Juergen Boehmer^{3,4,5}  | Franz Schöll⁶ | Frank M. Schurr⁷  | Hanno Seebens¹ 

¹Senckenberg Biodiversity and Climate Research Centre, Frankfurt, Germany

²Institut Mediterrani d'Estudis Avançats (CSIC-UIB), Global Change Research Group, Mallorca, Spain

³School of Geography, Earth Science and Environment, Faculty of Science, Technology and Environment, The University of the South Pacific (USP), Suva, Fiji

⁴Institute of Geography, Friedrich Schiller University Jena, Jena, Germany

⁵Institute for Applied Ecological Studies (IFANOS), Nuremberg, Germany

⁶German Federal Institute of Hydrology, Koblenz, Germany

⁷Institute of Landscape and Plant Ecology, University of Hohenheim, Stuttgart, Germany

Correspondence

Hanno Seebens
Email: hanno.seebens@senckenberg.de

Funding information

Federal Railway Authority of Germany, Grant/Award Number: 2017-U-10-1210

Handling Editor: Joseph Bennett

Abstract

1. The introduction and further spread of many alien species have been a result of trade and transport. Consequently, alien species are often found close to traffic infrastructure and urban areas. To contain and manage the spread of alien species, it is essential to identify and predict major routes of spread, which cannot be obtained by applying common modelling approaches such as species distribution models.
2. Here, we present a new model called CASPIAN to simulate the dispersal of alien species along traffic infrastructure and the establishment of populations along these routes. The model simulates simultaneous spread of species of up to eight different modes of transport along roads, railways and waterways. We calibrated and validated the model using two species that spread within Germany as case studies: the terrestrial plant *Senecio inaequidens* and the freshwater clam *Corbicula fluminea*, and performed a shortest path analysis to quantify the relative importance of individual routes for spread.
3. The application of the model yielded detailed predictions of dispersal and establishment for >600,000 segments of the traffic network throughout Germany. Once calibrated, the model captured the general spread dynamics of the two species with higher accuracy for the freshwater environment due to the higher quality of data available for the aquatic species.
4. The quantification of spread routes using the shortest path analysis revealed a clear backbone of major routes of spread, which varied depending on the type of traffic network and the starting points considered. Major routes of spread aligned with high traffic intensities, but high traffic per se did not necessarily result in high spread intensities.
5. *Synthesis and application.* By simulating the spreading dynamics of alien species along transport networks across multiple pathways, CASPIAN enables the

Maurizio Bagnara and Hanno Seebens contributed equally.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Journal of Applied Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

identification of major spread routes along different dispersal pathways and quantification of their relative importance, which helps prioritising pathways of introduction as required by international biodiversity goals such as the CBD Aichi targets.

KEYWORDS

biological invasions, dispersal, invasive species, modelling, neobiota, spread, traffic infrastructure, transport

1 | INTRODUCTION

The expansion and intensification of trade and transport over recent decades have caused the exchange of thousands of species worldwide (Chapman et al., 2017). Through the movement of commodities or means of transport, species can be transported over long distances and released at sites they would have never reached without human intervention (Hulme, 2021). Some of these so-called alien species established populations outside their native range and became an integral part of the local flora and fauna (Blackburn et al., 2011). The introduction of alien species can have far-reaching consequences and may affect local communities and global biodiversity patterns, for example, through the biotic homogenisation of spatially separated communities (Fricke & Svenning, 2020). Reducing further influences of alien species requires robust tools to quantify and predict their spread (Pyšek et al., 2020).

Trade—or transport in general—plays a crucial role for the spread of alien species, as introducing species accidentally or intentionally through trade remains the dominant pathway for most taxonomic groups (Saul et al., 2017). It has been repeatedly shown that the intensities of transport and imports are closely related to the number of alien species found in a region (Chapman et al., 2017; Levine & D'Antonio, 2003; Westphal et al., 2008). The close relationship between transport networks and the spread of alien species allows using transport intensities as proxy variables to estimate the number of alien species exchanged (Banks et al., 2015). Using transport data as a predictor allows improving predictions of the spread of alien species through the acquisition of huge amounts of data available for transport networks.

Dispersal and local establishment are two major factors influencing the spread of alien species (Floerl et al., 2009). The process of dispersal often involves multiple pathways of natural and human-mediated transport, which may happen simultaneously. Moreover, even for a single introduction pathway, the dynamics of dispersal can be complex. For instance, individual ships can carry species in various ways and connect many different sites (Banks et al., 2015). Thus, species released at one site may originate from any of the sites visited by the ship before (Seebens et al., 2019). Spreading dynamics of alien species can, therefore, be difficult to grasp using simple statistical models and require more complex modelling approaches.

The potential distributions of alien species are commonly estimated using species distribution models (SDMs). SDMs statistically relate species distribution data to local environmental or socio-economic variables to estimate new ranges of potential occurrence (Fournier et al., 2019). SDMs can provide valuable information about the potential ranges of alien species (Faulkner et al., 2020), are readily available and comparatively easy to apply. However, SDM-based estimates of habitat suitability may be biased by the lack of considering population dynamics and dispersal (Schurr et al., 2012). For example, a species might be absent from potentially suitable habitats because it has not yet dispersed to them (Pagel et al., 2020). Therefore, a more realistic approach to simulating the dynamics of biological invasions involves the prediction of both dispersal and local establishment in a combined way (Chapman et al., 2016; Seebens et al., 2013).

In recent years, there has been much progress in the application and development of SDMs to detect suitable habitats, while accounting for dispersal dynamics has been done less frequently (but see, e.g., Bullock et al., 2008; Chapman et al., 2016; Hudgins et al., 2017; von der Lippe & Kowarik, 2007). The process of human-mediated dispersal of alien species has been investigated for a variety of species, and dispersal kernels have been developed and parameterised, which can be used for predicting the spreading dynamics of alien species (Bullock et al., 2008; von der Lippe & Kowarik, 2007). It has also been shown that the routes of spread can be well depicted using the intensity of traffic (Seebens et al., 2013). The spread of individual species can be modelled with comparatively simple models (Chapman et al., 2016), and it is possible to predict the next invaders based on traffic dynamics (Seebens et al., 2016). Nevertheless, most existing models have a limited focus on single dispersal pathways or do not distinguish between pathways, which hinders quantifying their relative importance, although ways of transport might be very different for the same species (e.g., natural plus human-mediated spread; Gilbert et al., 2004). Particularly for countries with dense and closely interlinked transport networks, a cross-modal approach seems, therefore, essential to predict the spread and occurrence of alien species. However, thus far, there is no model available that can simulate the dispersal and establishment of organisms across transport modes simultaneously.

Here, we first introduce CASPIAN (Calculating Alien Species Probability of Invasion Along Networks), a new model to simulate the spread of alien species along and through networks of traffic and traffic infrastructure across multiple pathways. The model considers various pathways of dispersal such as attachment to vehicles, natural dispersal or airstream for terrestrial and aquatic species and simulates spreading dynamics along these pathways simultaneously. Secondly, we calibrate model parameters and validate model results using two case studies in Germany, representing the spread of a terrestrial plant and an aquatic mussel. Finally, we apply network analysis to identify the major routes of spread and investigate the relationships between traffic and alien species spread. We were particularly interested in answering the following questions: (1) how well can one simulate the spread of alien species using traffic information at a country scale, (2) which transport modes are most important for simulating the spread dynamics of individual species and (3) which are the most important routes of spread predicted by the model?

