Methods in Ecology and Evolution

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Full title: Rapid spatial risk modelling for management of early weed invasions: balancing ecological complexity and operational needs

Running title: Rapid spatial modelling of weed invasion risk

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Abstract

1. When an invasive alien 'weed' emerges in a previously uninhabited landscape, land managers must respond quickly to facilitate effective eradication or containment, and minimize long-term negative impacts. However, on-ground management decisions are often made under time, knowledge and capacity constraints. Spatially explicit tools for assessing invasion risk rapidly and under uncertainty would help land managers to better target interventions.

2. We developed a generic methodology that integrates (i) interactions between ecological risk factors and invasion processes affecting both the potential suitability for population growth and the actual susceptibility to propagule introduction from source populations with (ii) spatially explicit data in (iii) a probabilistic Bayesian network modelling framework. Our methods focused on the operational needs of land mangers responding to weed incursions, streamlining data and knowledge collection, simplifying model calibration, and facilitating adoption via a collection of user-friendly web apps called **riskmapr**.

3. We tested the generality of our methodology on two contrasting weeds (the rainforest tree *Cecropia* spp. and the cactus *Cylindropuntia rosea*) that are targeted for containment and local eradication in Queensland, Australia. Case study models were calibrated from published knowledge about abiotic and biotic factors affecting suitability for, and

susceptibility to, weed invasion. Validation of annual risk maps against weed detections in subsequent years showed that models accurately predicted the field-observed progression of each invasion to date.

4. We developed a rapid spatial risk modelling methodology that is theoretically comprehensive and practically simple. Our streamlined methods and open access implementation using **riskmapr** facilitate adoption by land managers. Models and risk maps can be used to target interventions or improve spatially explicit understanding of the risk factors and processes driving early weed invasions.

5.

Keywords: Bayesian network, emerging invasive weeds, incursion response, invasion risk, non-native plants, spatial model, suitability, susceptibility

Introduction

Across the globe, alien plant species are a major threat to biodiversity and agricultural industries (Wilson, Panetta & Lindgren 2017). While negative impacts are usually dominated by few widely established invasive 'weeds' (Sinden *et al.* 2004), new alien plants are continuously introduced across borders, regions or landscapes (Dodd *et al.* 2015), some of which have the potential to become serious problems. As such an invasive weed emerges, there is often a distinct lag phase, during which population growth and spread is slow. This initial post-entry incursion phase is followed by rapid expansion and ultimately widespread dominance when most negative impacts are realized (Wilson, Panetta & Lindgren 2017). Early and rapid response to weed incursions may bring greatest opportunities with regard to facilitating eradication or containment, and minimizing long-term costs of management and impacts (Adams *et al.* 2015; Wilson, Panetta & Lindgren 2017). However, successfully

responding to an incursion requires delimiting the extent of an infestation, removing each

detected individual (and thereby preventing it from producing new propagules), controlling

the dispersal of propagules, and finding and controlling new individuals where further

dispersal has occurred (Panetta & Lawes 2005; Panetta 2007; Panetta & Cacho 2012). In

practice, these management objectives are not easily achieved, especially when time,

resources and knowledge about the spatial processes (e.g. dispersal pathways, habitat

requirements) contributing to invasive spread are limited (Fletcher & Westcott 2013).

Instead, on-ground decisions on where to monitor and how to intervene are often based on

rules-of-thumb about the spatial distribution of risk (e.g. prescribed buffer zones of 500m in

Erbacher *et al.* 2008 or 2km in Graham 2017). Spatially explicit tools for assessing invasion

risk rapidly and under uncertainty are needed that enable land managers to better target

interventions.

Management of early weed invasions essentially aims at preventing a population from

persisting (eradication), or confining it within a well-defined area (containment). Hence,

understanding what processes drive population persistence, and how these processes play out

in the landscape, will aid management (Fletcher & Westcott 2013). Theory suggests that

population persistence in a landscape context depends on two general ecological processes:

local population growth and connectivity between local populations (Hastings 2014). These

processes have been conceptually refined, divided into measurable entities, and applied to the

specific context of biological invasions (Panetta 2007; Savage & Renton 2014; O'Reilly-

Nugent *et al.* 2016). Here, we adopt the conceptual framework and terminology proposed by

Smith *et al.* (2012) to describe weed invasion risk.

Smith *et al.* (2012) distinguish between two measures of risk: suitability for, and

susceptibility to, invasion. Suitability is an attribute of the landscape describing its potential

to support a growing weed population. It is decomposed into two invasion processes:

"establishment" refers to dormancy release, germination and recruitment of offspring, and "persistence" refers to survival, growth and reproduction of mature plants (Smith *et al.* 2012; note the difference to "population persistence" as in Hastings 2014). Both processes may be influenced by many abiotic and biotic factors (Soberon & Peterson 2005; Holloway & Miller 2017). Suitability is often viewed as a static and site-specific attribute (Marshall *et al.* 2013; van Klinken, Murray & Smith 2015), but may also be affected by landscape context or environmental change (Murray, Stokes & van Klinken 2012; O'Reilly-Nugent *et al.* 2016). Susceptibility to invasion depends not only on potential suitability, but also on the actual arrival of propagules from connected source populations (Smith *et al.* 2012). It is thus dependent on a third invasion process "propagule pressure" (termed "introduction" in Smith *et al.* 2012), which refers to both the supply of propagules and their movement over short, or long, distances (Panetta & Cacho 2012; Savage & Renton 2014; O'Reilly-Nugent *et al.* 2016; Jordano 2017). Propagule supply may be affected by factors such as source population abundance and reproductive biology, while propagule dispersal may involve a suite of vectors such as wind, water, animals or humans (Benvenuti 2007; Vittoz & Engler 2007).

