



Research Article

Mapping risks of pest invasions based on the spatio-temporal distribution of hosts

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Abstract

Surveying multiple invasive pest species at the same time can help reduce the cost of detecting new pest invasions. In this paper, we describe a new method for mapping the relative likelihood of pest invasion via plant propagation material in a geographic setting. The method simulates the invasion of a range of pest species, including arrival in an uninvaded area, spread, and survival in a novel landscape, using information on the spatial and temporal distribution of the suitable host crop species and tentative knowledge of the spread and survival capacities of the target pests. The methodology is applied to a gridded map in which each map cell represents a site in a landscape. The method uses stochastic simulations to depict plausible realizations of the invasion outcomes and estimate the distribution of pest invasion likelihood for each cell in the area of concern. The method then prioritizes the cells based on the stochastic invasion outcomes using a pairwise stochastic dominance rule and a hypervolume indicator. We demonstrate the approach by assessing the relative likelihood of pest invasion for strawberry production in Finland. Our method helps to differentiate sites in a landscape using both the estimates of pest invasion risk and their uncertainty. It can be applied to prioritize sites for plant health surveys and allocate survey resources among large geographic regions. The approach is generalizable and can be used in situations where knowledge of the harmful pest species is poor or nonexistent.

Key words: biological invasions, dispersal kernel, hypervolume, pest risk assessment, propagule pressure, risk management, stochastic dominance

Introduction

Introductions of invasive pest species into new areas with trade and transportation have resulted in extensive ecological and economic impacts worldwide (Meyerson and Reaser 2003; Perrings et al. 2005; Hulme et al. 2008; Pejchar and Mooney 2009). In response to the threats, various pre-border biosecurity measures, such as trade restrictions, have been implemented to prevent incursions of invasive pest populations. However, the recent increase in the rate of plant pest introductions to new areas (Santini et al. 2013; Essl et al. 2015) indicates that pre-border measures do not prevent all introductions, which

highlights the importance of implementing post-border measures to manage invasive threats.

The main objective of the post-border risk management of invasive pests is eradication and containment of new pest outbreaks (Hulme 2006; Pyšek and Richardson 2010). The feasibility of eradication and containment depends on the biological characteristics of the pest species and the size of the area invaded by the pest prior to its detection (Pluess et al. 2012a; Pluess et al. 2012b). When the pest has spread to a large area, eradication is often deemed unfeasible due to the high cost, non-target damage or low probability of eradication success (Simberloff 2009a; Pyšek and Richardson 2010; Pluess et al. 2012a; Pluess et al. 2012b).

A rapid response is often the preferred action against early invaders (Pyšek and Richardson 2010). However, in some cases, delaying eradication and gathering more data has been shown to be preferable (Sims et al. 2016), for example to avoid acting against pests of minor importance, which might be a waste of resources (Kenis et al. 2007). Nevertheless, informed decisions on management actions can only be made after the initial detection and evaluation of the state of the established pest population, and thus even the wait-and-see approach discussed by Sims et al. (2016) is likely to benefit from early detections.

To detect new invasions in time, surveys aimed at the early detection of invasive pests need to be targeted as efficiently as possible. Several pest species-specific models have been developed to predict the level of pest risk in a geographic domain using information on the biophysical preferences of the pest species and spatial data depicting key environmental factors, such as the distribution of host plants and climate (Venette et al. 2010; Magarey et al. 2011; Baker et al. 2012; Venette 2015). Several risk modeling frameworks have been proposed to facilitate consistency in pest risk assessments and support a rapid response to novel invasions (see Koch et al. 2009; Pitt et al. 2009; Yemshanov et al. 2009; Kehlenbeck et al. 2012; Robinet et al. 2012; Parnell et al. 2014; Savage and Renton 2014). Geographic representations of the results of such models are typically termed pest risk maps (Venette et al. 2010).

Notably, pest-specific approaches are highly dependent on data concerning the behavior of invasive organisms and may not be feasible for assessing the risks of new (or anticipated) invaders, for which the required data are normally lacking (Venette et al. 2010; Ward 2016). Hence, generalized pest risk mapping methods that target multiple invasive pests, including unrecognized threats, relevant to a particular host resource and geographic region could be beneficial for risk management, and in some circumstances might be the only option when species-specific data are not available (Hudgins et al. 2017).

Generalized risk mapping approaches that do not focus on a single species would require either a meta-model that estimates the risk from several species-specific models or a coarser model that uses only the proxy factors that are assumed to have a co-directional effect on all pests (Hudgins et al. 2017). A major challenge in constructing a risk model of this type is to include, despite the lack of data on the new invasive organism, sufficient realism in the modeling framework to keep the assessment meaningful (Parry et al. 2013; Savage and Renton 2014; Venette 2015; Hudgins et al. 2017). Although there have been some studies on generalized risk mapping

methods and invasion hotspot analysis (e.g. Margosian et al. 2009; Colunga-Garcia et al. 2010a; Colunga-Garcia et al. 2010b; Koch et al. 2011; Colunga-Garcia et al. 2013; Hudgins et al. 2017), the approach remains largely unexplored. Because generalized risk mapping methods have the potential to enhance post-border risk management, more attention is needed to advance this concept.