2 | MATERIALS AND METHODS

2.1 | Data

2.1.1 | Traffic networks

All traffic data sets used in this study were made available by the commercial engineering consultancy agency SSP Consult (<https://www.ssp-consult.de/>). Traffic data were represented as georeferenced networks of traffic infrastructure (roads, railways and waterways) and associated traffic densities (i.e., number of cars, trucks, trains or ships passing per day along individual segments of the networks) in Germany. The networks consisted of nodes and links, with nodes representing sites of changing network properties such as road crossings and river mouths or changing link characteristics such as road size or speed limit, while links denote the segments connecting nodes. The railway network consisted of the full operational network of railways in Germany. The road network included all sizes of roads except roads maintained at the lowest administrative level. We merged the road and railway networks to allow species to spread along both within the same simulation, identifying the intersections where roads and railways crossed and including them as additional nodes within the merged network (subsequently referred to as the terrestrial traffic network). This network consisted of 260,829 nodes and 634,817 links with a median length of 1 km.

The network of waterways includes canals and river segments maintained by German agencies for commercial shipping and, thus, covered major waterways in Germany. It consisted of 321 nodes and 666 links with a median length of 13 km.

For all networks, passenger and cargo transport were distinguished. Traffic intensities for inland shipping and railways were obtained in full extent from official reports and time schedules provided by the Clearing House Transport of the German Aerospace

Center (<https://www.dlr.de/cs/en/desktopdefault.aspx/tabid-701/>). As this information was not available for roads, road-based traffic intensities were obtained from an individual-based traffic model developed by SSP Consult, which simulates the movement of individual trucks and cars based on official traffic census data provided by the Clearing House Transport. Traffic simulations by SSP Consult have been frequently used to develop the Federal Transport Plans for Germany. Due to the lack of data to verify model results, we do not present results for the simulation of containers and wooden pallets within Germany, although these means of transport are included in CASPIAN.

2.1.2 | Environmental data

Environmental data were required to characterise the terrestrial and aquatic habitats of species. The terrestrial habitat was characterised using land cover data from the "CORINE Land Cover European seamless vector" database (version v18_5) based on satellite images from the European Union's Earth Observation Programme Copernicus (<https://land.copernicus.eu/pan-european/corine-land-cover>). It provides 44 classes of land covers with a 100m positional accuracy. For each segment of the terrestrial traffic model, the proportions of land cover were extracted within a 50m corridor to both sides of each network link. We aggregated the classes into five major categories of land covers: urban/industrial areas, croplands, pastures, forests and wetlands (see Table S1 in Supporting Information).

For the freshwater environment, consistent measurements of the environmental conditions across all waterways within Germany are lacking, and individual data sets had to be integrated. Since waterways used for commercial shipping are heavily modified water bodies with continuous shoreline stabilisation and little spatial heterogeneity, we only used mean annual water temperature and electric conductivity as environmental variables. These variables were identified as useful proxies to characterise freshwater habitats (Schöll, 2000, 2013) and were available from permanent measurement stations throughout Germany. Measurements were available at 4–11 sampling stations at the river systems of Elbe, Rhine, Weser and Oder, and were interpolated to cover segments between sampling stations. For extrapolations to cover tributary rivers, the low variation in environmental parameters (Figure S1) allowed for selecting the measures of the closest stations and assigning them to the respective water bodies. For each variable, time series over a period of 5 years were aggregated to obtain annual mean values. Thus, these variables described general trends in spatial heterogeneity in environmental conditions such as high conductivity towards coastal areas and higher temperature of the Rhine system (Figure S1).

2.1.3 | Species data

Species occurrence data were used to calibrate model parameters and to validate model results. Ideally, such a data set would satisfy the

following requirements: (1) belonging to a species alien to Germany, which is likely to be transported via traffic or disperse along traffic infrastructure, (2) being in the form of presence/absence data, (3) possessing high spatial accuracy and a large spatial extent and (4) possessing temporal resolution to reconstruct the spread trajectory. In addition, the accuracy of model predictions increases with the amount of available data and the spatial and temporal resolution of data. However, not meeting all requirements does not preclude running the model, as we show in our case study (see below), but the user should be aware of the limitations when applying the model.

Among terrestrial species, no data set perfectly matched our purpose. As a compromise, we digitised maps showing the distribution of the vascular plant *Senecio inaequidens* at different decades in Germany (Figure S2; Heger & Boehmer, 2005). *Senecio inaequidens* is a terrestrial perennial species native to South Africa, which started to spread through Central Europe in the 1970s and is commonly found along roads and railways (Heger & Boehmer, 2005). In the time period considered here, the range expansion of *S. inaequidens* in Germany was dominated by spread from an introduction site in Belgium (Lachmuth et al., 2010). *Senecio inaequidens* is known to spread mostly along roadsides and railway embankments, although it is also found in other rural habitats (Ernst, 1998; Griese, 1996). The maps already provided some first indications of spreading dynamics along major roads from Western to Eastern Germany (Figure S2). The occurrences were only available at a comparatively coarse resolution of raster cells with an edge size of ca. 10 km. If the species was recorded for a particular cell, we, therefore, assumed that the species was found throughout the whole cell. We used data from 1989 and 1997 for model calibration and for 2004 to validate model results. The calibration was restricted to the northwest part of Germany to obtain a balance of presence and absence values (indicated as a box in Figure S2). The validation was carried out for the whole of Germany in order to exploit the full extent of available data.

For the aquatic realm, we could identify one data set for *Corbicula fluminea*, which closely matched the requirements. *C. fluminea* is a small freshwater clam native to East Asia and has been likely introduced through shipping (Schöll, 2013). For this species, the spread processes have been reconstructed (Schöll, 2000, 2013), and samples could be obtained from various surveys conducted by the German Federal Institute of Hydrology. Here, we used data covering the main spread period from 1990 to 1999 (Figures S2). Samples were not available for canals. We used the time period 1990–1996 to calibrate the model parameters and the years 1997–1999 for model validation.

2.2 | The CASPIAN model

CASPIAN simulates the dispersal of species by traffic and along traffic infrastructure and the establishment of new populations along these routes in terrestrial and aquatic environments (Figure 1). The model covers spread dynamics associated with transport networks such as roads, railways and inland waterways. For each link, the model calculates three probabilities: (a) the probability of introduction $P(I)$

describes the probability that individuals of a species disperse from node i to node j along link k_{ij} . Species may disperse via different modes of movement, which we refer to as 'pathways', such as attachment to a vehicle or natural dispersal. $P(I)$ is calculated using pathway-specific dispersal kernels or functional forms of transport intensities, where dispersal kernels were not possible to implement (Table S2). (b) The probability of establishment $P(E)$ determines the probability that the species is able to establish a new population at a given site as a function of local environmental conditions. (3) The probability of invasion $P(Inv)$ combines $P(I)$ and $P(E)$ and describes the probability that a species reaches a new site and establishes a population there. The details of these calculations are provided in the following.

2.2.1 | Probability of introduction

Several relevant pathways have been implemented in CASPIAN to consider a range of different modes of dispersal: natural dispersal, attachment to vehicles, airstream, hull fouling and ballast water (see Supporting information text for a detailed description of the dispersal modes). For each pathway, a functional form f and initial parameter values were obtained from literature (Table S2). In addition, functions describing the introduction by transport of wooden pallets and inside containers were implemented.