Commonly not all these variables and processes affecting population persistence are empirically understood, especially in the context of early weed invasions. Hence, a suite of modelling tools and frameworks for estimating population persistence and range dynamics based on underlying ecological mechanisms and spatial processes have been developed (Lurgi *et al.* 2015). Several of these were specifically designed for simulating biological invasions (Williams *et al.* 2008; Pitt, Kriticos & Dodd 2011; Fennell *et al.* 2012; Robinet *et al.* 2012; Savage & Renton 2014; Adams *et al.* 2015).

Here we aimed to develop a generic methodology for estimating the likelihood of population persistence in early weed invasions (henceforth termed "invasion risk") that is theoretically comprehensive and practically simple. Our specific objectives were to (i) integrate invasion

processes affecting both the potential suitability for local population growth and the actual susceptibility to propagule introduction from connected source populations within a coherent, spatially-explicit modelling framework; (ii) facilitate implementation within the time, knowledge and capacity constraints commonly faced by land managers responding to weed incursions; and (iii) test the generality of the modelling methodology, and evaluate its performance, by applying it to two contrasting case study species.

Materials and methods

Bayesian network models

In Bayesian network (BN) models, 'parent nodes' are linked to 'child nodes' via directed causal relationships in a graphical influence diagram. Each network node has at least two mutually exclusive states, which exhaustively capture its total range of numerical values or discrete conditions. Causal effects and interactions between multiple influential parent nodes are quantified in conditional probability tables (CPT) behind each child node. Due to their probabilistic properties, BNs are suited to assessing risk under uncertainty (Fenton & Neil 2013).

When implementing Smith *et al.*'s (2012) spatially explicit framework as a BN model, the two measures of invasion risk (suitability and susceptibility) are linked to invasion processes (establishment, persistence and propagule pressure), invasion processes to measurable risk factors, and risk factors to remotely sensed or mapped spatial proxies. Based on the state of each risk factor proxy at a given location, invasion risk can thus be modelled, and mapped. The BN approach has been extensively applied to model invasion risk for diverse weed species (Murray, Stokes & van Klinken 2012; Marshall *et al.* 2013; van Klinken, Murray & Smith 2015).

Here, we adapted Smith *et al.*'s (2012) spatially explicit BN modelling approach to the needs of rapid incursion response. We focused on three areas of methodological improvement: (i) streamline conceptual model development, including guidance on risk factor identification, model structure and spatial proxy selection, (ii) simplify predictive model calibration via a "ranked node approach", and (iii) facilitate adoption via a collection of user-friendly web apps called **riskmapr** to run predictive models and generate risk maps. We elaborate on each area below. An overview of the methodological workflow is provided in Fig. 1. Concrete examples for each step are provided as part of our case studies (below and Appendix S1, Supporting information). A detailed user guide for applying our methodology to other species is provided in Appendix S2, Supporting information.

Fig. 1. Rapid risk modelling workflow. For each methodological step, we summarize its overall purpose, required tasks and suggested methods.

Conceptual model development

We reviewed the literature for abiotic and biotic factors commonly identified as influencing plant establishment and persistence (Soberon & Peterson 2005; Marshall, Lewis & Ostendorf 2012; van Klinken, Murray & Smith 2015), or propagule pressure (Benvenuti 2007; Vittoz & Engler 2007). On that basis, we devised a comprehensive yet compact typology of risk factors affecting suitability for, and susceptibility to, plant invasion that can be applied to any species (Fig. 2). Risk factors for suitability were further grouped into the overarching themes climate, vegetation / land use, soil, topography, and disturbance. Risk factors for susceptibility were grouped into propagule supply and two categories of dispersal modes – linear, and diffuse (distance-dependent).

Fig. 2. Typology of risk factors affecting suitability (incl. establishment and persistence) for, and susceptibility to, plant invasion.

In our methodology, knowledge about relevant risk factors is gathered via desktop research and a risk factor weighting assigned using a traffic light system (where red = highly, amber = moderately, and green = somewhat important, Fig. 1, step 1). This process is similar to common non-spatial pest risk assessments, and can accommodate detailed expert knowledge or empirical data, if available. Next, risk factors are structured according to which invasion process (establishment, persistence or propagule pressure) is affected and combined in a conceptual model (Fig. 1, step 2). We let each risk factor influence only one process, which may simplify ecological realities but avoids issues with 'double counting' (Marshall *et al.* 2013). In order to be able to map invasion risk, remotely sensed or mapped proxies to represent each risk factor, as well as spatial data on weed detections, are gathered (Fig. 1, step 3). Each risk factor is also assigned several discrete states (typically relating to a high, moderate and low risk level). Defining risk factors and their states to be specific and measurable will help matching spatial proxy attributes to one of these risk factor states.