In this paper, we describe a generalized method for mapping the likelihood of pest invasion via plant propagation material to enable the prioritization of pest surveillance efforts. The method simulates the invasion process (i.e. arrival in an uninvaded area, spread, and survival of a novel pest population) for a range of pests that may cause damage to a crop species of interest. The simulation only requires information on the spatial and temporal distribution of the crop species and tentative knowledge of the spread and survival capacities of the target pests. The outcome of the simulation describes the relative likelihood of pest infestation of a crop species in different geographic locations. The results can be used to guide plant health inspections in locations where the likelihood of invasion is high. We demonstrate the methodology with a case study that assesses the pest invasion risk for strawberry production in Finland based on the recent cropping history.

Description of the generalized pest risk mapping method

Basic assumptions

For many crop species, the spatial distribution of the production sites changes over time in rotation with other crop species. For harmful invasive pests, crop rotation in an agricultural landscape creates a fragmented and dynamic network of habitats with a suitable host resource. We assume that the spatial and temporal distribution of suitable habitats in a landscape affects the likelihood of pest invasions, and the infestations are most likely to occur at the sites where the production of a crop species is most concentrated in space and time. This assumption follows the basic idea of spatial ecology that population dynamics in a fragmented landscape depend on the size and lifespan of the habitat patches and connectivity between the patches (see Fahrig 1992; Hanski 1999; With 2004; Fahrig 2007), and it constitutes the basis of our generalized pest risk mapping method. We use information on the spatial and temporal distribution of crop production sites (i.e. sites with suitable host species) and tentative knowledge of the spread and survival capacities of the target pests to assess the spatial variation in

invasion likelihood of these pests. This is carried out by simulating the propagule pressure, spread, and survival of the pests in the geographic setting, applying a series of assumptions.

Foremost, we assume that the propagule pressure is correlated with the area of the host crop species, i.e., the number of individuals introduced to a given location in which they are not native (Lockwood et al. 2005). Specifically, we assume that 1) the volume of imports of propagation material of a host crop species to a given site depends on the production area of the crop species at that site, and 2) propagule pressure correlates positively with the amount of plant propagation material imported to a given site. The first assumption is based on the fact that imports of plant propagation material have been shown to be the most important transport pathways of invasive pest introductions (Brasier 2008; Liebhold et al. 2012; Santini et al. 2013; Hantula et al. 2014). The second assumption is based on the notion that propagule pressure is considered one of the most important factors explaining invasion success (Lockwood et al. 2005; Simberloff 2009b; Bradie et al. 2013).

We also assume that the likelihood of spread from an infested site declines with distance from the site according to the Cauchy dispersal kernel. This is because distance is considered a fundamental feature explaining the likelihood of spread in the spatial context (Nathan et al. 2012), and dispersal kernels, which estimate probability distributions over spread distances, are commonly used for characterizing the spread of invasive pests (Carrasco et al. 2010; Trotter and Hull-Sanders 2015; Withrow et al. 2015). The Cauchy kernel belongs to a group of fat-tailed dispersal kernels and is considered a good fit to the empirical pest dispersal data, because it is capable of capturing the rare long-distance dispersal events that have a significant impact on the population spread rates (Kot et al. 1996; Nathan et al. 2012). The Cauchy distribution has been widely used in estimating the spread of various organisms (see Mayer and Atzeni 1993; Shaw 1995; Xu and Ridout 1998; Meats and Smallridge 2007; Pitt et al. 2009; Luo et al. 2014).

We also assume that the absence of host plants negatively affects the ability of pests to survive and establish a viable population at newly invaded sites over time. Survival here refers to the capacity of pest organisms to sustain a population at a given site over time (e.g. the next growing season or longer).

Model application

Our generalized pest risk mapping model is applied to a gridded map where each map cell represents a site in a landscape. The model calculates the relative

likelihood of pest invasion in each cell. The model is run for multiple time steps over the forecast time horizon. At the beginning of the first time step, the value of all cells is set to zero. For each time step, the model performs the following simulation steps. First, the relative propagule pressure in each map cell is set as equal to the proportion of the area of the cell covered with the host crop species of interest at that time step. Thus, the total area of the cell defines the theoretical maximum of the relative propagule pressure at each time step. The spread is simulated from the entry foci (i.e. the cells where the pest is likely to arrive with plant propagation material) using the Cauchy dispersal kernel. Next, the resulting value of each cell is summed up to a relative likelihood of pest invasion of that cell over the previous time steps. Finally, the likelihood of pest survival in a cell is modeled using information on the presence/absence of the host crop species in that cell at a particular time step. This simulation procedure causes the relative likelihood of pest invasion to accumulate over time.