The functional form f describes the dispersal from node i to node j except for the pathways of ballast water, pallets and containers, which were estimated by cargo or traffic intensities at node j (Table S2) during 1/12 of a year (i.e., approximately 1 month). Road- and railway-based dispersal kernels describe the spread of a single propagule by a single vehicle. However, a population typically produces many propagules that are dispersed by multiple vehicles. To integrate $P(I)$ over all propagules and vehicles reported at this link, $P(I)$ was aggregated over all vehicles V moving from node i to j (Leung et al., 2004; Liebhold et al., 2017):

$$P(I)_{ij} = 1 - (1-f)^{\alpha V_{ij}}, \quad (1)$$

with α being a shape parameter describing how the number of propagules and vehicles translates into $P(I)$. The parameter α was implemented separately for airstream along roads (α_{FS}) and railways (α_{FR}), and for attachment to vehicles along roads (α_{AS}) and railways (α_{AR}). According to Equation 1, $P(I)_j$ of a single node j was derived from introduction probabilities of all links reaching j :

$$P(I)_j = 1 - \prod_i (1 - P(I)_{ij}). \quad (2)$$

For the pathways ballast water, pallets and containers, information about donor sites, where ships or commodities came from, was lacking. Only information about the number of ships per network link and the number of imported commodities was available. It was therefore assumed that $P(I)$ increases with the amount of released ballast water, delivered pallets and containers at the respective sites j .

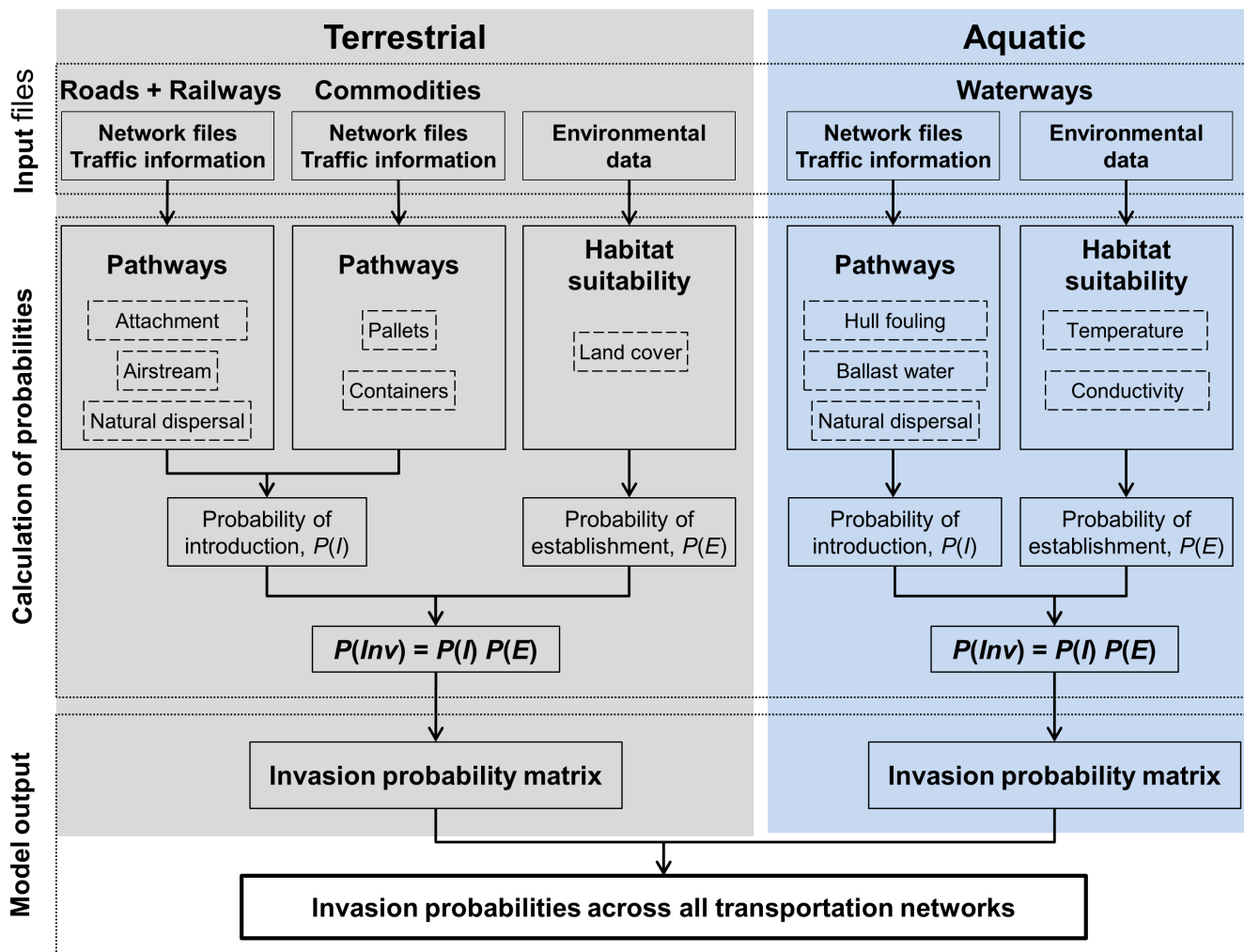


FIGURE 1 Schematic overview of CASPIAN. The model calculates invasion probabilities for terrestrial and aquatic organisms separately. The input variables represent the traffic networks (infrastructure + flows) and environmental data. Based on these data sets, the probabilities of introduction $P(I)$, establishment $P(E)$ and invasion $P(inv)$ were calculated. $P(I)$ was obtained using dispersal kernels specific to each pathway and applied to each segment of the traffic networks, which were then combined to get one $P(I)$ for each segment. $P(E)$ is calculated from habitat suitability and multiplied with $P(I)$ to obtain $P(Inv)$. The final $P(Inv)$ were then assigned to the spatial representation of the networks and exported as model output

2.2.2 | Probability of establishment

The probability of establishment $P(E)$ describes the foundation of a population at a new site and was approximated based on local habitat characteristics and species requirements, which we call 'habitat suitability'. Habitat suitability integrates the species' requirements and local environmental characteristics into a value ranging from 0 to 1, and translates into $P(E)$ (see below). CASPIAN is designed so that habitat suitability can be calculated in two alternative ways: The outcome of an SDM can be directly imported as a proxy for habitat suitability, which is then used to estimate $P(E)$ within CASPIAN. This, however, requires running an SDM beforehand. As an alternative, habitat suitability is calculated within CASPIAN based on data provided by the user. Both options are implemented in CASPIAN, but to showcase its application, we do not use the SDM approach here but use the simpler, less computer-intensive alternative as described below.

In the terrestrial case study, habitat suitability H along link s_{ij} was calculated from the percentage shares N of land cover classes n and the preferences I of the respective species for the corresponding land cover class: $H_{ij} = \sum_n (I_n N_{ijn})$. A preference of $I = 1$ for all land cover classes along s_{ij} would result in a maximum value of habitat suitability of $H_{ij} = 1$. The probability of establishment $P(E)_{ij}$ was then calculated from the product of the basic probability of establishment β_1 and H_{ij} : $P(E)_s = \beta_1 H_{ij}$. β_1 describes the probability of establishment under perfect conditions. In contrast to $P(I)$, $P(E)$ was calculated for links, thereby assuming that a species spreading along a link with probability $P(I)$ has the potential to establish a population along that link with probability $P(E)$.

For aquatic habitats, establishment probability was calculated as the Euclidean distance between the values of environmental parameters and species environmental optima: $P(E)_s = \beta_2 \sqrt{(T_s - \bar{T})^2 + (L_s - \bar{L})^2}$, where T denotes temperature and

L electric conductivity at link s , and \bar{T} and \bar{L} the respective species preference. β_2 describes the probability of establishment under perfect conditions. Environmental variables were normalised before calculation.

2.2.3 | Probability of invasion

The probability of invasion $P(Inv)_{ij}$ was calculated as the product of $P(I)_{ij}$ and $P(E)_{ij}$ and describes the probability that a species present at node i disperses towards node j along link s_{ij} and establishes a population along s_{ij} .