Predictive model calibration

When translating a conceptual model into a predictive BN model of invasion risk, previous research has relied on structured expert elicitation (Murray, Stokes & van Klinken 2012; Smith *et al.* 2012; van Klinken, Murray & Smith 2015) or empirical data (Marshall et al. 2013). This can be complex, time-intensive and ultimately impractical for land managers. Our methodology greatly simplified calibration of CPTs by implementing the ranked node approach suggested in Fenton, Neil and Caballero (2007) (Fig. 1, step 4). Here the discrete states of all model variables (parent and child nodes) are ordered by risk level and mapped

onto a numerical scale bounded by [0,100]. Each parent node is then assigned a weight representing its relative influence. We translated the risk factor weighting from step 1 above into numerical weights (where 3 = highly, 2 = moderately, and 1 = somewhat important). CPTs of child nodes are then computed as truncated normal distributions bounded on the interval [0,100] with a mean equal to the weighted mean of all influential parent nodes (Fenton, Neil & Caballero 2007).

We implemented the ranked node approach in the R statistical software (v 3.5.0; R Core Team 2018) as a collection of Shiny (Chang *et al.* 2017) web apps called **riskmapr**. Descriptions of statistical methods, a detailed walkthrough of our algorithm using a case study example, and references to R packages are provided in Appendix S2, Supporting information.

Spatial modelling and mapping

Methods for linking BN models to spatially-explicit data have recently proliferated, but often remained cumbersome (Johnson, Low-Choy & Mengersen 2012; van Klinken, Murray & Smith 2015). Ultimately, spatially-explicit BNs require a set spatial data files that specify the state of each risk factor included in the model at each location in (an appropriately defined) study area. Here, we simplify spatial integration procedures. We provide detailed guidance on preparing spatial risk factor proxies and weed detection records using GIS software (Fig. 1, step 5). The **riskmapr** web apps let users perform further customized geoprocessing tasks, run BN models of suitability and susceptibility, and generate risk maps in a graphical user interface that requires no interaction with the underlying source code (Fig. 1, steps 6 and 7).

In our methodological framework, suitability for weed invasion is modelled and mapped only once across the entire study area (Fig. 1, step 7a), based on the state of each risk factor at the

time of investigation (or more exactly, its spatial proxy at the time of mapping).

Susceptibility to invasion, however, dynamically responds to the supply and dispersal of propagules from source infestations. Hence, spatial proxies for propagule pressure must be referenced to a set of infestations detected during a specific timeframe. We suggest suitable "detection periods" can be derived from a weed's biological (e.g. fruiting seasons when new seeds are produced) or management (e.g. discrete periods when weed surveys have been conducted) context. For a given detection period, we model susceptibility only within a defined "dispersal risk area" where propagule introduction from any of the recorded source infestations is deemed likely given the identified dispersal modes. We suggest using published median and upper limit dispersal distances to define risk area thresholds (Vittoz & Engler 2007; Groves 2010; Tables S1.2, S1.3 and S2.2, Supporting information). We provide a custom **riskmapr** geoprocessing toolbox to generate spatial proxies for propagule supply and a range of dispersal modes for one, or several, detection periods of interest (Fig. 1, step 6). Together with spatial proxies for risk factors affecting plant establishment and persistence, tool outputs are used when modelling susceptibility to weed invasion using **riskmapr** (Fig. 1, step 7b).

Case study risk model development

Two contrasting weeds in the state of Queensland, Australia were selected to test the generality of our modelling methodology. Mexican bean tree (*Cecropia* spp.) invades disturbed rainforest habitats in tropical or subtropical areas, while the succulent Hudson pear (*Cylindropuntia rosea* and the similar *C. tunicata*) severely impacts on ecosystems and agriculture in semi-arid rangelands. In both cases, taxonomy has been somewhat unclear. For example, *Cecropia* in Queensland consists predominately of *C. peltata*, plus *C. palmata* and *C. pachystachya* (Graham 2017). Yet, information about infestations and species ecology has

mostly been confined to the genus level. While both species complexes do not constitute very recent incursions, (i) empirical data was available for multiple detection periods allowing us to evaluate model performance, and (ii) both are managed for containment and local eradication by the State's biosecurity agency similarly to early weed invasions at which our methodology is aimed. Knowledge about risk factors was gathered via desktop research and informal expert consultation. Spatial data was collected from openly accessible sources (Appendix S1, Supporting Information).

Mexican bean tree

Mexican bean tree (MBT) is a neotropical pioneer species. Fast growing and highly fecund, MBT invades and dominates early successional habitats in tropical and subtropical rainforests as well as other disturbed sites (Csurhes 2016). Our study area encompassed the 2 million hectare Wet Tropics bioregion in northern Queensland (Department of the Environment 2012), which contains most naturalized infestations of MBT recorded in Australia to date (Department of Agriculture and Fisheries 2017; Fig. 3a).

Here we assumed that MBT establishment (dense recruitment of seedlings) is most sensitive to vegetation and land use types of varying quality, but also depends on the availability of sufficient sunlight, and a favourable soil moisture content. MBT persistence (survival and fecundity of mature individuals) was influenced by dry season rainfall and elevation. To model susceptibility, we divided a data set of 320 detection records collected from 2008 to 2016 into 9 annual detection periods (May to April), which were broadly centred on the species' fruiting peak in the early wet season. Propagule pressure (amount of seeds likely arriving from source infestations) depended mostly on the presence and abundance of mature, seed-producing individuals (propagule supply) and the dispersal of seeds into the surrounding

landscape by flying animals (endozoochory mediated by bird or bat ingestion). Linear seed dispersal by flowing water (hydrochory) was considered less important. For each risk factor included in the model (Figs 4 and 5a), suitable remotely sensed or mapped spatial proxies were sourced, converted to raster format, projected to the reference system EPSG:28355, resampled to a 1 ha (100m x 100m) resolution, and reclassified to match the states of risk factors (Table S1.2, Supporting information; Froese & Hamilton 2017).

