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Prioritising plant-parasitic nematode species biosecurity risks using self organising maps

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Abstract The biosecurity risks from many plant-parasitic nematode (PPN) species are poorly known and remain a major challenge for identifying potentially invasive species. A self organising map (SOM) was used to prioritise biosecurity risks from PPN to the whole of continental Australia as well as each of the states and the Northern Territory separately. The SOM used the recorded worldwide distributions of 250 systematically selected species from 43 genera, and identified 18 different countries spanning Asia, Africa, North and Central America, Europe and the Pacific with very similar PPN assemblages to Australia as a whole. Many of the species in these countries are not recorded in Australia, and therefore pose a biosecurity risk. Analysed separately, the states and territories were identified as forming five separate clusters, each with a different region of the world, and with different characteristic PPN. Many of the PPN found in the regions clustered with an Australian state have not been recorded from anywhere in Australia, and others have very restricted distributions within Australia, thus posing different biosecurity risks. The SOM analysis ranked the risks of the different PPN based on likelihoods of establishment. The rankings confirmed the risks from frequently quarantined PPN, but more importantly identified species, which upon further investigation could be new threats. This method can be used to identify previously overlooked species for more detailed risk assessments.

Keywords Phytosanitary · Pest risk analysis · Pest list · New threats · Pest species assemblages

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Introduction

The number and taxonomic range of species moving around the world and the threat from invasive species have increased globally (Keller et al. 2011; Pimentel et al. 2005) with growing economic development

(Lin et al. 2007; Nunez and Pauchard 2010), movement of people (Tatem 2009; Tatem et al. 2006) and trade (Hulme 2009; Westphal et al. 2008), changing climates (Walther et al. 2009) and improved transport networks (Tatem and Hay 2007). Transport networks, in particular have expanded in extent, increased in connectivity and accelerated in speed (Hulme 2009; Tatem and Hay 2007). As a result, exotic species have more opportunity and faster means to move from one part of the world to another along transport networks that effectively bring geographically isolated but climatically similar regions closer (Ascunce et al. 2011; Floerl et al. 2009; Hulme 2009; Vilà and Pujadas 2001).

Although data are available for only a few countries, indications are that most countries have only acquired a few of the plant pests and pathogens which can adversely impact on their agricultural production and environment (Pimentel et al. 2005; Waage and Mumford 2008). This situation is beneficial economically because in the absence of invasive species, production is higher, losses are lower, management interventions are lower, indigenous ecosystems are protected, incidental environmental effects (e.g. destruction of plant and animals in the case of an incursion) are avoided, and market access and trade are facilitated (Cook et al. 2011b; Heikkila 2011; Hodda 2004; Keller et al. 2008). For any country then, biosecurity measures that effectively continue to prevent the establishment and spread of damaging pests and pathogens are the most effective and economical means of avoiding crop losses (Cook et al. 2011b; Hockland et al. 2006; Hodda and Cook 2009; Kahn 1991; Perrings et al. 2005; Pyšek and Richardson 2010; Sikora et al. 2005).

The challenge for any biosecurity agency charged with protecting a nation's agricultural production, is that not all potential invaders pose the same level of threat (Williamson and Fitter 1996). Some species are ill-suited to the climate, fail to adapt, or arrive with insufficient propagules, while others may not have suitable hosts or vectors to complete their lifecycles and are unable to establish viable populations (Hayes and Barry 2008; Kolar and Lodge 2001; Simberloff 2009). If these biosecurity risks can be assessed in an objective, repeatable way, resources can be prioritized to risk pathways and inspection regimes at a country's border can target those species with the greatest risks. In the context of this paper, the term biosecurity risk refers to the potential of an exotic pest to establish in a new range.

Self organising maps (SOMs) have been used to analyse species assemblages at the global scale to identify and rank potentially invasive species based on their likelihood of establishing in a particular country (Cereghino et al. 2005; Gevrey et al. 2006; Morin et al. 2013; Paini et al. 2010a; Vanninen et al. 2011; Worner and Gevrey 2006). A SOM is an artificial neural network, which recognises patterns in high dimensional data and is widely used in various research areas such as; molecular biology, medicine, geospatial analysis, mineral exploration, metrology, oceanography, data mining and financial risk analysis (Kohonen 2001). A SOM has two properties that make it especially suitable for identifying and prioritizing biosecurity risks. Firstly, a SOM can analyse large data sets, for example the worldwide distribution of up to 10,000 species on a standard desktop computer (Paini et al. 2011). This means that data from amongst the many pests and pathogens identified worldwide can be used in one analysis. Secondly, a SOM can handle the incomplete and suspect distribution records that often characterise pest and pathogen datasets. A SOM is resilient to up to a 20 % error in the species distribution dataset (Paini et al. 2010b) and has been shown to be highly efficient at ranking those species that can establish in a region above those that cannot establish (Paini et al. 2011).

In this paper we use a SOM to analyse the worldwide distributions of a large set of plant-parasitic nematodes (PPN) to identify and prioritise the biosecurity risks from these nematodes to Australia. PPN are a major group of pathogens, which cause losses estimated at between 8.8 and 14.6 % of total world crop production or US$100–157 billion annually (Abad et al. 2008; Koenning et al. 1999; Nicol et al. 2011; Sasser and Freckman 1987). Australia lacks most of the PPN that cause major losses elsewhere in the world, and quarantine is a major strategy of the Australian government to minimize any future losses (Hodda 2004; Hodda and Nobbs 2008). This is thus an excellent model system on which to apply the methodology and identify those PPN species most likely to establish in Australia.

From the SOM analysis we derive prioritised lists of the PPN posing the greatest biosecurity risks to Australia as a whole, as well as to each state and the Northern Territory. We also identify the countries or

regions most likely to be sources of species with the highest likelihoods of establishment. These rankings are supported by what is otherwise known of the biological and ecological characteristics (i.e. species preferences and adaptations compared to the establishment likelihoods) of the PPN.