The probability of occurrence of a population N at node j represents the accumulated $P(Inv)_j$ until time t . At the beginning of the simulation, N at all nodes was set to zero except at the starting nodes, where the species was assumed to occur initially ($N_{init} = 1$). The probability of occurrence at j is calculated as $N_j = N_i P(Inv)_{ij}$. In the case of multiple links, N_j is integrated over all links directed to j :

$$N_j = 1 - \prod_i [1 - (N_i P(Inv)_{ij})]. \quad (3)$$

In this way, the node status of all nodes was updated at each time step t , and the species started to propagate through the network.

2.3 | Model assumptions

As with all models, a number of assumptions had to be made to simplify and integrate the underlying processes into the model. Here, we outline major assumptions. A more detailed discussion can be found in the supplement.

First, a major assumption is that alien species spread only along traffic infrastructure, although in reality, species are able to move independently of the traffic infrastructure as well. This assumption might lower the predictive accuracy of the model. Nevertheless, as CASPIAN covers an important aspect of human-mediated spread often neglected in other spread models, it complements existing approaches.

Second, population dynamics and biotic interactions are not considered in the model, although both can play important roles for the dispersal and establishment of new populations. Population dynamics have been integrated into other model approaches, such as dynamic range models (Briscoe et al., 2019), which are often specific to individual taxa. However, in the general context applied here, the consideration of population dynamics is very challenging and requires additional data on demographics and a much longer computation time. Moreover, calibrating and validating the results of simulating population dynamics and biotic interactions would require detailed information of those, which is not available for our study system. However, CASPIAN can be connected to already existing models.

Third, the model assumes that species disperse from node to node within the traffic networks. This simplification arose from the model approach and the traffic network structure but should not affect the simulation at large scales, as links of the terrestrial network have an average length of 1 km. Thus, the resolution is still higher than provided in the data available for validating the model.

Several of these limitations are explicitly addressed in other modelling approaches, such as demographic distribution models or dynamics range models (Briscoe et al., 2019), but these approaches do not cover the dynamics of human-mediated spread. CASPIAN is, therefore, complementary to existing approaches and can facilitate higher predictive accuracy when simulating alien species spread.

2.4 | Case study

Two case studies of species spreading within Germany were conducted to calibrate model parameters and validate model results: the plant *S. inaequidens* as a model species for the terrestrial environment and the freshwater clam *C. fluminea* as a candidate to simulate spreading dynamics in the aquatic environment. For *S. inaequidens*, the pathways of natural dispersal, attachment and airstream for road and rail transport were considered. For this modelling exercise, habitat preferences were set to 1 for urban areas, 0.5 for arable land, 0.1 for pastures and zero for forests and wetlands, as *S. inaequidens* is commonly found in rural and disturbed areas on dry and sandy soils in Germany (Boehmer et al., 2001). For *C. fluminea*, hull-fouling, ballast water and natural dispersal were considered. Habitat preferences were set to 13°C and 100mS/m for temperature and conductivity, respectively, as this species is found in rivers throughout Germany except for colder waters in Eastern Germany and brackish estuaries (Schöll, 2013). Habitat preferences were based on expert knowledge and literature (Heger & Boehmer, 2005; Schöll, 2013) as we wanted to exemplify the application of CASPIAN rather than analysing species responses in more detail. The model was calibrated using a state-of-the-art Bayesian approach. A major advantage of the Bayesian approach is that it considers probability distributions of the parameter values, which allows estimating the uncertainty of the calibration results. A detailed description of the calibration approach is provided in the supplement.

Applying CASPIAN provided probabilities of spread and establishment of individual links and nodes, but these are difficult to interpret and generalise on a larger geographic scale. To obtain more general and large-scale results of the spreading dynamics, we applied a method from complex network science called 'shortest paths' (Albert & Barabasi, 2002). A shortest path denotes the shortest route between two nodes of a network. Usually, shortest paths are determined by minimising the sum of distances of all links between two nodes, but paths can also be described by other measures such as probabilities. Here, we calculated shortest paths as the route between any two nodes with the highest $P(I)$, indicating routes of the highest likelihood of spread. To calculate shortest paths, we applied the Dijkstra algorithm from the

R package IGRAPH (Csardi & Nepusz, 2006). As this algorithm requires measures that can be summed, we turned the multiplication into a summation by using log-transformed probabilities instead: $P(l) = 1 - \prod (1 - P(l)) = 1 - \exp\left[\sum \log(1 - P(l))\right]$.

We calculated shortest paths using $P(l)$ as we were interested in the identification of major routes of dispersal, but one could also use $P(l_{inv})$, which would take local establishment into account, and thus would consider more long-term dynamics. Shortest paths were calculated between a subset of random 200,000 pairs of nodes, which provides a good representation of the shortest paths of the whole network. Once the Dijkstra algorithm was applied to all pairs of nodes, we determined the number of shortest paths passing through a particular link. A high number of shortest paths associated with a certain link indicates that this link has been part of many shortest paths, thus representing a likely route of spread.

3 | RESULTS

For *S. inaequidens*, the calibration led to convergence over the course of 10^5 iterations (~33,000 for each chain), reaching a Gelman-Rubin index <1.1 (Figure S3). Overall, the quality of the model fit to the data for *S. inaequidens* was moderate (Percentage Correctly Classified [PCC] = 0.666, Figure 2). The validation revealed that the quality of model predictions fell slightly to a value of PCC = 0.661. Such a decrease in the model fit was expected since this test was performed using data from across Germany.

The calibration for *C. fluminea* converged after 10^5 iteration steps (~33,000 for each chain) with a Gelman-Rubin index <1.1, indicating acceptable convergence of the MCMC algorithm (Figure S4). With a PCC = 0.81, the model validation indicated that the model could reproduce the observed dispersion of *C. fluminea* well over the period of calibration (1990–1996). The validation step revealed a similarly high goodness-of-fit value (PCC = 0.84), indicating a good capacity to predict new occurrences outside the calibrated range (Figure 2). All functional forms f using the calibrated parameters are shown in Figure S5, while the parameter values and uncertainties are provided in Table S3.

For the combined road and railway network, the network analysis revealed a dense network of routes of low and intermediate importance, while a few routes emerged as the “backbone” of proliferation (Figure 3). This backbone is represented by a dominant North–South axis and a connection of major urban areas of Germany. The backbone varied slightly among the network types: in comparison to the full terrestrial network (Figure 3a), the dominance of the backbone routes became more apparent when using only the road or railway network with slightly different sets of major routes (Figure 3b,c). Therefore, switching between the road and railway network offers more opportunities for a species to spread. The major spread routes could also be identified from a fixed starting point such a major transport hub (such as Hamburg) or a single border entry point (Figure S6). Generally, routes with the highest probability of spread represented major traffic axes

in Germany, while links with a low traffic volume were of minor importance for the spread of alien species. However, routes with the highest traffic densities were not necessarily the main routes of dispersal: the number of shortest paths peaked at traffic intensities of around 40,000 vehicles per day (Figure S7). Routes with traffic volumes of more than 80,000 vehicles per day played a less significant role in the overall spread process, which was likely resulting from the fact that high traffic intensities appeared only locally while identified invasion routes integrated full sequences of suitable routes.

The waterway network consists of comparatively few links, which does not allow the selection of many alternative routes. Consequently, the major routes of spread along waterways represent the major transport routes: the Rhine system, including the canal to the Danube, and the Mittelland Canal through the northern river systems. The identification of shortest paths can also be restricted to certain areas or starting/ending nodes.

4 | DISCUSSION

CASPIAN represents a new model to predict the spread of alien species through and along traffic infrastructure. The model provides a number of unique features: (a) it considers a range of different modes of dispersal associated with traffic and traffic infrastructure, which enables simulating the dispersal along different pathways simultaneously; (b) it integrates various transport networks such as railways, roads and waterways across terrestrial and freshwater habitats, which allows the direct comparison of spread along different networks; (c) it has a modular structure, allowing the selection of individual pathways. Due to this modular structure, further mechanisms of dispersal and establishment can easily be incorporated. With these features, CASPIAN provides a novel way to integrate the complex dynamics of the spread of alien species and complements existing approaches for estimating population dynamics and habitat suitability.