We use the following calculations to estimate the relative likelihood of pest invasion. Consider a landscape (a gridded pattern) of $i \times j$ map cells, where i and j denote the spatial position of a site in a landscape. The relative likelihood of pest invasion for the ij^{th} cell in landscape L at the end of a simulation time step t can be estimated as:

$$L_{ijt} = (K_{ijt} + L_{ijt-1})z_{ijt} \quad [1]$$

where z_{ijt} is a coefficient that defines the likelihood of pest survival in a cell ij in time step t . If the crop species of interest is cultivated in the cell ij , at time step t , the z_{ijt} value is set to 1. When the crop species is not cultivated in the cell, the value z_{ijt} depends on the ability of the pests to survive in the absence of the host, with the survival likelihood z_{ijt} set between 0 and 1. The parameter L_{ijt-1} describes the relative likelihood of pest invasion in a cell ij in the previous time step $t-1$. K_{ijt} is the dispersal value based on the summation of dispersal kernels that predict the likelihood of pest arrival from all neighboring cells to a cell ij at time step t , and is calculated as follows:

$$K_{ijt} = \left(\sum_{k=1}^n \sum_{l=1}^m S_{ik,jl} \left(\frac{1}{1 + \frac{\|P_{ijt} - P_{kl}\|^2}{\sigma}} \right) \right) \frac{\sum_{i=1}^n \sum_{j=1}^m P_{ijt}}{\sum_{i=1}^n \sum_{j=1}^m S_{ik,jl}} \quad [2]$$

where P is the relative propagule pressure, which is the proportional area of a cell ik,jl covered with the host crop species of interest at time t , $S_{ik,jl}$ is a kernel-smoothed grid based on the relative propagule pressure value P , n and m denote the landscape size in spatial X and Y dimensions and k and l are auxiliary sub-indices in the summation equation of a two-dimensional kernel $S_{ik,jl}$, which denote the spatial position of a cell and enumerate all cells in the landscape. The parameter σ determines the degree of kernel smoothing, which in our case characterizes the probability distribution of the spread distances. The smoothing term is essentially a convolution kernel, which is a common numerical interpolation method of two-dimensional data. Kernel smoothing has been previously used in spatial simulations of epidemics (Brand et al. 2015), raster image processing and weather forecasting (Roberts and Lean 2008; Gilleland 2013; Sobash et al. 2016). In summary, the first part of Equation 2 sums up the dispersal kernels for the spread to a cell ij from all neighboring cells, and the resulting values are then rescaled so that the sums of the values in a landscape before and after the kernel smoothing match.

Individual pest species may differ in their spread behavior (which is captured by the parameter σ in Eq. 2) and ability to survive without a host (captured by the parameter z_{ijt} in Eq. 1). To depict the potential invasions of a range of pests, we define the parameters σ and z_{ijt} as probability distributions. These distributions cover plausible ranges of spread and survival capacities for different pest species that may invade the area of concern. We then estimate the probability distributions of pest invasion likelihoods for each cell ij in the landscape L via stochastic simulations of spread and survival using Equations 1 and 2. Each simulation calculates the likelihood of invasion for each cell ij using the σ and z_{ijt} values randomly sampled from their distributions.

Integrated pest risk map

Our model uses stochastic simulations to generate a set of uncertain plausible invasion scenarios for a given landscape. In practical risk assessments, decision-makers tend to misjudge uncertainty by a considerable margin (Kahneman et al. 1982) and may find a set of stochastic invasion scenarios confusing. Since the results are intended to support practical pest risk management, the stochastic assessments need to be aggregated into a simpler, single-dimensional form. In this case, risk prioritization should be based on comparing the distributions of pest invasion likelihoods between individual cells on the map. When multiple cells

must be compared, risk prioritization requires ordering of the distributions of invasion likelihoods for each individual cell.

In theory, if the distribution of invasion likelihoods could be approximated by a known functional form (such as the normal distribution), it would be possible to describe a set of plausible invasion scenarios (a distribution of maps) with first moments (e.g., mean values and variance). In our case, the extent of knowledge of the pest species and their spread and survival capacities is insufficient to characterize the shape of the distribution. Under such circumstances, ordering of multiple map cells in a geographic space can only be done by considering the entire distributions of the invasion likelihoods for each cell. In short, each map cell has a distribution of pest invasion likelihoods, and prioritizing the cells in a landscape requires ordering of these distributions in dimensions of high to low invasion risk. This task can be achieved using the hypervolume approach (Yemshanov et al. 2017). The method establishes the relative order of the distributions of invasion risk values without the need for estimating the first distribution moments. The hypervolume metric (HV) factors in the uncertainty of these multiple distributions, so that the final measure reflects the impact of both the expected likelihood of invasion and its variation, and does not require the distributions to conform to a known functional type. This is an important advantage over averaging methods that factor in uncertainty by depicting the invasion risk in dimensions of the mean invasion likelihood and its variance.

The HV method can be summarized as follows. We first depict the distributions of invasion likelihoods for individual map cells as cumulative distribution functions (CDF), so that each map cell is characterized by a CDF of invasion likelihood values. We then order these CDFs using the first-order stochastic dominance (FSD) rule (see Yemshanov et al. 2012, 2017). Ordering the sets of map cells via the FSD rule establishes their rank order along a gradient of pest invasion risk. Because the FSD rule considers the full distributions of values in the ranked sets, the uncertainty in the underlying distributions influences the outcomes of the ranking process. As described in Yemshanov et al. (2012), the FSD ranking creates “non-dominant” subsets. Within a non-dominant subset, the differences between CDFs are not big enough to establish preference order relationships via the FSD rule (see Levy 1992, 1998). Notably, the mathematical properties of the FSD rule allow a rational decision maker to treat a non-dominant subset as a single risk priority class.