Methods

Dataset

The dataset consisted of the distributions of 250 PPN species of greatest phytosanitary importance, based on a number of characteristics: pathogenicity or association with economically important crops; ability to act as virus vectors; interaction with bacterial and fungal pathogens; and quarantine or invasive status (Singh et al. 2013a). These species came from 43 genera. A database for the worldwide distribution of these species was created containing the accepted species name, and presence or absence. The presence or absence of species was obtained by searching for the scientific names and synonyms of the 250 PPN on the Web of Knowledge, CABI abstracts and Scopus databases. Synonyms were sourced from the database of nematode names created for the classification of phylum Nematoda (Hodda 2011). Publications reporting the distribution of these species were sourced and presence or absence recorded in the PPN distribution database. Distribution records for synonyms were then consolidated with the valid names. Distribution records on the CABI distribution map of plant diseases (CABI 2013), CABI crop protection compendium (CABI 2010) and CABI invasive species compendium (CABI 2011) and EPPO PQR (EPPO 2012) databases were retrieved, crosschecked and added to the PPN distribution database. Species without presence or absence information in a given region were assumed to be absent. This procedure produced 6,693 records of presence and 82,057 absence records from 355 world regions spanning 201 countries (large countries were further divided into counties, states or provinces).

SOM

The SOM model was implemented using the SOM toolbox (Vesanto et al. 2000) for MATLAB (MathWorks 2007). Details of the SOM algorithm, equations and the implementation can be found in Kohonen (2001) and Vesanto et al. (2000). Input into SOM was the PPN distribution data matrix [355 × 250] comprised of 250 neurons (one for each PPN species) connected to all 355 regions, thus forming 355 sample vectors of presence and absence records of the species at each of the sites. The linear initialization and batch SOM algorithms were used to model the PPN distribution data (Vesanto et al. 2000). The optimal SOM output size of 104 neurons was determined using the heuristic rule: $5 \times \sqrt{n}$ where n is the number of samples (Vesanto et al. 2000) and using the two largest eigen values from the dataset as the length and width of the SOM (Paini et al. 2011). A total of 52,000 iterations were used in the model, based on the recommended formula of 500× number of neurons (Kohonen 2001). The SOM output after analysing the PPN distribution was represented on a 13 × 8, hexagonal lattice of 104 neurons.

The SOM assesses species assemblages and associations to generate an index for every species in every region between 0 and 1 (Worner and Gevrey 2006). The SOM clusters countries and regions based on similarities in species assemblages and countries occupying the same neuron have the greatest similarity in species assemblage. Based on the similarities in species assemblages, the SOM analyses where a species has established and which other species are likely to establish in those same regions. The SOM index for a particular species in a particular neuron represents that species' strength of association with the species assemblages found in the countries or regions grouped in the neuron (Paini et al. 2010a, 2011; Worner and Gevrey 2006). Thus the index can be used as a representation of the likelihood of the species establishing in that country if it arrives and given that the host plant is present. The indices can then be used to rank all species, identifying those species most likely to establish in a particular country or region. The SOM clustering was used to identify countries or regions occupying the same neuron as Australia and its respective jurisdictions.

SOM indices for each species in each country, state or region were extracted from the SOM model output. Ranked lists for Australia as a whole and for each state; New South Wales (NSW), Queensland (QLD), South Australia (SA), Tasmania (TAS), Victoria (VIC), Western Australia (WA) and the Northern Territory (NT), were then extracted. The Australian Capital

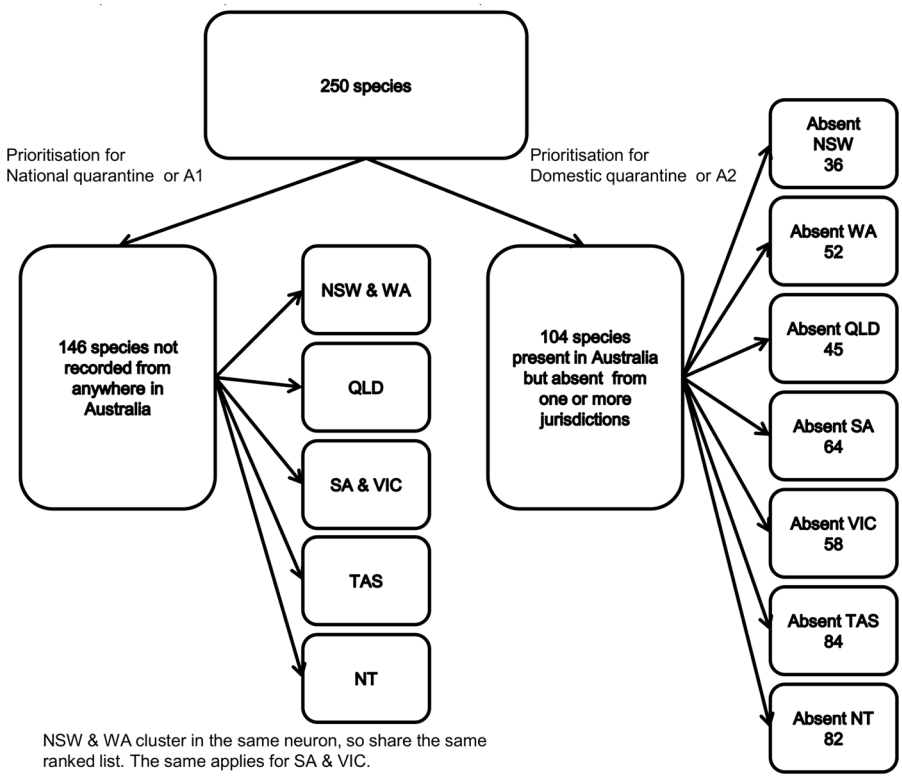

Fig. 1 Scheme for prioritisation of species for national and domestic quarantine

Territory was excluded from analysis because there is minimal agriculture and few records of PPN. While it was possible to generate a list for Australia as a whole, we wanted to account for the range of climatic and ecological characteristics found throughout Australia by generating jurisdiction specific lists. As such, we analysed each of the jurisdictions (the states and Northern Territory) for comparison with Australia as a whole. Spearman's rank correlation test was used to statistically compare the species rankings between Australia and each of its jurisdictions. The test was implemented in R (RDevelopmentCoreTeam 2010) using the "pspearman" package (Savicky 2009).

To prioritise species for national quarantine (i.e. A1 species are quarantined nationally), species recorded from anywhere in Australia (N = 104) were removed from the 250 species ranked list. The remaining species not recorded from anywhere in Australia (N = 146), were then ranked based on their SOM indices. Using these rankings, the top 50 species absent from Australia with the highest likelihood of establishment were determined for each of the jurisdictions.