The main novelty of CASPIAN is its ability to simulate different pathways (e.g., natural and human-mediated dispersal), transport modes (e.g., roads and railways) and invasion stages (i.e., introduction and establishment) simultaneously. Other studies have been conducted to model spreading dynamics along individual modes of transport, particularly for plants (e.g., Tackenberg, 2003; Wichmann et al., 2009) and marine species (Floerl et al., 2009; Seebens et al., 2013; Sylvester et al., 2011). An approach similar to ours has been applied to simulate the spread of common ragweed (*Ambrosia artemisiifolia*) along two transport pathways (Chapman et al., 2016). However, to our knowledge, CASPIAN is the first model that covers such a breadth of human-mediated pathways across the terrestrial and aquatic realm. This also represents a challenge because spread processes act on different spatial and temporal scales. Local spreading dynamics are influenced by local population dynamics and biotic interactions (Lemke et al., 2021), which are not covered in our approach (see discussion of assumptions in the Supporting information

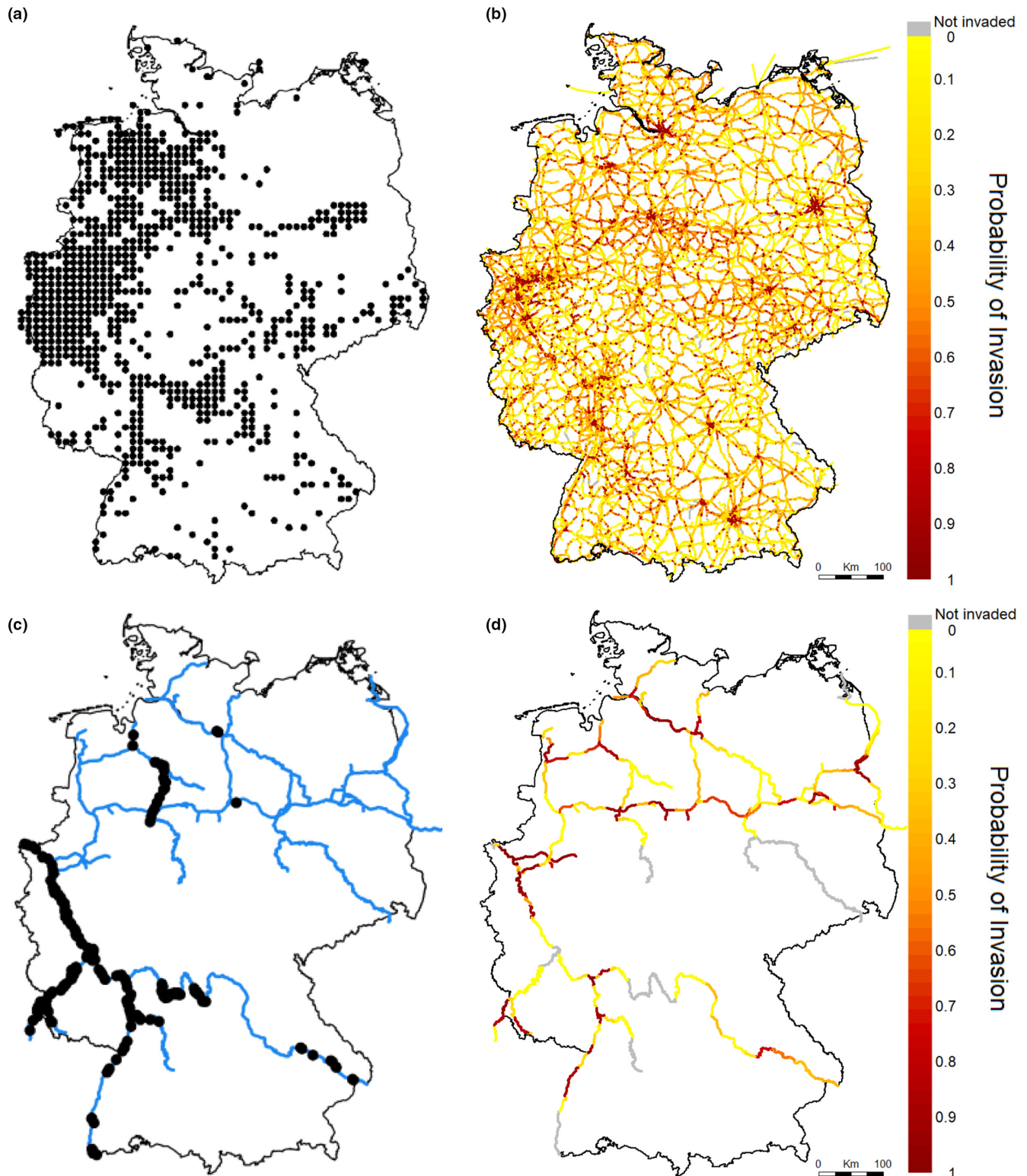


FIGURE 2 Observed (a, c) and predicted (b, d) locations of *Senecio inaequidens* (a, b) and *Corbicula fluminea* (c, d). Observed locations (dots) were obtained from previous studies and either provided in grid cells for *S. inaequidens* or along rivers and canals (blue lines) for *C. fluminea*. Predicted locations are shown for links of the terrestrial and aquatic transport networks, respectively

text). Nevertheless, our study provides a solid basis to implement population dynamics in a subsequent step.

For calibration and validation, we used data sets of regional invasion dynamics with a comparatively coarse spatial resolution

for the terrestrial case study. Therefore, the calibration was less sensitive for model parameters determining local spread processes. Indeed, our calibration did not result in significant changes of model parameters for airstream and natural spread compared