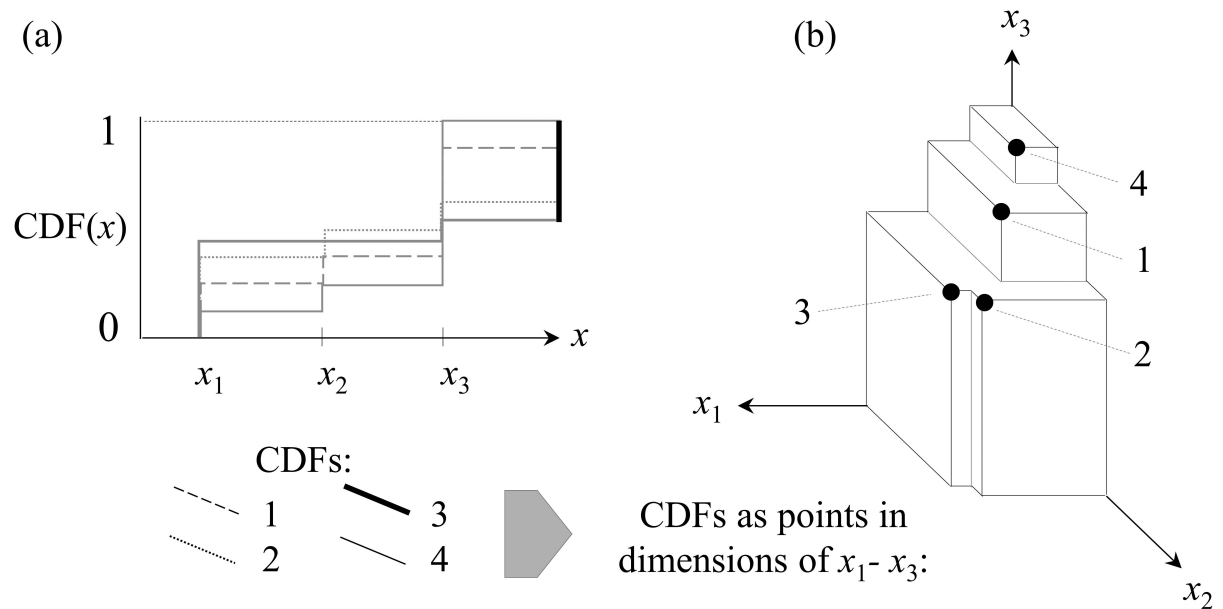


Figure 1. Geometric illustration of the hypervolume concept: a) an example of a non-dominant subset of four cumulative distribution functions (CDFs) sampled at three discrete intervals, x_1 , x_2 , and x_3 : CDF1 (0.25, 0.375, 0.875), CDF2 (0.375, 0.5, 0.625), CDF3 (0.45, 0.45, 0.55), and CDF4 (0.125, 0.25, 1); b) a depiction of the set of CDFs 1–4 as a frontier in dimensions of CDF sampling intervals x_1 – x_3 . The hypervolume of the set of CDFs 1–4 is the volume under the convex frontier of points 1–4 and a chosen reference point (with the coordinates 0,0,0).

The FSD rule can produce only ordinal rankings of CDFs. To characterize the quantitative positions of ranks in a gradient of pest invasion likelihood, each subset of CDFs should be characterized with a continuous measure. We estimate the positions of non-dominant sets with the HV metric. The HV metric has been widely used in multi-objective optimization to identify the positions of convex multi-dimensional frontiers (Brockhoff et al. 2008). For a non-dominant m -dimensional subset A , the HV metric can be defined as the volume of the m -dimensional space that is dominated by any point in subset A , but not dominated by the reference point r (Brockhoff et al. 2008, see Yemshanov et al. 2017).

We sample the CDFs in each ranked subset delineated with the FSD rule at m discrete intervals (Yemshanov et al. 2017). Geometrically, we depict each CDF, a member of a non-dominant subset delineated with the FSD rule, as a point in an m -dimensional space, where each dimension represents the m^{th} sampling interval of the CDFs (Figure 1). A subset of CDFs forms an m -dimensional frontier of points in the dimensions of these sampling intervals. For each subset, we then estimate a volume under the outermost convex boundary of that point cloud (Figure 1b) and above the reference point r with zero coordinates. Thus, each CDF (and a corresponding map cell) is characterized with the HV measure of

the ranked subset in which it falls. We use the HV measure as a proxy measure of the likelihood of pest invasion.

Case study: Assessing the pest invasion likelihood for strawberry production in Finland

We used strawberry production in Finland as a case study to demonstrate the new methodology. Strawberry is the most important commercially grown berry fruit in Finland, with a cultivation area of approximately 3300 ha. Practically all of the production is carried out in open fields and nearly all of the seedlings are purchased from other European countries. During the last three decades, at least four new strawberry pests have been introduced to Finland: *Phytophthora cactorum* in 1990 (Parikka 1990), *Colletotrichum acutatum* in 2000 (Parikka and Kokkola 2001), *Xanthomonas fragariae* in 2011 (EPPO 2011), and *Phytophthora fragariae* in 2012 (Parikka et al. 2017). The shipment of strawberry seedlings is suspected to be the main entry pathway for all of these pests. Notably, some strawberry pests that are present in other European countries have not been detected in Finland (EPPO 2018), but could easily be introduced via shipments of strawberry seedlings. Hence, strawberry production in Finland was considered an appropriate case study to demonstrate the new methodology.

