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# Potential spread of kiwifruit bacterial canker (*Pseudomonas syringae* pv. *actinidiae*) in Europe<sup>1</sup>

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Pest risk analyses (PRAs) are conducted to determine whether an organism is a pest and whether and how it should be regulated. Estimation of the potential area of establishment and pest spread are key factors of this analysis. Tools for modelling and mapping of these key factors have to be quick and easily applicable for a wide variety of organisms with limited data for parameterization. For this purpose, a dispersal kernel model based on a 2Dt-distribution had been developed in a European Union project (PRATIQUE). The aim of the present study was the evaluation of this spread model hitherto tested on insects, plants, fungi and nematodes in order to determine its applicability to bacterial pests. Therefore, the potential distribution and spread of kiwifruit bacterial canker *Pseudomonas syringae* pv. *actinidiae* in Europe was investigated based on climatic suitability and host plant availability. The results of the modelling were compared with the spread history of the pest in Europe. It is shown that this generic spread model can also be applied to a bacterial pest.

## Introduction

Increasing global trade transports a high number of potential pest species all over the world (Hulme, 2009). Pest risk analyses (PRAs) provide the scientific justification for phytosanitary measures against new, emerging or regulated plant pests which have the potential to cause unacceptable consequences in a defined area. The endangered area and potential spread of these organisms are key factors for evaluating the risk posed by an invasive plant pest (FAO, 2007). As the demand for risk mapping in PRAs increases, a simple, quick, applicable modelling tool for risk analysts is needed (Kehlenbeck et al., 2012). A set of generic spread models was developed in the framework of the European Union (EU) FP7 project PRATIQUE. They were expected to overcome the challenges of modelling spread in the PRA process. One of them, a dispersal kernel derived from a rotationally symmetric two-dimensional t-distribution (2Dtdistribution), has already been tested on various taxa such as insects (Diabrotica virgifera virgifera, Anoplophora chinensis), plants (Eichhornia crassipes), nematodes (Meloidogyne enterolobii, Bursaphelenchus xylophilus) and fungi (Fusarium circinatum) (Robinet et al., 2012, 2015), but not hitherto on bacteria. No previous modelling approaches examining the temporal and spatial spread of a

bacterial plant pest on a continental scale were found. The EU Project DROPSA ('Strategies to develop effective, innovative and practical approaches to protect major European fruit crops from pests and pathogens') started in 2014 and is intended to improve plant health strategies in fruit production and trade (Steffen et al., 2015). Within this project, it was aimed to verify the applicability of the dispersal kernel model for three bacterial pests of fruit crops. Here, the results for Pseudomonas syringae pv. actinidiae are presented. Pseudomonas syringae pv. actinidiae is the causal agent of kiwifruit bacterial canker. At present, bacterial canker is the most destructive disease of kiwifruit worldwide (Vanneste et al., 2013). The main symptoms on host plants (Actinidia species) are shoot wilt and dieback in addition to exudates from cankers on woody plant parts. The bacterium also causes necrotic leaf spots, leaf wilting and budrot (Froud et al., 2015). Severe infections cause plant death. A disease incidence of 40% is sufficient for up to 2/3 fruit loss (EPPO, 2012). From the late 1980s, P. syringae pv. actinidiae has caused important damage to kiwifruit orchards in Japan, the Republic of Korea and China (Froud et al., 2015). In 1992 it was detected in Italy, though observed economic damage was limited for 16 years (Vanneste et al., 2013). In 2007 and 2008 the first symptoms of the highly aggressive P. syringae pv. actinidiae biovar 3 were observed in kiwi orchards in Central and Northern Italy (Balestra et al., 2009b). The first economic losses became obvious in 2008 (EPPO, 2012). Afterwards, the bacterium spread into Calabria, Campania, Emilia-Romagna, Friuli-Venezia Giulia, Lazio, Piemonte and