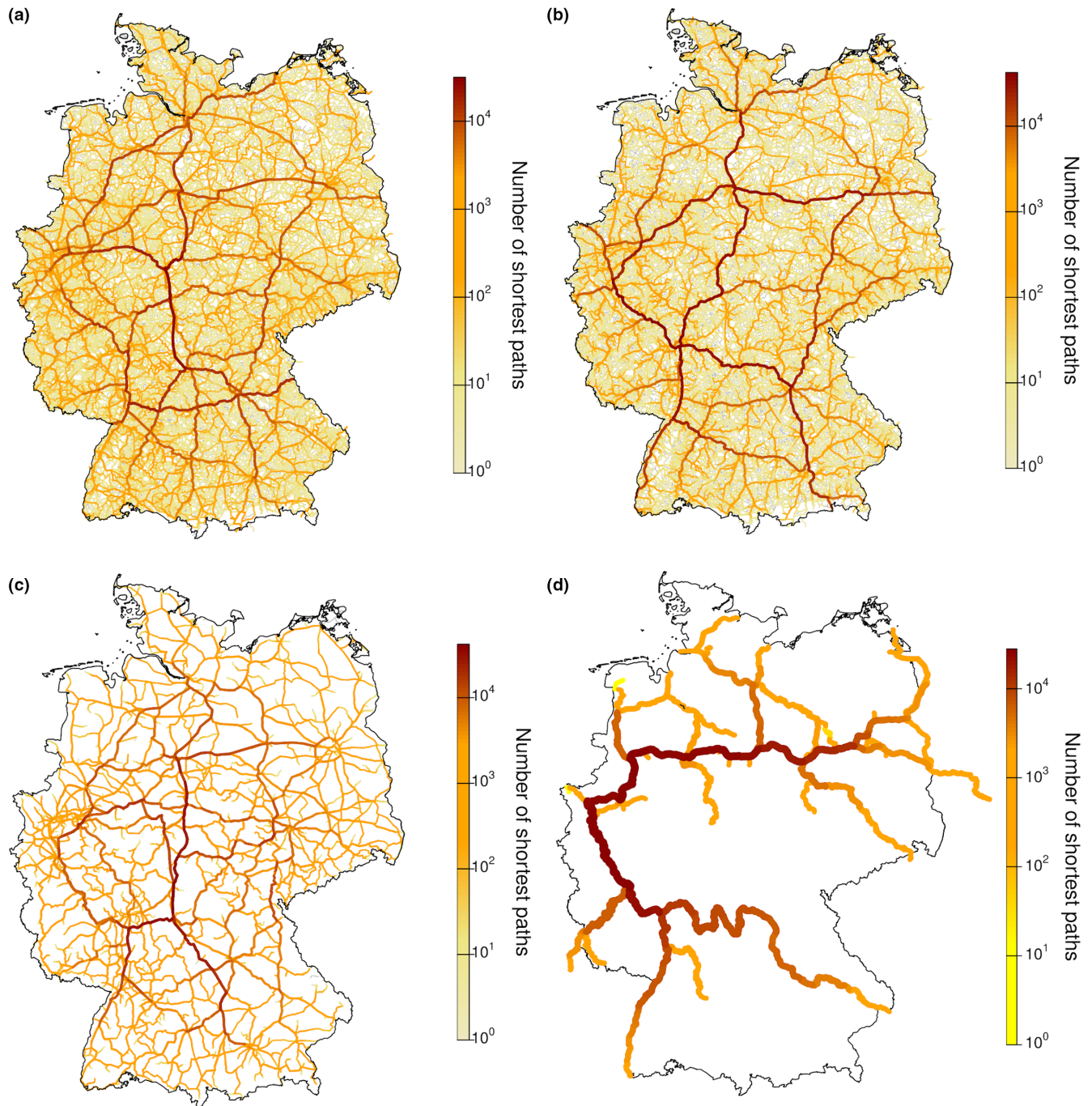


FIGURE 3 Likely routes of spread of alien species within Germany measured as the number of shortest paths going through a certain link. Routes were calculated for the road and railway network combined (a) and for the road (b), railway (c), and waterway (d) network alone. Calculation of shortest paths was based on introduction probabilities $P(l)$

to those values obtained from the literature. This either suggests that those values are appropriate as provided by other studies or that our calibration was not able to determine an improved fit. However, local spread processes were much better investigated in individual case studies (Bullock et al., 2008; von der Lippe et al., 2013). Hence, model parameters for short-distance spread obtained from the literature were likely more intensively tested and, therefore, more robust compared to model parameters determining long-distance spread, which were well identified with

our calibration. Available data were limited as samples were not taken in a consistent way across regions and times and are likely affected by varying sampling intensities and detection probabilities. Moreover, the availability of presence-only data limits the possibility of accurately predicting absences of species. This, however, results from low data quality and highlights the need for better data to refine future estimates.

Validating model results revealed that model predictions were moderate for *S. inaequidens*, which likely resulted from uncertainty

inherent in the observations used for calibration and the fact that the spread of this species is actually not restricted to traffic and traffic infrastructure (Heger & Boehmer, 2005). The coarse spatial resolution of the observations for that species likely reduced the efficiency and effectiveness of the calibration process. This could be partly addressed by using a Bayesian calibration approach, but this cannot compensate for all data limitations. Moreover, many isolated populations of that species were found throughout Germany in 2004 (Figure S2), which are unlikely to have been colonised from the initial starting points as observed in 1989. *S. inaequidens* might have been introduced to these sites in complex and multiple ways, including introductions from outside the study area, spread along routes outside the study area or dynamics independent of traffic, which are difficult to capture using CASPIAN. For example, *S. inaequidens* has been commonly found in disturbed areas (García-Serrano et al., 2004) and open ground along highways due to road maintenance work in Germany (Boehmer et al., 2001). This might explain the many isolated locations of that species, particularly in 2004 (Figure S2). Furthermore, *S. inaequidens* populations in more competitive environments evolved lower sensitivity to competition at the expense of delayed reproduction (Lachmuth et al., 2011). The demographic rates underlying its spread have thus probably changed during the invasion, a phenomenon that is not considered in the current version of CASPIAN.

The distribution of *C. fluminea* could generally be simulated well by our model with a few mispredictions (e.g., the wrongly predicted spread to eastern Germany). The lack of populations at these sites is likely a consequence of low winter temperatures preventing the establishment of persistent populations (Schöll, 2000). Unfortunately, information about winter temperatures was not available for all river systems and could therefore not be considered in our habitat suitability estimates. Moreover, the gaps in the distribution of the species between well-established populations may indicate multiple introductions at different sites (Figure S2). However, these gaps likely represent lacking data as the waterways between the populations were often canals, which were not sampled. It, therefore, seems likely that *C. fluminea* spreads continuously from West to East, as predicted by the model.

The processes of dispersal and establishment of alien species are more complex than considered in CASPIAN. Consequently, assumptions about the underlying processes had to be made (see Supporting information). For instance, we implicitly assumed that species only dispersed along traffic infrastructure or by vehicles and that local population dynamics do not influence spreading dynamics. These assumptions are not fully valid for our case studies, but this is an inevitable consequence of simplifying natural processes in a model. Furthermore, additional pathways and drivers such as recreational boating for the aquatic transport or dispersal beyond traffic infrastructure for the terrestrial spread may play a role and are promising candidates for model extension. Further model extensions could allow for more complex relationships between dispersal and habitat suitability (e.g., allowing for faster spread of individuals under unfavourable conditions as in the case of the emerald ash

borer Lutscher & Musgrave, 2017). A very promising extension of CASPIAN would be the integration of demographic distribution models, simulating population dynamics based on demographic data (Briscoe et al., 2019). This would provide population densities rather than presence/absence records of species and would allow for a more accurate consideration of propagule pressure, time lags and invasion potentials.

As it is currently implemented, CASPIAN simulates the process of establishment in a simplified way, as species' preferences are determined beforehand, and habitat suitability is calculated based on a comparatively low set of environmental variables. The rationale for doing so was that the main focus of CASPIAN is the integration of multiple pathways of human-mediated spread rather than estimating habitat suitability. To overcome this oversimplification, we designed CASPIAN so that habitat suitability estimated by other models such as SDMs or demographic distribution models (Briscoe et al., 2019; Pagel et al., 2020) could be imported and used as prior information for the estimation of $P(E)$. Demographic information can therefore be coupled to CASPIAN with relative ease, providing a more robust estimate of habitat suitability.

In conclusion, CASPIAN represents a new tool to simulate and integrate the spread of alien species along multiple pathways. The model has, therefore, the potential to close the gap, which still persists in many modelling studies, of not considering dispersal when estimating the spread potentials of alien species. Our model is not restricted to the transport network used in this study but can be applied to other networks such as the transport of firewood as sources for the introduction and spread of forest pests (Solano et al., 2021), recreational boating (Floerl et al., 2009; Ulman et al., 2019) or the movement along hiking trails (Anderson et al., 2015; Liedtke et al., 2020). Indeed, with appropriate data, the model could be calibrated and validated to any form of spread network. Moreover, CASPIAN represents a tool to quantify the relative importance of individual pathways and routes in complex networks involving multiple pathways of spread. A quantification of pathways and routes improves our basis for developing mitigation strategies to contain the spread of alien species. CASPIAN could support agencies and managers to prioritise pathways for management actions and policies as demanded by international biodiversity goals such as Aichi targets or formulated in the upcoming post-2020 biodiversity framework (CBD, 2021).