Data, parametrization, and analysis

We acquired the data on the geographic locations and sizes of strawberry fields for the years 2011–2015 from the Finnish field plot registry, provided by the Finnish Agency for Rural Affairs. We processed the data for each time step t (a year) into separate gridded maps with a 500-m spatial resolution, such that the map cell value represented the proportion of the cell area covered with strawberry cultivation in that cell in a given year. This value was used as a relative propagule pressure estimate (P) in a cell in a given year t .

We defined the distributions for the dispersal and survival parameters σ and z_{ijt} as plausible ranges that are expected to cover the majority of spread and survival capacities of novel pests of strawberry crops in Finland. For the dispersal parameter σ , we used a uniform distribution between 0 and 0.5. We assumed this range to account for both the natural and human-mediated spread of pests in the Finnish landscape. To parameterize the Cauchy dispersal kernel, we set the annual maximum spread distance to 20 km. This limit was based on the mean distance between neighboring strawberry fields (which was well below 20 km) and was intended to reduce the computational burden. With these assumptions, the proportion of pest individuals remaining in the entry foci after the dispersal phase ranged between 9% and 100%.

For the parameter z_{ijt} , which depicts the probability of survival without a host, we assumed a uniform distribution between 0 and 0.5. The lower limit 0 represents the survival of pests whose establishment is highly dependent on live host plants (such as obligate biotrophic plant pathogens). The upper limit 0.5 represents the survival potential of pests that are well adapted to surviving in the absence of the host plants (such as pathogens that produce long-lasting survival structures), and it was based on the survival potential of *Heteroderoidea* nematodes in Finland, which has been quantified by Tiilikkala (1991).

The model was implemented in R version 3.2.3 (R Core Team 2015), using the packages “raster” (Hijmans et al. 2016) and “Smoothie” (Gilleland 2013). All spatial data were prepared in ESRI ArcGIS 10.2 using the Spatial Analyst extension. We generated 100 plausible maps of pest invasion likelihoods by randomly sampling the values for the dispersal and survival parameters σ and z_{ijt} in individual map cells. Each map cell was characterized by a distribution of 100 invasion likelihood values. We then sampled the CDFs calculated from these distributions at 30 equal intervals to calculate the HV metric. Rankings with the FSD rule and HV

calculations were performed using a stand-alone program written in C++ that applied the hypervolume calculation algorithm from While et al. (2012).

We also evaluated the agreement between the HV metric and other simpler metrics that could be used to prioritize plant health surveys, namely the strawberry cultivation area between 2011 and 2015 and mean invasion likelihood values calculated from the distributions of 100 simulated invasion maps. To examine the impact of the dispersal (σ) and pest survival (z_{ijt}) parameters on the ranking outcomes, we simulated pest invasion scenarios with combinations of the minimum and maximum values of these parameters (i.e. σ , z_{ijt} = 0 and 0, 0 and 0.5, 0.5 and 0 and 0.5 and 0.5). We then compared the invasion likelihood values calculated with the different scenarios via pairwise Pearson correlation and calculated the match between the ranked subsets for the top 2% of cells with the highest invasion ranks.

Results

Our study area included 3611 map cells (500 × 500 m) with strawberries cultivated between 2011 and 2015. Based on the FSD rule, we delineated 140 ranks among these map cells. The higher ranks generally included fewer cells than the lower ranks (Figure 2). For example, the highest 20 ranks covered only 2% (73 cells) of the total area of strawberry cultivation, whereas the lowest rank alone covered over 60% (2194 cells) of the area. The HV values revealed distinct levels of stratification between the ranks. The HV values of the high ranks generally had larger differences between the individual ranks and were therefore more widely spread along the HV gradient than the HV values of the lower ranks (Figure 2). Figure 3 illustrates the example of spatial ranking for Northern Savonia, one of the most important strawberry production areas in Finland.

The ordinal ranks created with the FSD rule deviated slightly from the ranks based on the HV metric. This is because the hypervolume approach factors in the relative positions of the ranked sets, whereas the ranks based on the FSD rule are ordinal and evenly spaced along the gradient of high to low risk. However, both methods revealed similar broad-scale rank patterns, with Pearson’s correlation close to 1 ($p < 0.05$).

The risk ranking based on the HV metric was close to the ranking based on the strawberry cultivation area between 2011 and 2015 (Pearson’s $R = 0.93$, $p < 0.05$) (Table 1), although for some individual cells, the rankings substantially differed from each other (Figure 4). The agreement between the top 2% of cells with the highest HV ranks and strawberry cultivation areas was 84.9% (Table 2).

Figure 2. Ordinal ranks vs. the HV metric for the strawberry production cells in Finland (500 × 500 m cells) (dots). Gray bars show the proportion of cells in the different ordinal risk ranks. Only the cells with strawberry cultivation between 2011 and 2015 are shown.