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Veneto, and has thus infested all major kiwifruit growing areas in Italy. Biovar 3 has an incidence of up to 80-90% in several orchards in Italy (EPPO 2012). Rize Province in Turkey was affected in 2009. In 2010, the first infections were detected in Portugal (several orchards in the province of Entre-Douro-e-Mino) and France (Rhône-Alpes, few orchards). Records from Spain (Galicia, 3 orchards; plants imported from an Italian nursery) and Switzerland (a new commercial orchard in the Geneva canton) followed in 2011. In Germany, infected plants in a nursery in Bavaria and in a garden centre in Schleswig-Holstein were detected and destroyed in 2013. In the same year Slovenia reported two infected orchards (Vipavska Dolina). In addition the first occurrences in Georgia (municipality of Lanchkhuti) and in Corsica (France) were confirmed in 2013. The most recent first occurrence was in Greece (area of Drosero) in 2014. To date, P. syringae pv. actinidiae is present in Italy, France, Greece, Portugal, Turkey, Slovenia and Georgia, partly in restricted areas (EPPO Global Database, 2016). Thus, P. syringae pv. actinidiae biovar 3 has spread within 7 years to nearly all kiwifruit growing countries in Europe.

Within the current paper two spread scenarios based on climatic suitability and host plant availability are presented. Modelled past and potential future spread of *P. syringae* pv. *actinidiae* is pictured and compared with the real spread history of this pest in Europe. The most challenging characteristics concerning bacteria for parameter setting are discussed.

## Methods

#### **Climatic suitability input**

The dispersal kernel model estimates the spatial distribution and abundance of the pest species at a specific time. The model needs an input specifying the climatic suitability of the investigated area (Europe) for establishment of P. syringae pv. actinidiae. Therefore, a CLIMEX (Sutherst et al., 2007) output has been created, based on a climate data set from 1961-1990. Recent changes in the climate were not included. CLIMEX calculates two indices which are necessary for the spread model. The Ecoclimatic Index (EI) is the summarised annual climatic suitability based on weekly growth and stress indices. EI ranges from 0 to 100. If EI > 0, the organism is potentially able to establish in this cell. The Growth Index (GI) represents the the potential annual population growth of the organism during its favorable season. Prior to the present study, two CLIMEX datasheets of P. syringae pv. actinidiae were available (EPPO, 2012; Narouei Khandan et al., 2013). Both models were calibrated to match the model output to the worldwide reported distribution of the pest. The parameter settings, and therefore the resulting area of potential establishment in Europe, differ considerably between these models. The authors decided to use the model of Narouei Khandan et al. (2013) because of the biologically reasonable minimum,

optimum and maximum temperatures for the development of the bacterium and the extensive distribution data used for the iterative parameterization. Narouei Khandan et al. (2013) fitted the stress parameters in such a way that the majority of known occurrences resulted in climatically suitable and very suitable cells. This approach may produce misleading results, as every reported occurrence does not necessarily imply a successful long-term establishment and random introductions do not always appear in the climatic zones with the most favourable habitats for the pathogen. Additionally, the iterative parameterization based on the current distribution may imply incorrect climatic limitations if the organism still spreads. However, parameterization with physiological data alone is not possible for P. syringae pv. actinidiae without additional biological studies. The optimal and limiting temperature requirements of the pathogen differ notably in the available literature. While P. syringae pv. actinidiae grows in vitro in a temperature range between 4°C and 35°C with an optimum at 25°C, in vivo bacterial growth is strictly limited by plant defences to temperatures above 25°C (Gao et al., 2016). The inhibition of bacterial growth by wound-healing tissue around the infection at 25°C should be limiting for bacterial spread (Serizawa & Ichikawa, 1993; Young, 2012). There were conflicting reports on whether symptoms in Europe occur above 25°C or not (EPPO, 2012; Vanneste, 2013). Serizawa & Ichikawa (1993) concluded that the optimal range for bacterial growth on new canes is 10-18°C, while severe disease developed at 10°C and 15°C. Young (2012) stated that the severity of disease decreases gradually below 15°C.

The setting of stress indices is more problematic. While for many insect pests a known temperature leading to death within a given time is available, the authors are not aware

 Table 1. Parameter settings for CLIMEX adopted from Narouei

 Khandan et al. (2013), except the wet stress SMWS (marked with an asterisk)