Hudson pear

Hudson pear is a highly invasive, branched, succulent shrub of Mexican origin. It possesses a large environmental plasticity, disperses rapidly via detachable stem segments and is difficult to control (Deltoro *et al.* 2013). First introduced to Australia in the 1960s, the species has established localized populations across the continent. Our distributional data was limited to the state of Queensland, where the study area encompassed all Australian bioregions (Department of the Environment 2012) within semi-arid or arid agro-climatic zones (Hutchinson *et al.* 2005). In this vast 113 million hectare region, over 2800 detection records were collected at two naturalization sites between 2011 and 2017 (Department of Agriculture and Fisheries 2017; Fig. 3b).

We modelled Hudson pear establishment as a function of habitat type in both natural and managed land systems, and soil texture. Persistence was climate-dependent, with low annual rainfall and persistent night-time frost or intense day-time heat limiting long-term survival and growth. Unlike MBT, susceptibility to invasion could not easily be referenced to a reproductive period. While stem growth occurs mainly during the wetter summer, Hudson pear vegetatively reproduces anytime and at any life stage. However, distributional data was collected irregularly with up to 16 months between subsequent detections, allowing us to

define 6 separate 'detection periods', albeit of varying length and sampling intensity. In each

detection period, propagule pressure was most strongly affected by plant abundance

(propagule supply), and the linear dispersal of propagules by floodwaters (hydrochory).

Transportation of spiny stem segments by animals (epizoochory) or vehicles (agochory) was

considered moderately important. Spatial proxies for each risk factor included in the model

(Figs 4 and 5b) were pre-processed similar to MBT, except that a different projection

(EPSG:3577) and coarser resolution (200m x 200m = 4 ha) were chosen to increase

computational efficiency across the expansive study area (Table S1.3, Supporting

information).

Fig. 3. Study areas for Mexican bean tree (a) and Hudson pear (b) in Queensland, Australia.
Study areas are shown in grey. Locations of naturalized infestations used for modelling and validating susceptibility to invasion are shown in red (Mexican bean tree) and blue (Hudson pear). Detections of individual Hudson pear (yellow dots) refer to isolated garden specimens and were excluded from this study.

Fig. 4. Risk factors included in the case study risk models for Mexican bean tree and Hudson pear (with justification and colour coded by weighting). Further details on risk factors and spatial proxies, including references and data sources, are provided in Appendix S1, Supporting information.

Fig. 5. Conceptual Bayesian network model for Mexican bean tree (a) and Hudson pear (b).
Risk factors are colour coded by risk-factor weighting.

Case study risk model evaluation

For each case study, we evaluated the predictive performance of risk models with regard to

the historical progression of each invasion observed in the field (Department of Agriculture

and Fisheries 2017). For this purpose, we validated modelled susceptibility for each of the

defined detection periods against subsequently recorded weed detections. For MBT we used

records from the following three detection periods to allow for delays in germination,

maturation and detection in densely vegetated rainforest habitat (e.g. mapped 2012-13

predictions were validated against actual detections during 2013-14, 2014-15 and 2015-16;

Fig. 6c). For Hudson pear we used records from only two subsequent detection periods (e.g. 2015-16 predictions were validated against 2016-17 and late 2017 detections; Fig. 6d). While surveys were irregular and localized, resulting in potential detection delays, we assumed that propagules strike root quickly and are readily detected in the predominantly open rangeland vegetation once surveyed.

We report the Continuous Boyce Index (CBI) performance metric, which has previously been used to evaluate BN model predictions against presence-only observations (Hirzel *et al.* 2006; Froese *et al.* 2017). In this method, the full range of predicted susceptibility indices (i.e. the expected values from the BN model) is partitioned into a series of overlapping bins. For each susceptibility bin, the "predicted-to-expected (P/E) ratio" measures the proportion of detection records within the bin relative to the proportion of the validation background covered by the bin. Here, the background for a given susceptibility model was defined by the dispersal risk area around source infestations. The CBI measures the Spearman rank correlation coefficient of P/E vs. susceptibility and varies from −1 (poor prediction) through 0 (random) to +1 (perfect prediction) (Hirzel *et al.* 2006).

We also tested the robustness of the CBI of each case study model to variations in a range of input parameters, including (i) numerical values assigned to discrete risk factor states (Fig. 1, step 4), (ii) resolution of spatial risk factor proxies (Fig. 1, step 5), and (iii) uncertainty (standard deviation) in the truncated normal distribution used to compute model CPTs (Fig. 1, step 7). Validation and sensitivity analyses were performed in R using the **ecospat** package (Broennimann *et al.* 2017). Details of sensitivity analyses are provided in Appendix S3, Supporting information.

