


Predicting and managing plant invasions on offshore islands

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Abstract

Resources for biodiversity conservation are limited and it is therefore imperative that management actions that have the best chance of success are prioritized. Non-native species (NNS) are one of the key problems facing biodiversity conservation, so understanding how NNS disperse and establish can inform more effective conservation planning and management. Using a novel Bayesian belief network model, we investigated non-native plant dispersal on the approximately 550 islands along the Pilbara coast, Western Australia, and identified priority species and locations for targeted management. Of a total of around 9,000 weed arrivals onto the islands, 1,661 arrivals across 14 weed species had some probability of establishment. Suggested management actions in these cases would be education campaigns to inform visitors about the risk of accidental transport of propagules, quarantine programs, and eradication. For the seven weed species that arrived only via human dispersal and had a >10% chance of establishment on five islands, surveillance, and control of new arrivals would be the recommended management actions. Removal of propagule source populations would not be a cost-effective management strategy. The inherent flexibility of our model means that different objectives can be analyzed in a transparent way, making it a powerful tool for guiding effective targeted action, derived from an explicit decision-making framework.

KEYWORDS

Bayesian model, conservation management, island ecosystems, non-native plants, threatened species

1 | INTRODUCTION

Ecosystem invasion by non-native, or alien, species represents one of the biggest threats to biodiversity (Catford, Bode, & Tilman, 2018; Clavero & Garcia-Berthou, 2005;

Simberloff et al., 2013), driving species extinctions and adversely affecting ecosystem function through changes in species interactions (O'Dowd, Green, & Lake, 2003). Non-native species (NNS) can arrive into ecosystems naturally, mediated by wind or water dispersal

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(e.g., coconuts floating onto a new beach), or by animal transport (e.g., attached to birds). Arrival can also occur through human-mediated actions, which can be deliberate (e.g., bringing in a NNS for biological control), or accidental (e.g., seeds, spores or organisms on clothing, equipment, or vehicles moved from one place to another). Such human-mediated transport has occurred throughout human history (Hobbs, Valentine, Standish, & Jackson, 2018; Hulme, 2009). Although there are multiple sources and multiple dispersal pathways for species invasions, only 5–20% of NNS are actually detrimental to ecosystems (McGeoch et al., 2016).

NNS are managed at considerable cost: over US\$100 billion for 2005 in the United States (Pimentel, Zuniga, & Morrison, 2005), and A\$13.6 billion for 2011–2012 in Australia (Hoffmann & Broadhurst, 2016). Plants make up almost a third of the hundred “worst alien invasive species” globally (Luque et al., 2014). The impacts and costs of managing NNS plants are also large (Genovesi, Butchart, McGeoch, & Roy, 2013), with around A\$4 billion spent annually in Australia (Hoffmann & Broadhurst, 2016). Weed management for conservation can encompass many actions, ranging from eradication, or at least consideration of eradication feasibility, which is rarely assured, especially over larger areas (Panetta, 2015), control, through the clearing of certain areas in a landscape, habitat manipulation (e.g., fire), or reducing the number of individuals (e.g., through a decrease in seed production) (Panetta & Gooden, 2017; Walsh, Newman, & Powles, 2013), and education campaigns.

Islands are more vulnerable to NNS species than larger, more connected landscapes, and support many threatened and endemic species (Lohr, Wenger, Woodberry, Pressey, & Morris, 2017; Tershy, Shen, Newton, Holmes, & Croll, 2015). Quarantine and surveillance are the two key tools used to restrict the spread of NNS to islands. Quarantine is targeted at blocking source populations or dispersal pathways (Cope, Ross, Wittmann, Prowse, & Cassey, 2016; Faulkner, Robertson, Rouget, & Wilson, 2017), and surveillance is aimed at finding new NNS while their populations are still small or restricted enough to manage or eradicate (Moore et al., 2010; Whittle et al., 2013). Islands are also important sites for recreation, cultural, and industrial activities, which can all facilitate the establishment of NNS (Lohr et al., 2017) and reduce the success of quarantine actions (Boser et al., 2014). However, with adequate resources, a comprehensive biosecurity program can prevent the incursion and establishment of NNS into areas of high conservation value (Scott et al., 2017).