Index	Parameter	Values	Unit
DV0	Lower temperature threshold	5	°C
DV1	Lower optimum temperature	12	°C
DV2	Upper optimum temperature	20	°C
DV3	Upper temperature threshold	27	°C
SM0	Lower soil moisture threshold	0.5	_
SM1	Lower optimum soil moisture	0.8	_
SM2	Upper optimum soil moisture	2	_
SM3	Upper soil moisture threshold	3	_
TTCS	Cold stress temperature threshold	5	°C
THCS	Cold stress temperature rate	-0.00005	week <sup>-1</sup>
DTCS	Cold stress degree-day threshold	15	°C
DHCS	Cold stress degree-day rate	-0.0001	week <sup>-1</sup>
TTHS	Heat stress temperature threshold	30	°C
THHS	Heat stress temperature rate	0.0005	week <sup>-1</sup>
SMDS	Dry stress threshold	0.2	_
HDS	Dry stress rate	-0.005	week <sup>-1</sup>
SMWS*	Wet stress threshold*	3*	_
HWS	Wet stress rate	0.001	week <sup>-1</sup>

of these data for *P. syringae* pv. *actinidiae*. The bacterium is able to reproduce at very low temperatures within 24 h, therefore there was no need to determine a special limiting temperature sum (PDD). The authors adopted the parameter settings published by Narouei Khandan *et al.* (2013), except for the wet stress threshold SMWS because the published value was identical to and therefore in conflict with the upper optimum soil moisture SM1. The parameter settings are shown in Table 1.

In addition to this parameterization CLIMEX was run with and without an irrigation scenario, because kiwifruit plants require a large volume of water (Beutel, 1990), and at least in Italy kiwifruit orchards have irrigation systems (Testolin & Ferguson, 2009). For this scenario, irrigation in the months March to September was set to 5.6 mm per day on average as the total amount of water, including rainfall (Beutel, 1990).

#### Host availability input

Pseudomonas syringae pv. actinidiae is reliant on the presence of Actinidia species (Actinidia deliciosa, Actinidia chinensis, Actinidia arguta and Actinidia kolomikta). There are no natural Actinidia populations in Europe, but the growing area of commercial orchards and ornamental vines is increasing (EPPO, 2012). The area of potential establishment was limited to the commercial kiwifruit producing countries - Italy, Greece, France, Portugal, Spain, Montenegro, Bulgaria, Switzerland and Slovenia. The hosts were only considered as absent or present without a weighting of densities. As the location of the production sites within these countries was unknown, the authors assumed the presence of hosts all over the state territory. In countries without commercial kiwifruit production, the Ecoclimatic Index and the Growth Index of the pest were set to a value of 0. The production data for kiwifruit in Europe were taken from FAOSTAT (FAOSTAT, 2016).

#### Spread model parameters

The spread model runs on the open source software 'R' and the R code that was used for the application of the model is publicly available (Robinet *et al.*, 2012). It provides simulations on the spatial distribution and abundance of a pest species at a specific time. It considers population density in space and time and is able to take both natural spread and long-distance spread events by trade or other human assistance into account. The following parameters have to be determined to apply the model and run simulations:

- *Entry point*: the first record of *P. syringae* pv. *actinidiae* biovar 3 was in Italy in the Lazio region (12.8333 E, 42.8333 N) in 2008 (EPPO Global Database, 2016). This introduction point is considered in the model as an input file ('presencefile').
- Carrying capacity K: for the dispersal kernel model, the carrying capacity K of suitable cells is required. With

regard to the special feature of a bacterial disease with an unknown and uncountable number of bacteria per host plant, it was considered that the number of hosts (number of potential infections) was a good indicator of the carrying capacity. In Europe, Italy has the highest proportion of kiwifruit orchards with 24 327 ha (0.0807% of Italian state territory) harvested in 2012 (FAOSTAT, 2016). The planting densities of kiwifruit plants depend on the support structures used. In pergola systems up to 500 plants are grown per ha, while in T-bar orchards up to 740 plants are grown per ha (Testolin & Ferguson, 2009). In this model a mean density of 620 plants per ha is assumed. Based on these assumptions, the carrying capacity per grid cell (1579 km<sup>2</sup>) is calculated as follows:

K = 0.000807\*620 hosts per ha  $\times 100$  ha (conversion from ha to km<sup>2</sup>)  $\times 1579$  km<sup>2</sup> = 79 004 hosts per grid cell.

• *Initial population* N<sub>0</sub>: the initial population N<sub>0</sub> (population abundance as a percentage of the carrying capacity) is the supposed number of infected kiwifruit plants introduced at the entry point in Italy at t = 0 (year of entry). Just one infested plant is sufficient for propagation of *P. syringae* pv. *actinidiae*, therefore the authors set  $P_0 = 1$ :  $N_0 = 100 \times P_0/K = 100 \times 1/79\ 004 = 0.00127\% = 1.27 \times 10^{-3}\%$ .