Case study risk model results

Risk maps

Potential suitability for MBT and Hudson pear was mapped for each respective study area (Fig. 6a & b). In both case studies a substantial portion of the study area was modelled as suitable habitat. Nevertheless, there were substantial differences in the degree of risk. For MBT, about half (45%) of the study area was modelled as moderately suitable (index = 40-59), likely supporting scattered individual trees only. Highly or very highly suitable conditions (index = 60-100), which may support widespread moderate or high densities of the invader, covered one third (36%) of Queensland's Wet Tropics. Only 19% of the study area was modelled as unsuitable (index = 0-39), supporting, at best, isolated individual trees. For Hudson pear, however, the vast majority of the 113 million hectare study area contained highly (index = 60-80; 29%) or very highly (index = 80-100, 53%) suitable environments, with moderately and unsuitable areas limited to just 17% and 2% of the region respectively. These results are biologically and ecologically realistic, given (i) Hudson pear's reported plasticity combined with a comparatively uniform vegetation and land use structure in Australia's semi-arid grazing rangelands, and (ii) the availability of substantial tracts of protected tropical rainforest in the Wet Tropics bioregion, which is the primary habitat of MBT but may only support dense infestations at its margins or following localized disturbance.

Actual susceptibility to invasion during a given detection period was modelled only for the dispersal risk area around recorded source infestations (shown illustratively for one site each in Fig. 6c & d). Depending on abundance patterns within each infestation site, and suitability within the dispersal risk area, susceptibility varied substantially between detection periods.

Fig. 6. Mapped suitability for, and susceptibility to, invasion by Mexican bean tree (a and c) and Hudson pear (b and d). Panels a and b also show locations of naturalized infestations in red (Mexican bean tree) and blue (Hudson pear). Panels c and d show susceptibility for a local subset of recorded source infestations (location shown in a and b) during one detection period (black dots), compared to actually invaded sites recorded during subsequent detection periods (coloured dots).

Model evaluation

Validation plots showing plotted P/E ratios for all detection periods (Fig. 7a & b) reveal that in almost all cases, subsequent detections were much more likely recorded in locations predicted as highly susceptible to invasion than in areas with low or moderate susceptibility. For Mexican bean tree, CBI values ranged from 0.96 to 0.99, indicating highly accurate risk models (i.e. more actual detections as modelled risk increases). Performance metrics for Hudson pear were similar, except for one detection period (2013-14 predictions validated against 2015-17 detections). Here, one infestation was locally eradicated and hence no further individuals detected in areas predicted as high risk from the 2013-14 data. In the other infestation site, most subsequently invaded sites were located in areas predicted as moderately suitable, while most high risk areas actually remained weed-free. Both models discriminated between actually invaded and non-invaded locations only at susceptibility indices above ~60 (= high and very high risk of invasion). Moderate susceptibility (index = 40-59) did not translate into more actual detections in subsequent years than low susceptibility (index = 0-39). While any weed detections outside the dispersal risk area for which risk was modelled and mapped (e.g. detection record at bottom of Fig. 6d) were not adequately reflected in validation statistics, the number of such unanticipated detections remained low.

Sensitivity analyses indicated that the CBI of each case study model was robust to variations in (i) numerical values assigned to discrete risk factor states, (ii) resolution of spatial risk factor proxies, and (iii) standard deviation in the truncated normal distribution used to

compute model CPTs. Degenerate predictions were mostly limited to very coarse resolutions above 400ha (2km x 2km) per raster cell, and standard deviations close to '0' or above '40' which resulted in CPT probability distributions that were either too peaked or too flat to provide meaningful predictions (see Appendix S3, Supporting information).

Fig. 7. Validation plots comparing modelled susceptibility to invasion by Mexican bean tree (a) and Hudson pear (b) for all detection periods to actually invaded sites. The predicted-to-expected ratio (y axis) measures the proportion of invaded sites (recorded during subsequent detection periods) relative to the proportion of background pixels (i.e. the dispersal risk area around all source infestations within a detection period) on a continuous scale of predicted susceptibility index values (x axis). The Continuous Boyce Index (CBI) performance metric is also shown.

Discussion

We set out to develop a generic rapid risk modelling methodology that comprehensively captures the ecological complexity of weed invasions, while at the same time focusing on the operational needs of land managers responding to weed incursions. To this end, we built on an established modelling approach that integrates (i) interactions between ecological risk factors and invasion processes affecting both the potential suitability for population growth and the actual susceptibility to propagule introduction from source populations with (ii) spatially explicit data in (iii) a probabilistic BN modelling framework (Smith *et al.* 2012; van Klinken, Murray & Smith 2015). Our simplified methods, extensive guidance and open access implementation via **riskmapr** web apps facilitate adoption by land managers. By explicitly focusing on operational needs and protocols, our BN based methodology provides a useful alternative to mechanistic modelling tools that have previously been developed (Williams et al. 2008; Pitt, Kriticos & Dodd 2011; Fennell et al. 2012; Robinet et al. 2012; Savage & Renton 2014; Adams et al. 2015). Application requires three types of skills: familiarity with spatial analysis and available GIS data products, ecological and/or field knowledge of the target species, and limited scientific oversight.

In a first step, risk factors affecting plant establishment, persistence and propagule dispersal are identified. Our case studies demonstrated that this can be based on limited desktop research and informal expert consultation, similar to existing protocols for capturing knowledge about invasion risk (Downey *et al.* 2010). To further streamline knowledge capture across target species, we devised a typology of common risk factors. Yet, our framework can flexibly accommodate different levels of knowledge or uncertainty. Where feasible, structured expert elicitation or empirical data collection may be conducted to increase model robustness, and additional influential risk factors may be identified that are not yet adequately captured in our compact list.