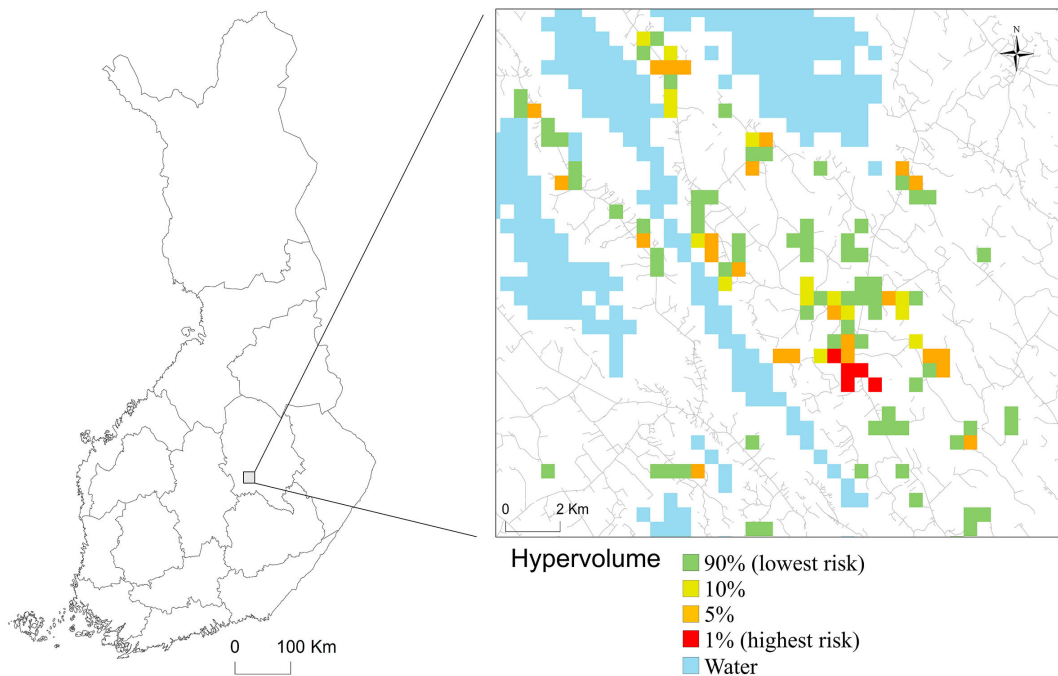
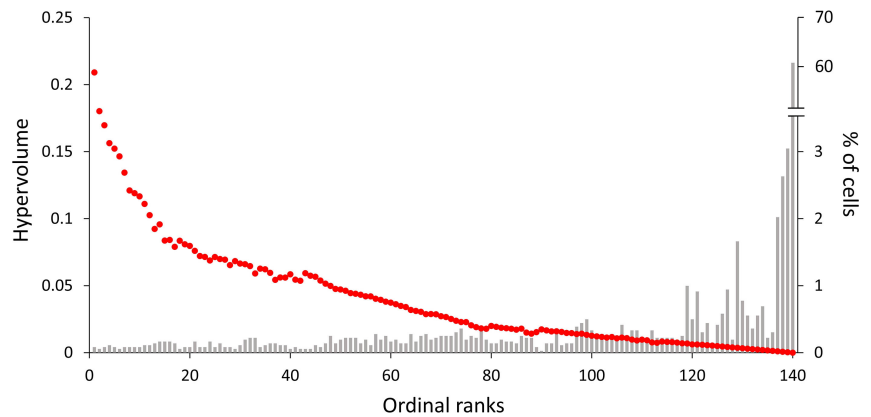


Figure 3. An example of the assessment outcome for Northern Savonia, eastern Finland. The cells with strawberry cultivation between 2011 and 2015 were categorized into four ranks based on the invasion likelihood values (i.e., first rank containing the top 1% of cells with the highest likelihood, the second rank between 1 and 5% of cells, the third between 5 and 10%, and the fourth containing more than 10% of all cells).

This implies that the methods, while depicting similar broad-scale patterns of pest invasion risk, assigned a portion of their highest values to different sites.

The rankings based on the HV metric and the mean invasion likelihoods had a high degree of similarity (Pearson’s $R = 0.97$, $p < 0.05$) (Table 1). Moreover, the agreement between the sets with the top 2% of the highest ranks calculated with these metrics was high (93.2%) (Table 2). This is unsurprising, because both rankings were calculated from the same set of invasion likelihoods.

We also compared the rankings based on the alternative model scenarios, which used different settings for the dispersal and survival parameters σ and z_{ijt} . The strongest pairwise correlation was recorded between the scenarios where the dispersal parameter (σ) was set to its minimum (0) and the survival parameter (z_{ijt}) to its minimum (0) or its maximum value (0.5) (Pearson’s $R = 0.99$, $p < 0.05$) (Table 1). This indicates that the survival parameter z_{ijt} did not significantly alter the geographical patterns of pest invasion likelihoods for strawberry production in

Table 1. Pairwise correlation between the rankings based on different risk priority metrics and assessment scenarios. Risk priority metrics and assessment scenarios: Hv – hypervolume metric, based on 100 invasion scenarios; Mean – mean likelihood of invasion, based on 100 invasion scenarios; Area – the strawberry cultivation area between 2011 and 2015; σ_{min}, z_{min} – the invasion scenario that used the minimum dispersal capacity ($\sigma_{min} = 0$) and minimum pest survival capacity ($z_{min} = 0$); σ_{min}, z_{max} – the scenario with the minimum dispersal capacity ($\sigma_{min} = 0$) and maximum pest survival capacity ($z_{max} = 0.5$); σ_{max}, z_{min} – the scenario with the maximum dispersal capacity ($\sigma_{max} = 0.5$) and minimum pest survival capacity ($z_{min} = 0$); σ_{max}, z_{max} – the scenario with the maximum dispersal capacity ($\sigma_{max} = 0.5$) and maximum pest survival capacity ($z_{max} = 0.5$). Only the cells with a positive strawberry cultivation area between 2011 and 2015 were compared.