AUTHORS' CONTRIBUTIONS

M.B. and H.S. conceived the study, developed the model and conducted all analyses; H.J.B., F.S. and F.M.S. provided data on species distributions and advice on environmental data; H.S., M.B. and L.N. wrote the manuscript with major inputs from all authors.

ACKNOWLEDGEMENTS

We thank Aidin Niamir for technical support in extracting CORINE land cover data, and Moritz von der Lippe and Tina Heger for advice

on species data. We thank the "BMVI Network of Experts" of the Federal Ministry of Transport and Digital Infrastructure (BMVI) of Germany for funding through the Federal Railway Authority of Germany (project number 2017-U-10-1210). We thank for their valuable input: Marion Leiblein-Wild (Federal Railway Authority, Germany); Katja Broeg, Nicole Heibeck, Mariusz Zabrocki (Federal Maritime and Hydrographic Agency of Germany); Daniel Esser, Andreas Sundermeier (German Federal Institute of Hydrology) and Pia Bartels (Federal Highway Research Institute of Germany). Open access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interests.

DATA AVAILABILITY STATEMENT

Environmental data sets are freely available online: land-cover satellite product (<https://land.copernicus.eu/pan-european/corin-e-land-cover>), temperature and conductivity for the river systems of Elbe (<https://www.fgg-elbe.de>), Rhein (<https://iksr.bafg.de/iksr/>), Weser (<https://www.fgg-weser.de>, <http://www.iksm-cipms.org>) and Oder (<http://geoportal.mkoo.pl>). Species occurrence data were obtained from published sources as described in the methods. Model code of CASPIAN is available as an R package via Zenodo <https://doi.org/10.5281/zenodo.4983252> (Bagnara & Seebens, 2021).

ORCID

Larissa Nowak  <https://orcid.org/0000-0002-1910-8041>

Hans Juergen Boehmer  <https://orcid.org/0000-0002-9176-4836>

Frank M. Schurr  <https://orcid.org/0000-0002-4518-0602>

Hanno Seebens  <https://orcid.org/0000-0001-8993-6419>

REFERENCES

- Albert, R., & Barabasi, A. L. (2002). Statistical mechanics of complex networks. *Reviews of Modern Physics*, 74(1), 47–97.
- Anderson, L. G., Rocliffe, S., Haddaway, N. R., & Dunn, A. M. (2015). The role of tourism and recreation in the spread of non-native species: A systematic review and meta-analysis. *PLoS One*, 10(10), e0140833. <https://doi.org/10.1371/journal.pone.0140833>
- Bagnara, M., & Seebens, H. (2021). CASPIAN - calculating alien species probability of invasion along Networks (1.0). Retrieved from <https://doi.org/10.5281/zenodo.4983252>
- Banks, N. C., Paini, D. R., Bayliss, K. L., & Hodda, M. (2015). The role of global trade and transport network topology in the human-mediated dispersal of alien species. *Ecology Letters*, 18(2), 188–199. <https://doi.org/10.1111/ele.12397>
- Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution*, 26(7), 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Boehmer, H. J., Heger, T., & Trepl, L. (2001). *Case studies on alien species in Germany*. German Federal Environment Agency.
- Briscoe, N. J., Elith, J., Salguero-Gómez, R., Lahoz-Monfort, J. J., Camac, J. S., Giljohann, K. M., ... Guillerá-Arroita, G. (2019). Forecasting species range dynamics with process-explicit models: Matching methods to applications. *Ecology Letters*, 22(11), 1940–1956. <https://doi.org/10.1111/ele.13348>
- Bullock, J. M., Pywell, R. F., & Coulson-Phillips, S. J. (2008). Managing plant population spread: Prediction and analysis using a simple model. *Ecological Applications*, 18(4), 945–953. <https://doi.org/10.1890/07-1128.1>
- CBD. (2021). *First draft of the post-2020 global biodiversity framework*. Secretariat of the Convention on Biological Diversity. Retrieved from <https://www.cbd.int/doc/c/d605/21e2/2110159110d84290e1afca98/wg2020-03-03-en.pdf>
- Chapman, D., Purse, B. V., Roy, H. E., & Bullock, J. M. (2017). Global trade networks determine the distribution of invasive non-native species. *Global Ecology and Biogeography*, 26(8), 907–917. <https://doi.org/10.1111/geb.12599>
- Chapman, D. S., Makra, L., Albertini, R., Bonini, M., Páldy, A., Rodinkova, V., Šikoparija, B., Weryszko-Chmielewska, E., & Bullock, J. M. (2016). Modelling the introduction and spread of non-native species: International trade and climate change drive ragweed invasion. *Global Change Biology*, 22(9), 3067–3079. <https://doi.org/10.1111/gcb.13220>
- Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. In *InterJournal: Vol. Complex Systems*. Retrieved from <https://igraph.org>
- Ernst, W. H. O. (1998). Invasion, dispersal and ecology of the south African neophyte *Senecio inaequidens* in The Netherlands: From wool alien to railway and road alien. *Acta Botanica Neerlandica*, 47(1), 131–151.
- Faulkner, K. T., Robertson, M. P., & Wilson, J. R. U. (2020). Stronger regional biosecurity is essential to prevent hundreds of harmful biological invasions. *Global Change Biology*, 26(4), 2449–2462. <https://doi.org/10.1111/gcb.15006>
- Floerl, O., Inglis, G. J., Dey, K., & Smith, A. (2009). The importance of transport hubs in stepping-stone invasions. *Journal of Applied Ecology*, 46(1), 37–45. <https://doi.org/10.1111/j.1365-2664.2008.01540.x>
- Fournier, A., Penone, C., Pennino, M. G., & Courchamp, F. (2019). Predicting future invaders and future invasions. *Proceedings of the National Academy of Sciences of the United States of America*, 116(16), 7905–7910. <https://doi.org/10.1073/pnas.1803456116>
- Fricke, E. C., & Svenning, J.-C. (2020). Accelerating homogenization of the global plant–frugivore meta-network. *Nature*, 585(7823), 74–78. <https://doi.org/10.1038/s41586-020-2640-y>
- García-Serrano, H., Escarré, J., & Sans, F. X. (2004). Factors that limit the emergence and establishment of the related aliens *Senecio inaequidens* and *Senecio pterophorus* and the native *Senecio malacitanus* in Mediterranean climate. *Canadian Journal of Botany*, 82(9), 1346–1355. <https://doi.org/10.1139/b04-097>
- Gilbert, M., Gregoire, J.-C., Freise, J. F., & Heitland, W. (2004). Long-distance dispersal and human population density allow the prediction of invasive patterns in the horse chestnut leafminer *Cameraria ohridella*. *Journal of Animal Ecology*, 73(3), 459–468. <https://doi.org/10.1111/j.0021-8790.2004.00820.x>
- Griese, D. (1996). Zur Ausbreitung von *Senecio inaequidens* DC. an Autobahnen in Nordostdeutschland. *Braunschweiger Naturkundliche Schriften*, 5(1), 193–204.
- Heger, T., & Boehmer, H. J. (2005). The invasion of Central Europe by *Senecio inaequidens* DC. - A complex biogeographical problem. *Erdkunde*, 59(1), 34–49. <https://doi.org/10.3112/erdkunde.2005.01.03>
- Hudgins, E. J., Liebhold, A. M., & Leung, B. (2017). Predicting the spread of all invasive forest pests in the United States. *Ecology Letters*, 20(4), 426–435. <https://doi.org/10.1111/ele.12741>
- Hulme, P. E. (2021). Unwelcome exchange: International trade as a direct and indirect driver of biological invasions worldwide. *One Earth*, 4(5), 666–679. <https://doi.org/10.1016/j.oneear.2021.04.015>
- Lachmuth, S., Durka, W., & Schurr, F. M. (2010). The making of a rapid plant invader: Genetic diversity and differentiation in the native