To prioritise species for domestic quarantine (i.e. A2 species are quarantined at jurisdiction level only), we used the list of 104 species present in Australia to generate lists of species absent from each jurisdiction. Species not recorded in the given jurisdiction (but found somewhere else in Australia) were then ranked based on their SOM indices and the top 10 species with the highest likelihood of establishment were determined. The scheme used here for prioritisation of species for national and domestic quarantine is presented in Fig. 1.

The top 50 and 10 species were chosen for prioritisation for national and domestic quarantine, respectively, because they represent a realistic number on which more detailed assessments can be completed within timeframes that will allow implementation of meaningful biosecurity measures if they are justified.

Results

Distribution of PPN

Of the 201 countries in the dataset, most had 20 or fewer PPN species reported as present (64 %), and only a few had more than 40 species reported (15 %)

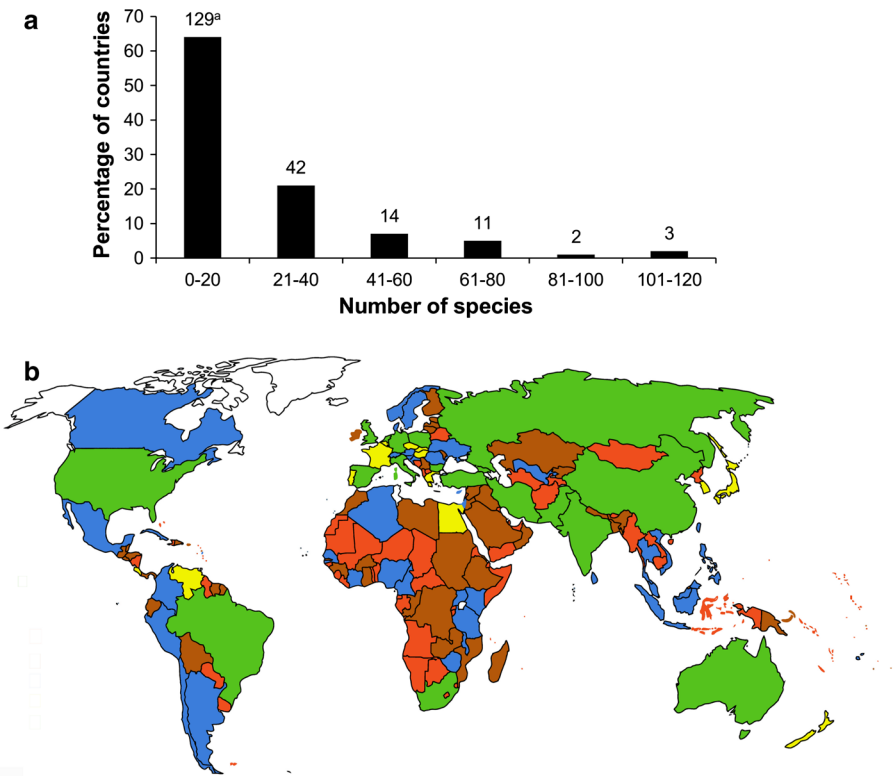

Fig. 2 **a** Percentage of countries on the database by number of reported PPN species. [a]Number on top of each column represents the number of countries. **b** Worldwide representation by number of PPN species reported. Key—*country colour coding* represents number of PPN species records: *orange* 1–10, *brown* 11–20, *blue* 21–40, *yellow* 41–60 and *green* 61–120. (Color figure online)

(Fig. 2a). No country had more than half of the 250 species investigated. Many of the countries with few records were developing countries or small islands (Fig. 2b). Most of the published species records came from countries with good nematological expertise, and most were from major agricultural areas, especially for large countries such as Australia, Brazil, Canada, China, India, Russia and USA.

SOM analysis

The 355 world regions were clustered into 88 neurons based on similarities in their PPN species assemblages. Most of the neurons (69 %) had four or fewer countries and regions while 16 neurons were empty (Fig. 3). A maximum of 26 countries and/or regions were clustered in one neuron. Generally the individual counties, states or regions of large countries with diverse climates were clustered into different neurons reflecting the differences in species assemblages between the smaller geographic units across these countries. Australia as a whole and the individual jurisdictions were clustered into five different neurons (Fig. 3). Similarly USA and its states were clustered into 20 different neurons (Electronic supplementary material 1). Species which were recorded in many countries generally had higher SOM indices than species with more restricted distributions.

Australia as a whole had the most similar PPN to South Africa (sharing the same neuron). When the jurisdictions were considered independently, 18 countries spanning; Asia (7), Africa (5), Central America (2), Pacific (2), Europe (1), and North America (1), were present in the same neurons (Fig. 3).

Considering each jurisdiction within Australia separately, SA and VIC were clustered together, as were NSW and WA, which were also clustered in the same neuron as Australia as a whole (Fig. 3). Regions clustered in the same neuron had the same SOM index for all species. Comparing the rankings of all species in each jurisdiction showed that climatically similar jurisdictions had similar PPN rankings (Table 1). All rankings for species in the individual jurisdictions were significantly positively correlated except TAS and NT, which had a significant negative correlation and TAS and QLD, which had no correlation (Table 2).

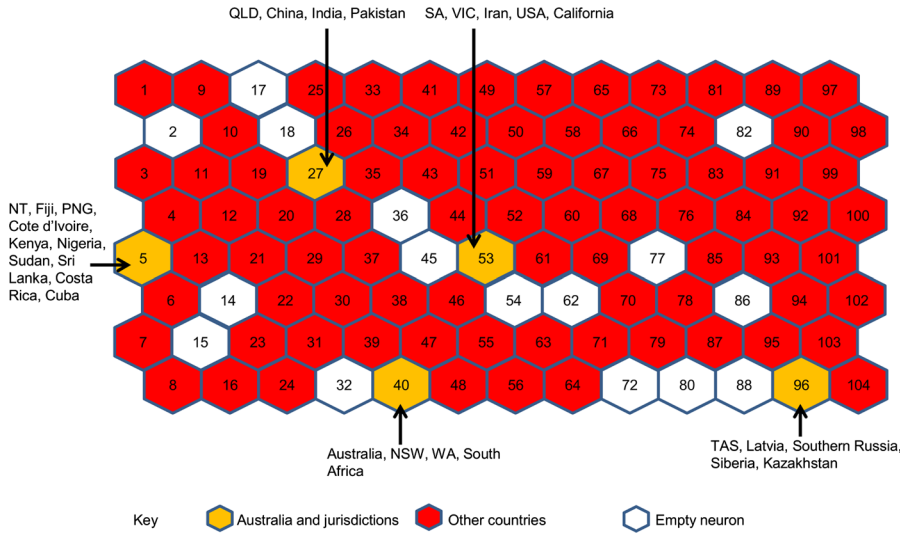

Fig. 3 SOM clustering of regions and countries with similar PPN assemblages to Australia as a whole and individual jurisdiction. Each *hexagon* represents a neuron on the SOM model output layer. Countries or regions with very similar PPN species assemblages to Australia and individual jurisdictions are clustered into the same neuron. The greater the distance between the neurons the greater the dissimilarity in PPN species assemblage between them. For a detailed list of all neurons and the SOM regional clustering, please refer to Electronic supplementary material 1