Next, interactions between risk factors and invasion processes are structured in a conceptual, graphical model, which is then translated into a predictive, numerical model. The BN approach allows both steps to occur within one coherent statistical framework, while also capturing the uncertainty in modelled interactions. In our implementation, predictive BN models were calibrated using simple weight expressions that describe invasion risk based on the relative importance of interacting variables. While this 'ranked node' approach had applied benefits in terms of modelling effort, speed, and replicability across target species (Fenton, Neil & Caballero 2007), it simplified the real ecological complexity in weed invasions. For example, assuming that the probability of a particular invasion outcome (e.g. plant establishment) can be computed as a truncated normal distribution centred on the mean state of a suite of risk factors did not allow for non-additive interactions, multimodal or skewed responses, limiting factors, or substitution relationships. Future research could extend our transparent implementation of the ranked node approach in R to non-normally distributed response functions, or data-driven methods for calibrating BNs (Fenton & Neil 2013).

In contrast to non-spatial risk assessments (Downey *et al.* 2010), our methodology places weed invasions into a specific spatiotemporal context by linking risk factors to spatial data.

We greatly improved spatial integration compared to previous BN applications (Johnson, Low-Choy & Mengersen 2012; van Klinken, Murray & Smith 2015) by developing a collection of user-friendly web apps called **riskmapr** to perform customized geoprocessing tasks, run BN models of suitability and susceptibility, and generate risk maps. We also provided detailed generic guidance as well as case study examples for collecting and pre-processing remotely sensed or mapped spatial proxies so that they adequately reflect risk factors and their discrete states.

To demonstrate the usefulness and generality of our modelling methodology, we evaluated the predictive performance of both case studies. Validation of annual risk maps against subsequent weed detections showed that locations predicted as highly susceptible to invasion were much more likely to be actually invaded by MBT and Hudson pear than locations with moderate or low susceptibility. These results suggest that surveillance and containment efforts can be confidently focused on highly susceptible areas, as these were indeed preferentially invaded in the existing data.

However, validation also revealed that there was little difference in actual weed detections between moderately susceptible and non-susceptible locations. This suggests that moderate invasion risk was overestimated in both case studies. This may stem from our parameterisation of dispersal distances from published averages (Table S2.2, Supporting information), and treatment of the resulting dispersal risk area in validation statistics. While median dispersal distances appear robust across native and introduced species (Flores-Moreno *et al.* 2013), there are likely large contextual differences in upper dispersal limits (e.g. ingestion by different bird species, attachment to different types of vehicles, transportation by fast or slow-moving floodwaters). Our risk thresholds may have overstated the likelihood of rare dispersal events, and therefore overestimated the area at risk of propagule introduction. A further issue may have contributed to overestimating risk in the

Hudson pear case study: while dispersal events (flooding, sporadic transportation of stem fragments by vehicles) are highly variable in inland Australia, such stochasticity was not incorporated here. Instead, mapped stream and road lines were assumed to carry the same dispersal risk across all landscapes and detection periods, irrespective of climatic conditions or vehicle density. However, false positives are preferred to false negatives in invasion models due to the potentially high cost of detection failures (Jiménez-Valverde *et al.* 2011). Additionally, a key application of BN models is to test hypotheses and subsequently update prior beliefs (van Klinken, Murray & Smith 2015). Here, this may involve revising upper dispersal limits based on validation results.

Some new weed detections were also located well outside the dispersal risk area around source infestations for which annual susceptibility was modelled, and predictive performance evaluated. These detections may have stemmed from rare natural long-distance dispersal events, which were not adequately captured in the average distances used in case study models (Vittoz & Engler 2007; Jordano 2017). Alternatively, they may have been due to translocation or repeat introduction (e.g. as garden plants). These human-mediated long-distance dispersal processes are difficult to predict or may be entirely disconnected from known source populations, and hence were outside the scope of our methodology. While detecting and controlling new weed infestations resulting from rare or random long-distance dispersal is arguably "key to slowing or stopping the spread of an invasive species" (Hastings 2014:25), we suggest that they are best managed by controlling propagule supply rather than attempting to predict and monitor dispersal (Panetta 2007; Panetta & Cacho 2012).

We envisage several avenues for further enhancing the utility of our methodology. While our **riskmapr** web apps provide a user-friendly interface for performing customized geoprocessing tasks, running models and generating risk maps, a significant portion of spatial data collection and pre-processing tasks remained 'outside' of automated workflows. Despite

the detailed guidance provided, linking risk factors to spatial proxies that are both ecologically meaningful and adequately discretised can be challenging and subjective. It requires familiarity with best-practice spatial data products available in a particular region, and a reasonable level of expertise in spatial analysis and data manipulation using GIS software. Future research may suggest 'default' risk factors and spatial proxies likely to influence the establishment, persistence and dispersal of different types of weeds. Such a weed typology may be based on life form (e.g. tree, shrub, vine, succulent, grass, forb), invaded habitat (e.g. forest, shrubland, grassland, cropland, desert, riparian, coastal, wetland) or functional traits (Wilson, Panetta & Lindgren 2017). Defaults may then be adjusted from specific knowledge where available. Developing a generic software tool that allows users to select risk factors, access and pre-process suitable spatial proxies, run risk models, and generate risk maps within one graphical user interface may further reduce technical barriers to adoption and subjectivity when modelling for diverse species and landscapes. A major challenge would be to curate and maintain a spatial database that is both perpetually updated and applicable to a wide range of species, regions, and levels of detail. Finally, future research could aim at integrating the two measures of invasion risk (potential suitability and actual susceptibility) with the economic and environmental impacts of invasions (e.g. see Holt, Leach & Schrader 2018).