 $N_0$  was included in the 'presencefile'.

- Scale parameter u: the scale parameter u gives the mean distance of spread (in km) in one direction per year. The distance of spread of *P. syringae* pv. *actinidiae* by rain, wind and vectors was studied in New Zealand (Rosanowski *et al.*, 2013). The vast majority (98%) of new infections were detected within a 10-km radius over a time period of 2 years. For 1 year, a mean distance of spread of 5 km (u = 5 km) was estimated.
- *Shape parameter* p: the shape parameter p represents the number of degrees of freedom and the shape of the distribution (thin-tailed versus fat-tailed). A fat-tailed kernel (small p) is recommended when occasional spread events, e.g. trade, over much longer distances than achieved by natural spread mechanisms, are likely to occur (Robinet *et al.*, 2012).

**Pathways:** *P. syringae* pv. *actinidiae* is able to spread 5 km per year by rain, wind and vectors (Rosanowski *et al.*, 2013). Human assisted long-distance spread occurs with infected plant material (grafting material, nursery plants and pollen) and contaminated biotic and non-biotic vectors (Tontou *et al.*, 2014; Froud *et al.*, 2015). Concerning the long distance between the kiwifruit growing regions in Europe compared with the high orchard density in New Zealand, human transmission by trade of nursery material was assumed to be the major mechanism of spread in the model, with a rate of minor (p = 5) and moderate regional spread (p = 10).

• *Multiplication factor*  $\lambda_{max}$ : the multiplication factor  $\lambda_{max}$  represents the maximum year to year multiplication that a population could achieve under optimal conditions in the

area of potential establishment. The multiplication factor was estimated by the number of hosts that can be infected per year. The infection rate of plants per year differs depending on plant cultivar and region. In Europe, infestation levels of up to 80% infested plants per orchard were described (Balestra *et al.*, 2009a). According to the host densities above, the multiplication factor was calculated as:

 $\lambda_{\rm max} = K \times 0.8 = 63 \ 203.$ 

• *Time period* t: the number of years after entry (*t*) has to be set for simulations. Considering  $t_0 = 2007$  as the first year of entry would mean that  $t_9 = 2016$  represents the current situation and, for example,  $t_{12} = 2019$  predicts a possible future situation.

#### **Results and discussion**

#### **Climatic suitability**

According to the CLIMEX settings for *P. syringae* pv. *actinidiae*, almost the whole area of Europe is potentially suitable for establishment (Fig. 1). The limiting factor for the pathogen in the north of Europe is cold stress. In the south-eastern part of Spain and in the middle of Turkey the pathogen is limited by drought stress. The maximum growth rate of the pest occurs on the Atlantic shoreline from south Portugal up to Ireland.

#### Climatic suitability and host availability

For the spread model, the authors limited the area of potential establishment to the commercial kiwifruit producing countries. Additionally the irrigation scenario was applied. The resulting area of establishment and growth potential of the population are pictured in Fig. 2. The irrigation setting predominantly influences the growth rate of *P. syringae* pv. *actinidiae*, with little impact on the area of potential establishment, compared with the setting without irrigation. The climatically unsuitable areas within Spain and Turkey disappear. The whole territory of all kiwifruit producing countries is suitable for the establishment of the pest. The growth rate of the pathogen is favoured by the humid climate of the coastal areas.

# Validation of the spread model compared with spread history

Kiwifruit plants require a large volume of water; therefore the irrigation scenario was used for modelling the spread (Figs 3 and 4). Figure 3 illustrates a minor regional spread and a very high long-distance spread event probability (p = 5). The predicted spread proceeds too fast compared with the spread history of the pest in Europe. Figure 4 shows a slightly higher rate of regional spread due to the natural spread capacity of P. syringae pv. actinidiae and a lower probability of long-distance spread events (p = 10). The scenario matches well the real spread of P. syringae pv. actinidiae in Europe, even though long-distance spread by infected plant material is a random, non-predictable process. The results still reflect the observed high frequency of introductions over a very short time within Europe and they provide a more realistic picture of population growth and regional spread in areas with higher orchard densities. Consequent eradication measures slightly slowed down the rate of spread and prevented widespread establishment and population growth of the pest in the past. Even though the pathogen did not reach the modelled infection density  $[N_t (\%)]$  of the carrying capacity], findings from nearly all predicted kiwifruit producing countries (except Bulgaria) in the risk area were known. The predicted spread with a higher shape parameter values (p = 15, p = 25) and the without irrigation scenario were considerably delayed and did not conform to the rapid observed spread of P. syringae pv. actinidiae in Europe in the past (data not shown).