	Hv	Mean	Area	σ_{min}, z_{min}	σ_{min}, z_{max}	σ_{max}, z_{min}	σ_{max}, z_{max}
Hv	x	0.97	0.93	0.96	0.96	0.94	0.93
Mean	0.97	x	0.95	0.98	0.98	0.98	0.97
Area	0.93	0.95	x	0.96	0.98	0.89	0.91
σ_{min}, z_{min}	0.96	0.98	0.96	x	0.99	0.93	0.91
σ_{min}, z_{max}	0.96	0.98	0.98	0.99	x	0.92	0.92
σ_{max}, z_{min}	0.94	0.98	0.89	0.93	0.92	x	0.98
σ_{max}, z_{max}	0.93	0.97	0.91	0.91	0.92	0.98	x

Table 2. Pairwise match between the sets of the top 2% of cells with the highest ranks based on different risk priority metrics and assessment scenarios. Risk priority metrics and assessment scenarios: Hv – hypervolume metric, based on 100 invasion scenarios; Mean – mean likelihood of invasion, based on 100 invasion scenarios; Area – the strawberry cultivation area between 2011 and 2015; σ_{min}, z_{min} – the invasion scenario that used the minimum dispersal capacity ($\sigma_{min} = 0$) and minimum pest survival capacity ($z_{min} = 0$); σ_{min}, z_{max} – the scenario with the minimum dispersal capacity ($\sigma_{min} = 0$) and maximum pest survival capacity ($z_{max} = 0.5$); σ_{max}, z_{min} – the scenario with the maximum dispersal capacity ($\sigma_{max} = 0.5$) and minimum pest survival capacity ($z_{min} = 0$); σ_{max}, z_{max} – the scenario with the maximum dispersal capacity ($\sigma_{max} = 0.5$) and maximum pest survival capacity ($z_{max} = 0.5$). Only the cells with a positive strawberry cultivation area between 2011 and 2015 were compared.

	Hv	Mean	Area	σ_{min}, z_{min}	σ_{min}, z_{max}	σ_{max}, z_{min}	σ_{max}, z_{max}
Hv	x	93.2	84.9	84.9	84.9	90.4	89.0
Mean	93.2	x	83.6	84.9	84.9	89.0	87.7
Area	84.9	83.6	x	93.2	93.2	75.3	75.3
σ_{min}, z_{min}	84.9	84.9	93.2	x	100	75.3	74.0
σ_{min}, z_{max}	84.9	84.9	93.2	100	x	75.3	74.0
σ_{max}, z_{min}	90.4	89.0	75.3	75.3	75.3	x	98.6
σ_{max}, z_{max}	89.0	87.7	75.3	74.0	74.0	98.6	x

Finland. The lowest correlation coefficient was recorded between the scenarios in which both the dispersal and survival parameters were set to either their minimum or maximum values, 0 and 0.5 (Pearson’s $R = 0.91, p < 0.05$) (Table 1). This indicates that dispersal parameter σ clearly affected the geographic patterns of pest invasion likelihoods for strawberry production in Finland.

A comparison of the top 2% of cells with the highest ranks revealed no difference between the scenarios in which the dispersal parameter σ was set to its minimum value (0) and the survival parameter z_{ijt} set to its minimum or maximum value (0 or 0.5) (Table 2). This indicates that the survival parameter z_{ijt} did not affect the spatial arrangement of the high-risk sites for strawberry production in Finland. This is unsurprising, because strawberry production at the high-risk sites in Finland was carried out in a continuous monoculture, i.e. the host resource was always available at those sites and the issue of pest survival without a host was not critical. The biggest disagreement between the top 2% of cells (74.0%) was recorded between the scenario in which the dispersal and survival parameters σ and z_{ijt} were set to their

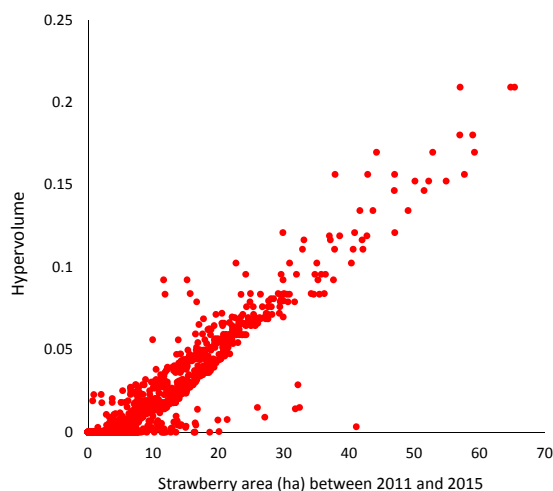


Figure 4. Hypervolume metric vs. the cultivation area of strawberry between 2011 and 2015.

maximum values (0.5) and the one in which the dispersal parameter σ was set to a minimum value (0) and the survival parameter z_{ijt} either to its minimum (0) or its maximum value (0.5) (Table 2). This further confirms that the dispersal parameter σ influenced the prioritization of pest invasion risk for strawberry production in Finland.