Modelling can improve decision-making for incursion response in several ways. The suitability maps generated by **riskmapr** are a marked improvement on climate-based range maps commonly used in weed risk assessments. Susceptibility maps may be used to direct on-ground surveillance and containment resources towards high risk areas. Perhaps most importantly, our methodology provides a comprehensive and consistent framework for structuring knowledge on the ecological risk factors and invasion processes driving weed invasion risk, and visualising their interactions on a map. It can support adaptive

management, where an initial risk hypothesis is rapidly generated, evaluated against field observations, and on that basis iteratively updated and reassessed.

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Authors' contributions

JGF and GH conceived the idea for this research; JGF, GH and AP designed the methodology; JGF collected data; JGF and AP analysed the data; JGF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data Accessibility

Shiny **riskmapr** web apps are available at the following URLs (note that availability is not guaranteed due to usage restrictions imposed by shinyapps.io):

riskmapr - geoprocessing tools: https://jens-g-froese.shinyapps.io/riskmapr_geoprocessing

riskmapr - suitability model: https://jens-g-froese.shinyapps.io/riskmapr_suitability

riskmapr - susceptibility model: https://jens-g-froese.shinyapps.io/riskmapr_susceptibility

The underlying R code can be downloaded at https://github.com/apear9/riskmapr for local app deployment and further development. The GitHub repository also includes spatial data that can be used to reproduce case study results using **riskmapr**, as well as R code and data

to reproduce sensitivity analyses

(https://github.com/apear9/riskmapr/tree/master/sensitivity_analysis). A ZIP file containing a

current version of the GitHub repository has been published to Zenodo

(https://doi.org/10.5281/zenodo.3347111). Users of **riskmapr** may access the case study data

directly via the "Download case study data" tool of the **riskmapr - geoprocessing tools** app.

A README file is included with the data archive, containing a description of its contents

and how they should be used.

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Step	Purpose	Tasks and methods
Step 1. Risk factors	Identify risk factors for establishment, persistence and propagule pressure	• Review published/grey literature and consult expert practitioners or scientists • If feasible, conduct structured expert elicitation and/or collect empirical data • Justify reasons for including / excluding each risk factor and assign risk factor weightings (template in **Table S.2.1, Supp. information**)
Step 2. Conceptual model	Construct conceptual model of suitability for, and susceptibility to, invasion	• Link each identified risk factor to one invasion process (**Fig S.2.1, Supp. information**) • Define each model variable (invasion risk, invasion processes, risk factors) with reference to the target species (**Table S.2.3, Supp. information**)
Step 3. Spatial data	Source spatial data and link proxies to identified risk factors	• Source remotely sensed or mapped proxies representative of each risk factor • Assign discrete risk factor states (**Table S.2.3, Supp. information**) • Source weed detection records, containing information about detection date and abundance / reproductive status
Step 4. Predictive model	Calibrate a predictive Bayesian network model using ranked nodes	• Assign numerical values (on a scale bounded by [0,100]) to each discrete risk factor state (**Table S.2.3, Supp. information**) • Revise risk factor weightings and translate into numerical weight (1,2 or 3)
Step 5. GIS pre-processing	Prepare spatial proxies for risk factors and weed detection records using GIS	• a. Study area reference raster: define spatial extent, resolution and projection • b. Risk factor proxies: rasterize, classify attributes to match risk factor values • c. Linear dispersal mode proxies: rasterize, classify as '1' vs. 'NA' • d. Weed detection records: clean, add abundance per record, divide into detection periods of interest (e.g. active infestations for future prediction)
Step 6. riskmapr geoprocessing tools	Prepare spatial proxies for propagule pressure during a specified detection period using riskmapr	• Run **riskmapr - geoprocessing tools** for each detection period of interest (**https://jens-g-froese.shinyapps.io/riskmapr_geoprocessing**) • Apply tools as required to prepare spatial proxies for propagule supply and all identified dispersal modes
Step 7. riskmapr models	Model invasion risk (suitability and susceptibility) using riskmapr and map results using GIS	• a. Run **riskmapr - suitability model** once across the entire study area (**https://jens-g-froese.shinyapps.io/riskmapr_suitability**) • b. Run **riskmapr - susceptibility model** for each detection period of interest (**https://jens-g-froese.shinyapps.io/riskmapr_susceptibility**) • Map model results (risk index and uncertainty) using GIS