# Spread predictions for *P. syringae* pv. *actinidiae* in Europe

Without continuing control measures, the model with minor natural spread (p = 5, Fig. 3) predicts a spread within 3 years into every kiwifruit producing country. After 5 years the whole area in these countries would be potentially infested. Saturation of the carrying capacity (every available host infested) is reached after 8 years ( $t_9 = 2015$ ). No further spread is possible in this system. With a shape parameter of p = 10 (Fig. 4), the model predicts the infestation of every kiwifruit producing country after 5 years.



Fig. 1 Area of potential establishment (left: orange areas, EI > 0; white areas, EI = 0; EI, ecoclimatic index) and growth index (GI) [right: graduated colours from white (GI = 0) to red (GI = 100)] of *P. syringae* pv. *actinidiae* in Europe based on climatic suitability; GI and EI created with CLIMEX, plotted with the software 'R' assuming that no irrigation is applied. [Colour figure can be viewed at wileyonlinelibrary.com].



**Fig. 2** Area of potential establishment (left: orange areas, EI > 0; white areas, EI = 0; EI, ecoclimatic index) and growth index (GI) [right: graduated colours from white (GI = 0) to red (GI = 100)] of *P. syringae* pv. *actinidiae* in Europe based on climatic suitability and host plant availability with irrigation setting in the summer months; GI and EI created with CLIMEX, plotted with the software 'R'. [Colour figure can be viewed at wileyonlinelibrary.com].

The whole area of potential establishment in Europe is affected in the year 2016 (t = 9), and full saturation of the system is reached after 12 years, in 2019. In reality,

*P. syringae* pv. *actinidiae* appeared in all kiwifruit growing countries in the EU except Bulgaria within 7 years, despite intensive eradication measures.



**Fig. 3** Modelled spread of *P. syringae* pv. *actinidiae* over 8 years from 2008 to 2015 (p = 5) with an assumed irrigation scenario in the summer months. Population abundance (% of carrying capacity) shown in graduated colours from white ( $N_t < 10^{-6}$ %) to yellow, orange and red ( $N_t \ge 10$ %); grey means no data. [Colour figure can be viewed at wileyonlinelibrary.com].



**Fig. 4** Modelled spread of *P. syringae* pv. *actinidiae* over 12 years from 2008 to 2019 (p = 10) with an assumed irrigation scenario in the summer months. Population abundance (% of carrying capacity) shown in graduated colours from white ( $N_t < 10^{-6}$ %) to yellow, orange and red ( $N_t \ge 10$ %); grey means no data. [Colour figure can be viewed at wileyonlinelibrary.com].

## Conclusions

The areas of potential establishment and predicted spread of the model with a moderate regional and mainly humanassisted spread (p = 10) fit well the recorded spread history and actual occurrence of *P. svringae* pv. actinidiae in kiwifruit growing countries in Europe. Within 7 years P. syringae pv. actinidiae spread into all potential suitable countries except Bulgaria. The model predicts this extent after 5 years, without eradication and containment measures. The rapid saturation of the carrying capacity in the model reflects the high climatic suitability of these areas and therefore the high damage potential of P. syringae pv. actinidiae in European kiwifruit growing areas. It has to be considered that this model accounts for a worst case scenario, with the assumption that every vulnerable host within a grid cell could be infected within a year, and does not include a latency period; therefore the maximum multiplication rate is very high. Additionally, the model input indicates an evenly high host density in kiwifruit producing countries and therefore overestimates the growth rate and potential spread.

The non-kiwifruit producing countries in Europe are climatically suitable for the establishment of the pest, and therefore infection of ornamental plants is possible. However, isolated infected host plants would not promote noticeable natural spread of the pathogen.

Spread modelling of bacterial pests with the dispersal kernel model developed in PRATIQUE is challenging due to bacterial characteristics compared with insect pests or plants, in particular. The high number of potential bacterial individuals per host, together with the exponential reproduction and unknown number of generations per year, limit the ability to rate population density, carrying capacity and number of starting populations. The number of infested hosts seems to be a suitable alternative for parameterizing these values.