Limited resources for management and conservation mean that managers must prioritize areas for quarantine operations and routine surveillance. However, lack of baseline data and expertise for site-specific modeling in

management agencies make it difficult to identify which NNS are most likely to reach, establish, and spread to specific locations. Risk assessments that set out to identify the greatest threat for an area are often in the form of ranked lists of species (Gordon, Tancig, Onderdonk, & Gantz, 2011; Pheloung, Williams, & Halloy, 1999). However, these do not typically consider the vulnerability of sites to the establishment of new populations of incoming NNS species, and so have limited application for informing the spatial prioritization of surveillance (Lohr et al., 2017). Pest risk maps are similarly limited, in terms of spatial scale discrepancies, data deficiency, and accessibility for managers (Dahlstrom, Hewitt, & Campbell, 2011).

Given the logistical and financial difficulties with managing islands, individually or in groups (Carrion, Donlan, Campbell, Lavoie, & Cruz, 2011), it is important to prioritise which islands and what type of management interventions (e.g., quarantine, surveillance, or control) are worth investing in for conservation management success. We therefore set out to develop a new method for predicting the annual biosecurity risk for a group of islands along the Pilbara coast in Western Australia. The method accounts for the complex inter-relationships between non-native plant species' source populations and locations, their dispersal pathways, likelihood of dispersal, and their destination islands. Using novel “Biosecurity BBN” software (Supplementary Material; Lohr et al., 2017), based on Bayesian belief network (BBN) models, we estimated, for each island, the total number of propagules of each non-native weed species arriving each year, via multiple dispersal pathways, and the annual risk of establishment for each NNS, for 16 weed species and 556 islands. The aim was to inform more focused, effective, and cost-effective, species-specific conservation management. In particular, we aimed to identify hotspots of natural weed dispersal sources and islands where weed spread was driven solely by human activity, so that appropriate management interventions could be formulated. Our methods are broadly transferable and applicable and can be used to inform planning and management in any island system.

2 | METHODS

2.1 | Study area

The Pilbara islands ($n = 556$), off the central coast of Western Australia (Figure 1), are typically small and widely dispersed over approximately 30,000 km² of ocean, extending along more than 700 km of coastline