Environmental suitability for plant invasion	
Climate	Temperature (mean, minimum or maximum)
	Rainfall (mean, minimum or maximum)
Topography	Elevation
	Slope / aspect or similar
Soil	Type / texture
	Moisture
	Nutrients
	pH
Vegetation / land use	Type
	Canopy cover
	Ground cover
Disturbance	Fire
	Flooding
	Human
	Biological (consumption or competition)
Susceptibility to plant invasion	
Propagule supply	
Dispersal diffusion	Animals ground (esp. epizoochory or endozoochory)
	Animals flying (esp. epizoochory or endozoochory)
	Wind (anemochory)
Dispersal linear	Water (hydrochory)
	Humans (esp. agochory)
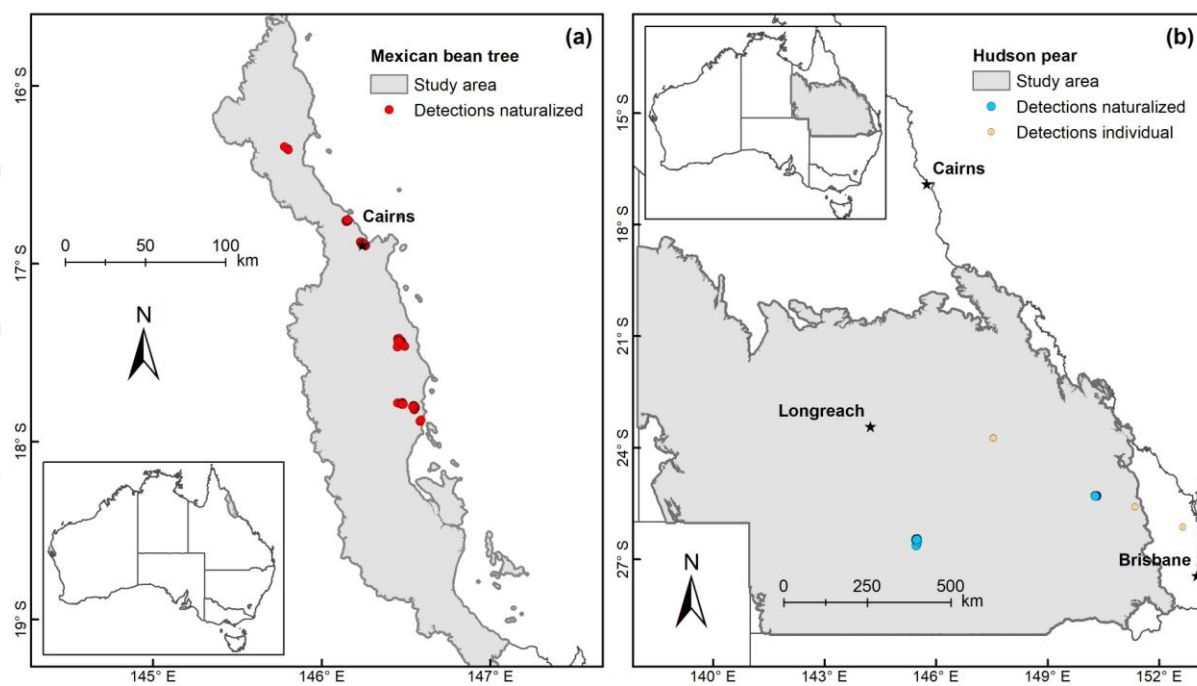
Risk factor		Mexican bean tree (*Cecropia* spp.)	Hudson pear (*Cylindropuntia rosea*)
Climate	Temperature	Intolerant to frost – N/A in study area	Prefers warm/hot climates with mild winters Tolerates some, but not persistent, frost or heat
	Rainfall	Prefers wet (sub-)tropical rainforest climates Tolerates wet-dry (sub-)tropical savanna climates	Prefers semi-arid climates Tolerates drought but not very arid desert
Topo-graphy	Elevation	Grows mainly in lowland rainforests	N/A
	Slope / aspect	N/A	N/A
Soil	Type / texture	N/A	Shallow-rooted, prefers lighter soils Tolerates various but not heaviest / infertile soils
	Moisture	Prefers well-draining soils Does not establish on saturated or dry soils	N/A
	Nutrients	N/A	N/A
	pH	N/A	N/A
Vegetation / land use	Type	Prefers disturbed rainforest habitats Also establishes in other open sites (riparian, roadside, gardens)	Grows in a variety of natural or managed habitats May not establish on intensively managed land, in closed forest or wetlands
	Canopy cover	Prefers full sunlight, esp. seedlings Tolerates some shade but not closed canopies	N/A
	Ground cover	N/A	N/A
Distur-bance	Fire	N/A	N/A
	Flooding	Important risk factor for 'linear dispersal'	Important risk factor for 'linear dispersal'
	Human	Human disturbance important for risk factors 'vegetation type' and 'canopy'	N/A
	Biological	N/A	N/A
Propagule supply		Matures in 3 years; fruits seasonally and seeds prolifically with 4-month early wet peak	Reproduces vegetatively from segments and fruit Germinates opportunistically upon soil contact
Dispersal diffusion	Animals ground	N/A	Spiny segments attach to fur of livestock, domestic, native or feral animals
	Animals flying	Frugivorous bats & birds ingest seeds	N/A
	Wind	N/A	N/A
Dispersal linear	Water	Dropped seeds spread by running water	Segments moved by floodwaters over several km
	Humans	Long-distance dispersal as garden plant – N/A	Spiny segments attach to vehicles, equipment or clothing over several km

3x weighting = highly important	2x weighting = moderately important	1x weighting = somewhat important

Validation against Mexican bean tree detections

Legend

— Detections 2009-12: CBI = 0.976
— Detections 2010-13: CBI = 0.992
— Detections 2011-14: CBI = 0.962
— Detections 2012-15: CBI = 0.965
— Detections 2013-16: CBI = 0.996
— Detections 2014-17: CBI = 0.983

Validation against Hudson pear detections

Legend

— Detections 2012-14: CBI = 0.967

— Detections 2013-15: CBI = 0.993

— Detections 2015-17: CBI = -0.285

— Detections 2017: CBI = 0.984