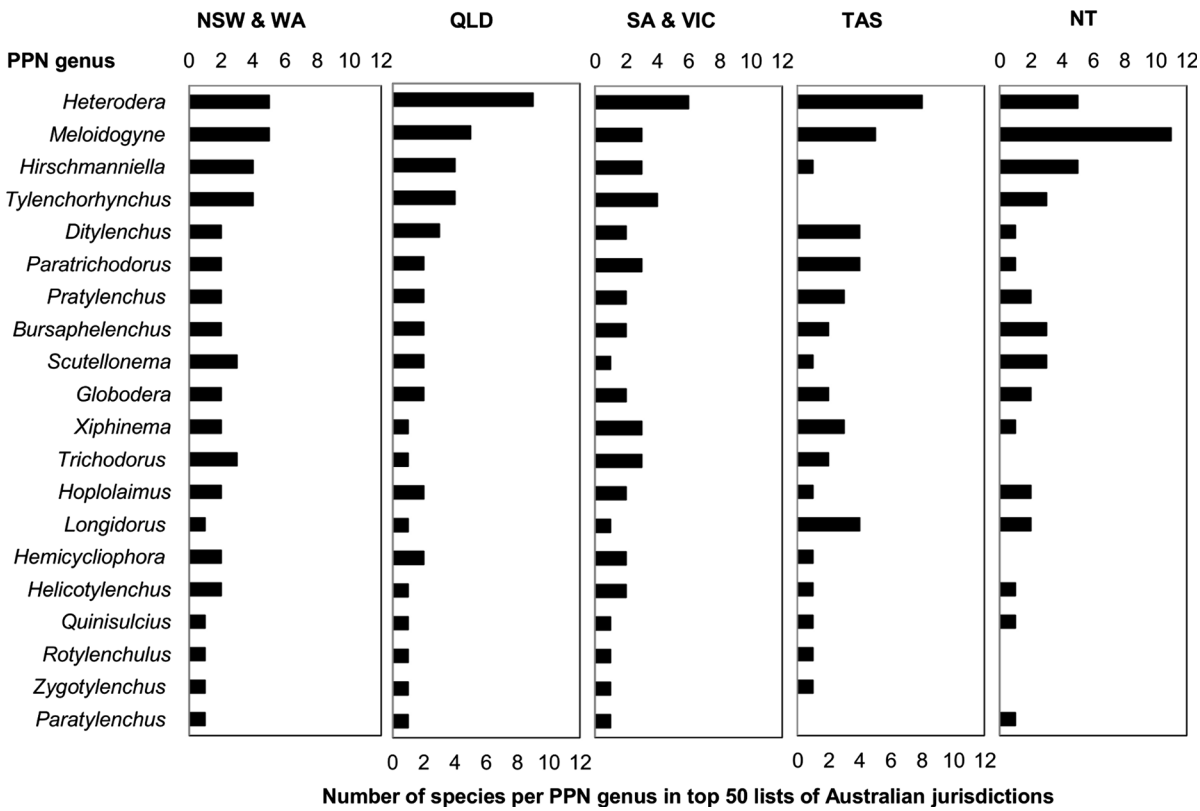

Fig. 4 PPN genera in top 50 lists of 4 or more Australian jurisdictions

Table 1 Rank comparison of PPN species in top 50 lists of Australia as a whole and individual jurisdiction within

Species[a]	Ranks[b]					
	AUST	NSW and WA	QLD	NT	SA and VIC	TAS
Hirschmanniella oryzae	**1**	**1**	**1**	**1**	**6**	80
Ditylenchus destructor	**2**	**2**	**12**	71	**1**	**1**
Heterodera glycines[a]	**3**	**3**	**7**	**16**	**4**	**31**
Bursaphelenchus xylophilus[a]	**4**	**4**	**16**	**40**	**3**	**15**
Helicotylenchus microcephalus	**5**	**5**	**5**	**3**	**23**	62
Hirschmanniella spinicaudata	**6**	**6**	**13**	**5**	**13**	98
Tylenchorhynchus nudus	**7**	**7**	**3**	**35**	**12**	64
Meloidogyne graminicola	**8**	**8**	**6**	**7**	**29**	96
Zygotylenchus guevarai	**9**	**9**	**32**	107	**2**	**7**
Quinisulcius acutus	**10**	**10**	**15**	**13**	**9**	**28**
Paratylenchus minutus	**11**	**11**	**14**	**9**	**33**	107
Scutellonema bradys	**12**	**12**	**10**	**4**	**37**	101
Tylenchorhynchus brassicae	**13**	**13**	**8**	**47**	**25**	83
Hirschmanniella gracilis	**14**	**14**	**11**	**44**	**19**	**14**
Ditylenchus medicaginis	**15**	**15**	**18**	54	**30**	**45**
Longidorus pisi	**16**	**16**	**17**	**18**	**31**	61
Globodera tabacum	**17**	**17**	**24**	**31**	**22**	**25**
Trichodorus primitivus	**18**	**18**	53	77	**5**	**9**
Xiphinema californicum	**19**	**19**	**29**	72	**20**	**21**
Hemicycliophora poranga	**20**	**20**	**50**	51	**8**	85
Trichodorus cedarus	**21**	**21**	**30**	83	**32**	58
Meloidogyne chitwoodi	**22**	**22**	74	69	**7**	**12**
Pratylenchus fallax	**23**	**23**	**34**	87	**18**	**19**
Heterodera filipjevi[a]	**24**	**24**	**21**	80	**16**	**10**
Heterodera zeae	**25**	**25**	**2**	**45**	**50**	72
Hoplolaimus indicus	**26**	**26**	**4**	**25**	**42**	**44**
Hoplolaimus columbus	**27**	**27**	**19**	**26**	**47**	95
Meloidogyne enterolobii	**28**	**28**	**22**	**6**	68	69
Xiphinema diversicaudatum	**29**	**29**	55	82	**14**	**5**
Paratrichodorus teres	**30**	**30**	**47**	99	**27**	**32**
Meloidogyne partityla	**31**	**31**	**46**	67	**38**	78
Globodera pallida[a]	**32**	**32**	**26**	**14**	**11**	**4**
Heterodera goettingiana	**33**	**33**	**43**	89	**10**	**6**
Tylenchorhynchus cylindricus	**34**	**34**	**42**	**41**	**15**	51
Hemicycliophora similis	**35**	**35**	**40**	75	**40**	**35**
Tylenchorhynchus agri	**36**	**36**	**35**	56	**43**	60
Trichodorus similis	**37**	**37**	72	98	**28**	**26**
Pratylenchus delattrei	**38**	**38**	**25**	**33**	72	104
Paratrichodorus nanus	**39**	**39**	**36**	78	**46**	**34**
Heterodera oryzae	**40**	**40**	**28**	**24**	57	110
Rotylenchulus macrodoratus	**41**	**41**	**39**	108	**39**	**33**
Helicotylenchus vulgaris	**42**	**42**	80	122	**17**	**38**
Bursaphelenchus mucronatus	**43**	**43**	**45**	**48**	**35**	**2**