- and invaded range of *Senecio inaequidens*. *Molecular Ecology*, 19(18), 3952–3967. <https://doi.org/10.1111/j.1365-294X.2010.04797.x>
- Lachmuth, S., Durka, W., & Schurr, F. M. (2011). Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: The role of genetic Allee effects, adaptive and non-adaptive evolution. *New Phytologist*, 192(2), 529–541. <https://doi.org/10.1111/j.1469-8137.2011.03808.x>
- Lemke, A., Buchholz, S., Kowarik, I., Starfinger, U., & von der Lippe, M. (2021). Interaction of traffic intensity and habitat features shape invasion dynamics of an invasive alien species (*Ambrosia artemisiifolia*) in a regional road network. *Neobiota*, 64, 155–175. <https://doi.org/10.3897/neobiota.64.58775>
- Leung, B., Drake, J. M., & Lodge, D. M. (2004). Predicting invasions: Propagule pressure and the gravity of allee effects. *Ecology*, 85(6), 1651–1660.
- Levine, J. M., & D'Antonio, C. M. (2003). Forecasting biological invasions with increasing international trade. *Conservation Biology*, 17(1), 322–326. <https://doi.org/10.1046/j.1523-1739.2003.02038.x>
- Liebold, A. M., Brockerhoff, E. G., & Kimberley, M. (2017). Depletion of heterogeneous source species pools predicts future invasion rates. *Journal of Applied Ecology*, 54(6), 1968–1977. <https://doi.org/10.1111/1365-2664.12895>
- Liedtke, R., Barros, A., Essl, F., Lembrechts, J. J., Wedegärtner, R. E. M., Pauchard, A., & Dullinger, S. (2020). Hiking trails as conduits for the spread of non-native species in mountain areas. *Biological Invasions*, 22(3), 1121–1134. <https://doi.org/10.1007/s10530-019-02165-9>
- Lutscher, F., & Musgrave, J. A. (2017). Behavioral responses to resource heterogeneity can accelerate biological invasions. *Ecology*, 98(5), 1229–1238. <https://doi.org/10.1002/ecy.1773>
- Pagel, J., Treurnicht, M., Bond, W. J., Kraaij, T., Nottebrock, H., Schutte-Vlok, A. L., Tonnabel, J., Esler, K. J., & Schurr, F. M. (2020). Mismatches between demographic niches and geographic distributions are strongest in poorly dispersed and highly persistent plant species. *Proceedings of the National Academy of Sciences*, 117(7), 3663–3669. <https://doi.org/10.1073/pnas.1908684117>
- Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., ... Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, 95(6), 1511–1534. <https://doi.org/10.1111/brv.12627>
- Saul, W.-C., Roy, H. E., Booy, O., Carnevali, L., Chen, H.-J., Genovesi, P., Harrower, C. A., Hulme, P. E., Pagad, S., Pergl, J., & Jeschke, J. M. (2017). Assessing patterns in introduction pathways of alien species by linking major invasion data bases. *Journal of Applied Ecology*, 54(2), 657–669. <https://doi.org/10.1111/1365-2664.12819>
- Schöll, F. (2000). Die Temperatur als verbreitungsregulierender Faktor von *Corbicula fluminea* (O.F. Müller 1774). *Hydrologie und Wasserbewirtschaftung*, 44, 318–321.
- Schöll, F. (2013). Verbreitung der Körbchenmuschel *Corbicula fluminea* (O. F. Müller 1774) in Abhängigkeit von der Wassertemperatur in deutschen Bundeswasserstraßen. *Lauterbornia*, 76, 85–90.
- Schurr, F. M., Pagel, J., Cabral, J. S., Groeneveld, J., Bykova, O., O'Hara, R. B., Hartig, F., Kissling, W. D., Linder, H. P., Midgley, G. F., Schröder, B., Singer, A., & Zimmermann, N. E. (2012). How to understand species' niches and range dynamics: A demographic research agenda for biogeography. *Journal of Biogeography*, 39(12), 2146–2162. <https://doi.org/10.1111/j.1365-2699.2012.02737.x>
- Seebens, H., Briski, E., Ghabooli, S., Shiganova, T., MacIsaac, H. J., & Blasius, B. (2019). Non-native species spread in a complex network: The interaction of global transport and local population dynamics determines invasion success. *Proceedings of the Royal Society B: Biological Sciences*, 286(1901), 20190036. <https://doi.org/10.1098/rspb.2019.0036>
- Seebens, H., Gastner, M. T., & Blasius, B. (2013). The risk of marine bio-invasion caused by global shipping. *Ecology Letters*, 16(6), 782–790. <https://doi.org/10.1111/ele.12111>
- Seebens, H., Schwartz, N., Schupp, P. J., & Blasius, B. (2016). Predicting the spread of marine species introduced by global shipping. *Proceedings of the National Academy of Sciences of the United States of America*, 113(20), 5646–5651. <https://doi.org/10.1073/pnas.1524427113>
- Solano, A., Rodriguez, S. L., Greenwood, L., Dodds, K. J., & Coyle, D. R. (2021). Firewood transport as a vector of forest pest dispersal in North America: A scoping review. *Journal of Economic Entomology*, 114(1), 14–23. <https://doi.org/10.1093/jee/toaa278>
- Sylvester, F., Kalaci, O., Leung, B., Lacoursière-Roussel, A., Murray, C. C., Choi, F. M., Bravo, M. A., Therriault, T. W., & MacIsaac, H. J. (2011). Hull fouling as an invasion vector: Can simple models explain a complex problem? *Journal of Applied Ecology*, 48(2), 415–423. <https://doi.org/10.1111/j.1365-2664.2011.01957.x>
- Tackenberg, O. (2003). Modeling long-distance dispersal of plant diaspores by wind. *Ecological Monographs*, 73(2), 173–189.
- Ulman, A., Ferrario, J., Forcada, A., Seebens, H., Arvanitidis, C., Occhipinti-Ambrogi, A., & Marchini, A. (2019). Alien species spreading via biofouling on recreational vessels in the Mediterranean Sea. *Journal of Applied Ecology*, 56(12), 2620–2629. <https://doi.org/10.1111/1365-2664.13502>
- von der Lippe, M., Bullock, J. M., Kowarik, I., Knopp, T., & Wichmann, M. (2013). Human-mediated dispersal of seeds by the airflow of vehicles. *PLoS One*, 8(1), 1–10. <https://doi.org/10.1371/journal.pone.0052733>
- von der Lippe, M., & Kowarik, I. (2007). Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conservation Biology*, 21(4), 986–996. <https://doi.org/10.1111/j.1523-1739.2007.00722.x>
- Westphal, M. I., Browne, M., MacKinnon, K., & Noble, I. (2008). The link between international trade and the global distribution of invasive alien species. *Biological Invasions*, 10(4), 391–398.
- Wichmann, M. C., Alexander, M. J., Soons, M. B., Galsworthy, S., Dunne, L., Gould, R., Fairfax, C., Niggemann, M., Hails, R. S., & Bullock, J. M. (2009). Human-mediated dispersal of seeds over long distances. *Proceedings of the Royal Society B: Biological Sciences*, 276(1656), 523–532. <https://doi.org/10.1098/rspb.2008.1131>

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Bagnara, M., Nowak, L., Boehmer, H. J., Schöll, F., Schurr, F. M., & Seebens, H. (2022). Simulating the spread and establishment of alien species along aquatic and terrestrial transport networks: A multi-pathway and high-resolution approach. *Journal of Applied Ecology*, 59, 1769–1780. <https://doi.org/10.1111/1365-2664.14184>