Discussion

The proposed pest risk mapping method is suitable for assessing the relative likelihood of potential infestations when a valuable crop resource is expected to be threatened by a range of pest species. The method can be applied in many practical situations when knowledge of the biology of the pests is lacking and analysts can only acquire some proxy data on the factors contributing to the success of invasions (such as the distribution of susceptible crop species and general assumptions about spread rates and pest introduction pathways). The method combines the outcomes of randomized simulations of a range of pest introductions when the pests are assumed to have different spread behavior and ability to survive without a host plant. It also accounts for the temporal dynamics of potential pest entries and the availability of a host resource in a landscape over time.

Our methodology helps make better use of uncertain data regarding threatening pest invasions in practical risk management. When knowledge of the potential invasions is poor, a rational decision maker would target early detection surveys based on the abundance of the suitable host crop species. Our methodology provides decision makers with additional insights into where the pest invasions are more likely occur given the spatio-temporal distribution of the crop species of interest and tentative assumptions concerning the spread and survival capacities of the threatening pest species.

Our results revealed moderate differences between the rankings based on the HV measure and the area of strawberry production. The degree of similarity between the rankings acquired by the two approaches depends on the spatio-temporal distribution of the host crop species and the assumptions about the capacities of the pests to spread and survive in a novel landscape. The main benefit of using the presented methodology is that it factors in the temporal and spatial variation in the host crop species and the uncertainty about the spread and survival potential of the pests. The uncertainty associated with the assessed risk values is an important decision-making variable that in theory should be directly incorporated into the final risk estimates (Venette et al. 2010).

While the approach is not intended to provide a comprehensive depiction of the pest invasion process, it can be used to assess the likelihood of invasion for early pest detection programs when knowledge of the invasive organisms is essentially nonexistent. For example, in Finland, plant health inspectors will be using risk maps produced with the presented methodology to prioritize sites for plant health surveys. The method could also be used to allocate limited pest surveillance resources among different regions. In this case, risk priority maps can be used as inputs for optimization-based models designed to find, under a limited budget, an optimal pest survey strategy for a particular crop species (see Mehta et al. 2007; Hauser and McCarthy 2009).

Technical aspects

Our method used the size of the production area as a surrogate for relative propagule pressure. In the context of crop production, the production area is a reasonable proxy for propagule pressure. This is because the production area is likely to affect the amount of imported plant propagation material, and larger areas would require greater volumes of propagation material. The volume of imported plant propagation material positively influences propagule pressure (Leung et al. 2012), since the propagation material is an important pest introduction pathway (Brasier 2008; Liebhold et al. 2012; Santini et al. 2013; Hantula et al. 2014). Other factors, such as the size of the urban population, the area of commercial-industrial land use (Colunga-Garcia et al. 2010a), and the volume of imports arriving in a particular area (Bradie et al. 2013; Colunga-Garcia et al. 2013) have also been used as indicators of propagule pressure. Propagule pressure could also be affected by the origin of the propagation material (e.g. farm, province, or country), and the resistance of the used cultivar.

Our method assumed that the relative likelihood of invasion at a given site is equal to the relative propagule pressure estimated by modeling pest arrival, spread, and survival at that site. Propagule pressure affects the probability of invasion (Lockwood et al. 2005; Simberloff 2009b), and their relationship has been quantified in several studies (e.g. Leung et al. 2004; Drake and Lodge 2006; Bradie et al. 2013). Often, this relationship may be nonlinear due to the Allee effect, which causes small populations to be prone to extinction (Leung et al. 2004). Nevertheless, when information on the absolute propagule pressure (i.e. the number of introduced individuals) is lacking, the assumption of a linear relationship between propagule pressure and invasion likelihood feels justified.

We used the Cauchy dispersal kernel to estimate the spread rates of pests from the entry foci. Despite their popularity, it has been argued that single-event dispersal kernels are too simple for modeling the realistic spread of invasive pests, because they do not take into account knowledge of the pest's biological traits and interactions with the environment (Chapman et al. 2015). However, in knowledge-poor situations, the simplicity of the approach can also be considered a major advantage when detailed information on the biophysical preferences of a new invasive pest is lacking (Ward 2016). For example, Hudgins et al. (2017) showed that simple dispersal kernels could be used to explain the spread of a range of pest species. Potentially, gravity models, which assume that movement of propagules between two sites depends on the characteristics of the sites and the distance between them (Bossenbroek et al. 2001; Douma et al. 2016), could be combined with dispersal kernel models to better estimate spread in spatially diverse landscapes. Gravity models could be used to spatially adjust the cell-specific dispersal parameters, but would require more data on the environmental preferences of individual pest species. More stringent data requirements may limit the potential application of gravity models, or other more complex models, in situations where knowledge of the biophysical preferences and environmental tolerances of individual pest species is lacking.

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