Table 1 continued

Species[a]	Ranks[b]					
	AUST	NSW and WA	QLD	NT	SA and VIC	TAS
Meloidogyne ethiopica	**44**	**44**	51	**22**	74	**40**
Scutellonema clathricaudatum	**45**	**45**	**38**	**2**	75	115
Scutellonema unum	**46**	**46**	76	**19**	63	**49**
Tylenchulus palustris	**47**	**47**	75	74	51	77
Hirschmanniella imamuri	**48**	**48**	**44**	**42**	73	97
Bitylenchus vulgaris	**49**	**49**	**20**	53	71	81
Merlinius microdorus	**50**	**50**	54	109	**34**	54
Heterodera cajani	51	51	**9**	**46**	86	121
Meloidogyne paranaensis	52	52	73	**43**	58	99
Heterodera carotae[a]	53	53	**48**	91	**44**	**13**
Aphelenchoides sacchari	55	55	**23**	**49**	85	86
Xiphinema bricolensis	56	56	103	128	**26**	**43**
Heterodera sacchari	57	57	**27**	**11**	88	120
Punctodera punctata	59	59	98	68	**24**	**3**
Dolichodorus heterocephalus	61	61	82	**27**	60	68
Hemicriconemoides litchi	62	62	**31**	52	89	122
Anguina agropyri	65	65	104	127	**36**	**39**
Meloidogyne indica	67	67	**33**	106	91	123
Nacobbus aberrans	69	69	99	84	**41**	**30**
Heterodera latipons[a]	70	70	100	97	**21**	**8**
Aphelenchoides arachidis	71	71	84	**23**	79	116
Ditylenchus angustus	74	74	**37**	**15**	87	105
Longidorus martini	76	76	81	**36**	84	**48**
Pratylenchus convallariae	78	78	56	90	82	**41**
Pratylenchus mediterraneus	80	80	105	115	**45**	**36**
Punctodera matadorensis	81	81	106	116	**49**	**42**
Bursaphelenchus cocophilus	82	82	90	**8**	81	67
Meloidogyne coffeicola	83	83	77	**50**	93	102
Paratrichodorus allius	85	85	107	**21**	**48**	**16**
Heterodera oryzicola	86	86	**41**	79	110	126
Meloidogyne brevicauda	87	87	**49**	**28**	111	**50**
Longidorus attenuatus	88	88	57	96	94	**20**
Pratylenchus sudanensis	92	92	61	**12**	107	92
Longidorus leptocephalus	98	98	111	132	65	**17**
Anguina graminis	100	100	109	130	66	**22**
Paratrichodorus tunisiensis	101	101	112	129	69	**23**
Xiphinema ifacolum	103	103	91	**10**	103	113
Meloidogyne africana	104	104	67	**17**	120	125
Meloidogyne artiellia	112	112	119	126	67	**11**
Heterodera ciceri	113	113	121	121	77	**29**
Heterodera hordecalis	119	119	126	131	104	**27**
Heterodera daverti	120	120	110	70	127	**46**
Ditylenchus gigas	126	126	135	120	126	**18**

Table 1 continued

Species[a]	Ranks[b]					
	AUST	NSW and WA	QLD	NT	SA and VIC	TAS
Longidorus macrosoma	130	130	138	140	124	**24**
Meloidogyne salasi	132	132	120	**20**	134	137
Ibipora lineatus	133	133	123	**34**	135	117
Meloidogyne oryzae	134	134	124	**37**	136	139
Radopholus citri	135	135	125	**39**	139	140
Meloidogyne minor	136	136	140	143	129	**37**
Ditylenchus weischeri	138	138	142	144	131	**47**
Hirschmanniella miticausa	141	141	133	**29**	141	141
Meloidogyne arabicida	142	142	134	**30**	142	142
Subanguina hyparrheniae	143	143	136	**32**	143	138
Meloidogyne acronea	144	144	137	**38**	144	136

Species marked [a] are already on high priority pest list for Australia, species indicated in bold are in the top 15 ranked species for one or more jurisdictions in Australia and could represent possible new threats

[b] Ranks in bold represent species in the top 50 ranks of the respective jurisdiction

Table 2 Spearman's rank correlation of PPN species ranks for Australia as a whole and individual jurisdiction within

	AUST	NSW and WA	QLD	NT	SA and VIC	TAS
AUST	1					
NSW and WA	1	1				
QLD	0.880[a]	0.880[a]	1			
NT	0.469[a]	0.470[a]	0.591[a]	1		
SA and VIC	0.906[a]	0.906[a]	0.651[a]	0.230[a]	1	
TAS	0.423[a]	0.423[a]	0.150	−0.222[a]	0.644[a]	1

[a] Significant correlation

PPN not recorded in Australia as a whole

Of the species not recorded in Australia, the top 50 PPN with the highest likelihood of establishing in Australia as a whole should they be introduced were from 23 genera (Table 1). All of the top 50 PPN for Australia as a whole were also ranked in the top 50 for two or more of the individual jurisdictions within Australia considered separately, and 80 % of these species (N = 40) were ranked in the top 50 for at least 5 jurisdictions (Table 1; also see Electronic supplementary material 2 for a list of all species and their SOM indices). The highest ranked species was *Hirschmaniella oryzae*, followed by *Ditylenchus destructor* and *Heterodera glycines* (Table 1).