There are some uncertainties left with regard to the key biological factors necessary for the climatic input, for example the in situ temperatures which are optimal for development and spread of P. syringae pv. actinidiae. There is a lack of reliable thresholds and information about the impact of stress on the population. The authors did not find any information about lethal effects of cold or heat stress and are not aware if P. syringae pv. actinidiae populations decline or just remain inactive under unfavourable conditions. The model would interpret this stress as lethal and every affected grid cell as unsuitable for establishment. In this way the area of potential establishment may be underestimated for bacterial pests. Another point is the identity and origin of known outbreaks of P. syringae pv. actinidiae, which can be essential for determining the spread history, calculated spread distances and derived climatic requirements. Recent studies showed that there are several genetically distinct strains responsible for the worldwide epidemic of P. syringae pv. actinidiae (Cunty et al., 2015). Because there is on-going research on the characterization and identification of *P. syringae* pv. *actinidiae* populations, this model does not consider further discrimination between different haplotypes, strains and potential new pathovars (i.e. *P. syringae* pv. *actinidifoliorum* and the Spanish *P. syringae actinidifoliorum* look-alike, etc.), which can be relevant for the spread history (number of introductions, spread distances), thus adding some uncertainty to the results. This model involves climatic suitability and host availability in the investigated area, though other aspects (e.g. interspecific competition, management practices, geographical barriers and other factors) will also influence the spread of the disease.

Although there are many uncertainties, the model fits well with the spread and known distribution of *P. syringae* pv. *actinidiae*. In general, the dispersal kernel seems to provide a suitable tool for predicting bacterial spread.

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# Dissémination potentielle du chancre bactérien du kiwi (*Pseudomonas syringae* pv. *actinidiae*) en Europe

Des analyses de risque phytosanitaires sont conduites afin de déterminer si un organisme est nuisible, s'il doit être réglementé, et comment il doit l'être. La prédiction de sa zone d'établissement potentiel ainsi que l'évaluation de sa dissémination sont des facteurs clefs de cette analyse. Les outils de modélisation et de cartographie de ces facteurs clefs doivent être rapides et faciles à utiliser sur une grande diversité d'organismes, et ce en utilisant un nombre limité de données de paramétrage. A cet effet, une fonction de dispersion avait été développée au sein d'un projet européen (PRATIQUE) sur la base d'une distribution de Student à deux degrés de liberté (2Dt). L'objectif de la présente étude est l'évaluation de ce modèle de dissémination, jusqu'à présent testé sur insectes, plantes, champignons et nématodes, pour déterminer s'il est également applicable aux bactéries. Pour cela, la distribution et la dissémination potentielle en Europe du chancre bactérien du kiwi, Pseudomonas syringae pv. actinidiae, est étudiée sur la base de la pertinence climatique ainsi que la disponibilité en plantes hôtes. Les résultats de cette modélisation ont été comparés à l'historique de la dissémination de cet organisme nuisible en Europe. Il est ainsi démontré que ce modèle générique de dissémination peut également être appliqué à des bactéries.

## Потенциальное распространение бактериального рака киви (*Pseudomonas syringae* pv. *actinidiae*) в Европе

Анализ фитосанитарного риска (АФР) проводится для того, чтобы определить, является ли тот или иной организм вредным, и каким образом он должен регулироваться. Ключевыми факторами этого анализа являются оценка потенциальной зоны акклиматизации и вредного организма И его распространения. Инструменты для моделирования и составления карт этих ключевых факторов должны быть быстрыми и легкими в применении для широкого круга организмов с ограниченными данными для параметризации. Чтобы достичь этого, в рамках проекта EC PRATIQUE была разработана модель ядра распространения, полученная на основе 2D-распределения Стьюдента. Пелью настоящего исследования была оценка этой модели распространения, до сих пор проверенной только на насекомых, растениях, грибах и нематодах, с тем, чтобы определить возможность её применения к вредным бактериям. Для этого было исследовано потенциальное распределение и распространение бактериального рака киви Pseudomonas syringae pv. actinidiae в Европе на данных о пригодности основании климата И доступности растений-хозяев. Результаты были историей моделирования сопоставлены С распространения этого вредного организма в Европе. Исследование демонстрирует, что эта обобщенная модель распространения может быть также применена к бактериальным вредным организмам.

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