There were five species from each of the genera *Heterodera* (Cyst Nematodes) and *Meloidogyne* (Root-Knot Nematodes) ranked in the top 50 for Australia as a whole (Table 1). Other genera with many species ranked in the top 50 included *Hirschmanniella*, *Tylenchorhynchus* (Stunt Nematodes), *Scutellonema* (Spiral Nematodes) and *Trichodorus* (Stubby-Root Nematodes).

When the jurisdictions within Australia were considered separately, *Heterodera* and *Meloidogyne* each had three or more species ranked in the top 50 for every state (Fig. 4). The other PPN genera mentioned above also contained species in the top 50 for five or more jurisdictions. In addition, another 14 genera contained species ranked in the top 50 for at least four jurisdictions (*Ditylenchus, Paratrichodorus, Pratylenchus, Bursaphelenchus, Globodera, Xiphinema, Hoplolaimus, Longidorus, Hemicycliophora, Helicotylenchus, Quinisulcius, Rotylenchulus, Zygotylenchus* and *Paratylenchus*). Altogether 12 genera had species ranked in the top 50 for three or less jurisdictions: *Anguina, Nacobbus, Punctodera* (SA, VIC, TAS); *Bitylenchus* (NSW, WA, QLD); *Hemicriconemoides* (QLD); *Aphelenchoides* (QLD, NT); *Merlinius* and

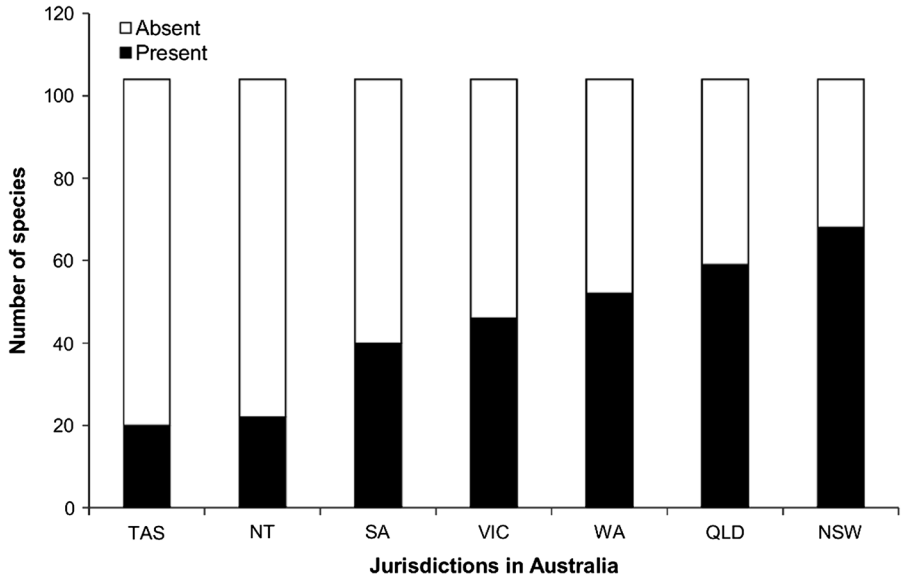

Fig. 5 PPN species recorded in Australia, presence and absence by jurisdictions

Tylenchulus (NSW, WA); *Dolichodorus, Ibipora, Radopholus* and *Subanguina* (NT) (Table 1).

PPN species present in Australia

Of the 104 PPN recorded from Australia, most (64 %) were found in three jurisdictions or less: only about one-third of the PPN species present (36 %) were widespread (in more than three jurisdictions). Of the species recorded from Australia, the numbers per jurisdiction varied from 20 (TAS) to 68 (NSW) (Fig. 5). PPN species from 19 genera already present in Australia were ranked in the top 10 for jurisdictions where they are not recorded (Electronic supplementary material 3). These PPN generally had higher SOM index values and thus a stronger association with the Australian jurisdictions than the species totally absent from Australia.

PPN species absent from particular jurisdictions, and most frequently ranked in the top 10 for other Australian jurisdictions included *Aphelenchoides besseyi, Cactodera cacti, Globodera rostochiensis, Helicotylenchus pseudorobustus, Hemicriconemoides mangiferae, Heterodera fici*, *Paratrichodorus porosus, P. renifer, Pratylenchus scribneri*, *Quinisulcius capitatus, Rotylenchulus parvus, R. reniformis, Tylenchorhynchus annulatus, T. claytoni* and *Xiphinema index* (Electronic supplementary material 3). Species from the genera *Pratylenchus, Heterodera, Xiphinema, Paratrichodorus* and *Tylenchorhynchus* were commonly ranked in the top 10 for five or more jurisdictions (Electronic supplementary material 3).

Discussion

Use of SOM to assess biosecurity risks

The basis of using SOM to assess biosecurity risks is that species assemblages integrate the complex interactions of the biotic, abiotic and anthropogenic environments (Begon et al. 1996; Gevrey et al. 2006; Paini et al. 2010b; Worner and Gevrey 2006). All the species in a particular place will have broadly similar niches and form an assemblage (Wisz et al. 2013; Worner and Gevrey 2006). Geographic units sharing many species of an assemblage will also share similar niches and ecological characteristics (Ferrier and Guisan 2006; Wisz et al. 2013; Worner and Gevrey 2006). Thus, if a particular species is missing from an assemblage at a particular place, but is found in other regions with otherwise similar assemblages, then it is likely to be able to establish in the place where it is absent and should be regarded as a biosecurity risk.

An advantage of a SOM analysis is that it is based on patterns in species assemblages and their resulting associations with each other, rather than simple pairwise comparisons of species between regions. SOM analyses and the resulting indices can differentiate

biosecurity risks from many species from all over the world to any given region (Paini et al. 2010a, 2011; Worner et al. 2013; Worner and Gevrey 2006). In this study PPN and Australia were evaluated but any other country included in the dataset could have been analysed similarly. Another advantage is that the SOM index is based on a consistent mathematical calculation of similarity of species assemblages between regions and is more objective than qualitative observations (Paini et al. 2010b). All the species and regions are evaluated using the same framework in the SOM model; hence the SOM index and species rankings between regions are also comparable.

The SOM approach also has some limitations. The quality of dataset used is an important contributor to the limitations of any predictive modelling approach including SOM (Elith et al. 2006; Morin et al. 2013; Wisz et al. 2008). The species selected or represented on a dataset, the correctness of presence and absence of a species and the thoroughness of surveys are all inherent limitations. Only some species that may pose a biosecurity risk are listed on widely used databases such as the CABI crop protection compendium, invasive species compendium and EPPO databases. In the present study, a very comprehensive list of PPN species of phytosanitary importance was compiled (Singh et al. 2013a) and used for the SOM. Of the 250 PPN species analysed, only 97 PPN species were listed in the databases listed above. Indeed, studies such as this are one way to identify other species to add to such databases.

The observation that the majority of countries in the world have 20 PPN species records or less, demonstrates the paucity of nematological expertise and scarcity of nematode surveys for most parts of the world (De Waele and Elsen 2007; Nicol et al. 2011; Powers et al. 2009). The lack of PPN species distribution records can result from low sampling effort rather than true absence of species in data poor regions and countries. This can distort understanding of species biogeography (Bello et al. 1986; Coomans 2002; Navas et al. 1993) and hence is an inherent limitation to using patterns of species assemblage to determine the risks from invasive pest species. Countries and/or regions with fewer than 10 species present are more difficult for the SOM to generate an accurately ranked list (Paini et al. 2011). Nevertheless, a SOM analysis is able to cope with up to 20 % errors in the species distribution dataset without causing large changes in species rankings (Paini et al. 2010b). Even allowing for the incomplete data, it is apparent that the distributions of most damaging PPN are still restricted. This was evident within countries in the present study, and presence of biogeographical patterns in nematode species distributions has also been observed elsewhere (Coomans et al. 2001; Ferris and Ferris 1985; Ferris et al. 1976; Porazinska et al. 2012). The power of SOM to make assessments of similarities in species distribution even with incomplete data (Paini et al. 2011) suggests that the lists generated here should be trustworthy.

Another limitation is that the SOM approach does not provide a measure of the impacts from a species. Therefore the SOM index and species rankings can only be considered as a preliminary measure of biosecurity risks. For instance a species with medium probability of establishing in a region but likely to cause high economic or environmental impact is likely to be rated as of greater importance by experts than a species which has a high probability of establishing but with low economic or environmental impact (Paini et al. 2010a, b).

Expert opinion is commonly used to prioritize invasive species for quarantine or management actions based on their knowledge of the damage and impact species have. However, the process is susceptible to biases depending on knowledge of the taxonomic group, the time available and other external influences (Burgman et al. 2011; Martin et al. 2012). These biases may result in differences of opinion between experts especially when evaluating large numbers of species (McGeoch et al. 2012; Paini et al. 2010b). Another pitfall of using expert opinion is that biosecurity risks may be underestimated when there is uncertainty and a lack of information on the impacts of a species (McGeoch et al. 2012). The biosecurity risks from many PPN may not have been realised due to lack of information and uncertainty (Singh et al. 2013b). When using a systematic approach such as a SOM analysis, the abovementioned biases can be avoided and there is considerable potential for identification of species which could establish and later become invasive in a particular region.

There are thousands of potential pest species from highly diverse groups such as nematodes, fungi or arthropods and resources to thoroughly evaluate all are not available. Therefore the SOM analysis can be used to rank species, and those with high likelihoods of

establishment (SOM indices) can be prioritised for further, more detailed analysis of potential impacts (Cook et al. 2011a, b; Morin et al. 2013). Targeted investigation on species with good chances of establishment could be used to point out species which could become new threats to a particular region.

For example, in the present analysis *Helicotylenchus microcephalus* ranked third for NT and fifth for NSW, QLD and WA and has been reported from many hosts (including economically important crops such as sugarcane, chickpeas, soybean, citrus, grapevine, and ornamental plants) from 20 different countries (PPN distribution database, this study). However, the biology and damage caused by *H. microcephalus* is not well known, and after qualitative evaluation based on expert opinion only, it was classified as low risk to Northern Australia (Hodda et al. 2012). However, considering the high likelihood of *H. microcephalus* establishing in Northern Australia based on SOM index, classification as low risk could be an underestimation of the biosecurity risks by experts. Thus such species are good candidates for further investigation.

In addition to prioritising species, the clustering of countries and regions with similar PPN species assemblages can be used to identify pathways linking these countries and regions to Australia for further analysis and quarantine targeting. Regions which have similar pest species assemblages can act as donors of invasive species (Paini et al. 2010b; Worner and Gevrey 2006). For instance WA and NSW have very similar PPN species assemblages except *H. pseudorobustus, P. scribneri* and *R. reniformis* which occur in WA, but not in NSW. These three species have high SOM indices for NSW (0.82–0.65) and therefore have a high probability of establishing in that state if they were to arrive. Based on this information, the potential pathways for these species between NSW and WA can be targeted during risk assessments. Similar findings have been reported for insects in the USA, where the greatest risks from exotic insect species came from other states within the USA with very similar insect species assemblages (Paini et al. 2010a).

Although quarantine is mostly controlled at a national level (as, for example, in Australia, and the USA), smaller geographic units may be better for analysis and identifying threats, especially for large countries like Australia. Were they countries rather than states or territories, WA, QLD and NT would be the tenth, eighteenth and twentieth largest in the world. Using smaller units captured more variation in PPN assemblages than using the country as a whole, as shown by the divergent lists of threats for the different states, and the different positions of the neurons.

Using smaller units also meant that fewer species were recorded in each, and there was a greater likelihood of false absences. However, the SOM was able to deal with the fewer records from individual jurisdictions well, and produce results consistent with known climatic and other differences. In addition to climate, other biotic (such as crops, cropping history), abiotic and anthropogenic factors (history of colonization, trade, and even research on particular taxa) which affect the known species distributions are taken into account by SOM when clustering regions. Although NSW and WA differ climatically, their clustering into the same neuron can be explained by their similarity in crops and their history of nematological research.

Particular implications for Australia

All PPN listed on the high priority pest list by Plant Health Australia (PlantHealthAustralia 2012) that are absent from Australia were ranked in the top 15 species of one or more of the jurisdictions considered. This supports the ranking based on expert opinion from these species. The SOM rankings also identified a further 32 PPN species not yet on the priority lists of Plant Health Australia and ranked them in the top 15 for one or more jurisdictions. Species currently not on the high priority pest list but having similar likelihoods of establishment as currently known high priority pests for Australia could be targeted for more detailed analysis. More detailed analysis of these species could result in identification of some as new threats to Australia.

The majority of the species (76 % N = 29/38) ranked in the top 15 biosecurity risk for any of the jurisdictions were of more general importance for the country as a whole since they occurred in the top 50 for four or more of the individual jurisdictions. For instance *H. oryzae*, ranked first for QLD, NSW, WA and NT is also ranked sixth for SA and VIC (with SOM index range of 0.65–0.31). Such a ranking indicates *H. oryzae* can establish in any of the six jurisdictions. This is further supported by evidence from literature confirming the wide ecological tolerance of *H. oryzae* (i.e. survival in moderate to heavy

clay soils including flooded soils; soil pH range 5–9, and soil temperatures ranging 10–34 °C (Babatola 1981; Fortuner 1976; Maung et al. 2012). The evidence from this species indicates that many of the PPN species posing greatest biosecurity risks may have relatively wide environmental ranges.

PPN species from both temperate and tropical regions posed risks to Australia, with 18 countries having very similar species assemblage to that of at least one Australian jurisdiction. These countries include major trading partners with frequent travel pathways linking to Australia. Hence, PPN potentially invasive to Australia could come from a wide range of countries via a wide range of pathways. The risks from a wide range of PPN species to Australia overall is not unexpected given the diverse range of climates and crops, together with the 18 different agro-climatic regions (Hutchinson et al. 2005; Hutchinson et al. 1992). That risks from different PPN varied among jurisdictions is also expected. There is scope for different targeting of quarantine species for different jurisdictions in a country the size and climatic variability of Australia. TAS and NT have greatest difference in climate and illustrate the scope for different targeting of species. While we do not imply that species with likelihood of establishing in other jurisdictions should not be targeted by another jurisdiction (see above for species with wide environmental ranges), it is logical for quarantine inspectors in TAS to spend relatively greater sampling effort on species which are more likely to establish in TAS, SA, VIC, NSW and WA than on species which are less likely to establish. Given the microscopic size and difficulties in detecting PPN and other similar microscopic pests (Ferris et al. 2003; Rajan 2006), targeted sampling effort can make a difference. For example, consignments of root vegetables, bulbs, nursery stock and other goods with the potential to carry targeted nematode species may be sampled more vigilantly to improve chances of detection.

The species ranks for all states in Australia except TAS and NT were positively correlated; indicating some similarity in risks from PPN species. Tasmania and Northern Territory had the greatest difference in their species assemblages indicated by the distance separating the respective neurons. TAS and NT have contrasting climates and there are thus strong indications that PPN species posing high phytosanitary risks to TAS do not pose the same levels of risk to NT, and vice versa. For example, *H. oryzae* is the top ranked species for NT, NSW, WA and QLD, but is ranked 80th for TAS. *H. oryzae* is an important pest of rice and is known mainly from countries or regions with climates suitable for growing rice (CABI 2013) and is likely to be of minor importance for TAS, because of unfavourable conditions for rice cultivation. Similarly *Scutellonema clathricaudatum* prefers warm (30–36 °C) tropical climates (Baujard and Martiny 1995) so was identified by SOM as of greatest risk to NT (ranking 2nd) and low risk to TAS (ranking 115). By contrast, *D. destructor* was ranked by SOM as the most important species for TAS, SA and VIC and second most important for NSW and WA but relatively unimportant (ranking 71) for NT. Elsewhere, *D. destructor* is of known importance in countries/regions with cold-temperate climates, and is adapted for surviving in cold climates (Svilponis et al. 2011). It is unable to withstand excessive desiccation (Sturhan and Brzeski 1991) and the monsoonal conditions in NT would be unfavourable for it, particularly during the dry season. These examples illustrate that the SOM rankings generally accord with PPN habitat preferences where they are known.

The clustering of jurisdictions in Australia based on PPN species assemblages (this study) was similar to the SOM clustering of jurisdictions based on insect (Paini et al. 2010b) and fungal species assemblages (Paini et al. 2011). In all three SOM analyses, the country as a whole and its jurisdictions were clustered into 5 different neurons. It thus seems that PPN, fungi and insect species assemblages differ similarly among jurisdictions. SA and VIC consistently clustered in one neuron in all three analyses, indicating these jurisdictions had very similar species assemblages of all three pest groups. All three taxa assemblages seem to capture the climatic, biotic, and abiotic characteristics of each region and all include pests of agricultural crops.

Other modelling methods have also used species assemblages to predict future invaders but with different datasets and model parameters (Diez et al. 2012; Hui et al. 2013). While the SOM model uses species presence and absence data to determine species assemblages more complex models can integrate additional information on species naturalisation and invasion history to build predictive models which provide a probabilistic score on the likelihood of establishment (Diez et al. 2012). The time invasive species spend as part of an assemblage also affects the characteristics of a species assemblage and can be integrated in models for

predicting future invaders (Hui et al. 2013). Compared to the two recent studies, the SOM model uses a relatively simple species presence and absence dataset which is more readily available for plant pests and pathogens than the datasets on invasion histories (Diez et al. 2012) and the invasion residence time of species (Hui et al. 2013). The Bayesian model (Diez et al. 2012) and the functional modularity model (Hui et al. 2013) both require input from experts in the model development and are more complex than the SOM model used in this study.

Conclusions

Based on this and previous studies (Morin et al. 2013; Paini et al. 2010a, b, 2011; Worner and Gevrey 2006) we suggest the use of a SOM analysis as complementary to expert opinion especially when analysing biosecurity risks from large numbers of pest species. A SOM analysis is a systematic approach, which is free from bias and can provide a preliminary assessment of risks as well as an independent means of cross-validating lists derived through expert elicitation. Systematic assessments generally increase the consistency and reliability of biosecurity risk assessments across geographies (Gordon et al. 2008; Hayes 2003; Holt et al. 2006). The prioritised PPN species from this study could be used for cross validation of expert opinion and also be used for more detailed risk analysis including information on other important variables such as pathogenicity, host range, pathways and association with disease complexes.

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