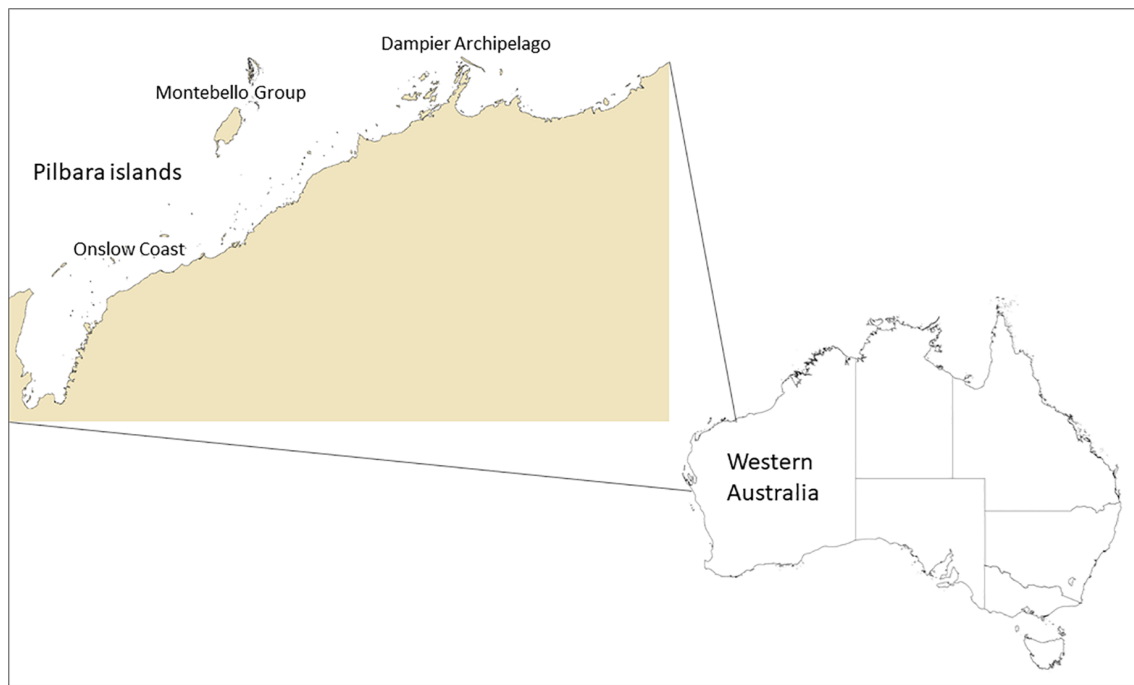


FIGURE 1 Location of the Pilbara Islands, and selected island groups, off the coast of Western Australia

(Lohr et al., 2017). The islands range in size from Gndaroo Island (3 ha) to Barrow Island (202 km²), and have a total area of approximately 690 km², with 1,600 km of coastline. Many of the islands are isolated, and the adjacent human population density is low, with 45,000 people along the nearby mainland coast (ABS Stat, 2015). Several of the islands are refuges for threatened and endemic species, and most are important breeding sites for seabirds and marine turtles. In spite of their remoteness, protection through quarantine is difficult because most biosecurity resources are located in a few coastal towns, and 10% of the local population are boat owners (ABS Stat, 2015; Department of Transport, 2014), giving people easy, and largely unregulated, access to the islands. Indeed, only 22 of the islands have quarantine regulations, with the remainder having minimal, or no, biosecurity measures in place. Some 403 non-native plant species have been documented on the Pilbara islands (Lohr, Lohr, Keighery, & Long, 2016).

2.2 | Model structure and inputs

BBNs are mathematical models that use Bayes' rule to compute the likelihood (i.e., posterior distribution) of a target variable given evidence (Korb & Nicholson, 2010; Russell & Norvig, 1995). BBNs consist of a graphical structure, containing variables represented as nodes, arcs (conditional dependencies or relationships) between

variables, and conditional probability tables associated with each node (Figure S1.1). The conditional probability tables report the strength of the relationship between each combination of possible values of each variable. BBNs can synthesize most types of data and are thus useful for applications in data-limited environments, for scenario analysis, across a range of alternative scenarios and assumptions (Smith, Howes, Price, & McAlpine, 2007). They can also be used to inform where further research would most improve model confidence (Marcot, 2006; Marcot, Holthause, Raphael, Rowland, & Wisdom, 2001). A full description of how BBNs work is given by Uusitalo (2007).

In our “Biosecurity BBN” (see Supplementary Material 1 for details, Appendix S1), models representing human-mediated and natural dispersal pathways for weed species propagules were developed. We considered recreational and industrial visitation, ocean currents, floodwaters, and wind currents. A further model estimated the probability of NNS establishing a new population given the estimate of the number of arrivals per annum (Figure S1.1, lower right). The outputs of the model consisted of two spreadsheets: the first one detailed all arrival events of each weed to each island under the dispersal pathway(s) used by the propagule. The second spreadsheet listed the probability of establishment of each weed on each island.

Empirical data, data from the literature, and expert elicitation were used to parameterize the dispersal

models, which were developed using the GeNIe BBN tool (available at <http://www.bayesfusion.com/>) (Supplementary Material 1, Appendix S1; Lohr et al., 2017). The propagule arrival probabilities for each dispersal pathway were combined for each species as inputs to the establishment sub-model to generate a probability of establishment for each NNS on each island. Propagule pressure is linked to invasion success or failure (Nunez, Moretti, & Simberloff, 2011; Von Holle & Simberloff, 2005), and is a function of propagule size (number of introduced individuals), number of distinct introduction events (each with its own propagule), and the spatial and temporal patterns of propagule arrival (Lockwood, Cassey, & Blackburn, 2009). Establishment is defined as the ability to survive, reproduce, and expand spatially and numerically. Expert knowledge and the scientific literature were used to define the establishment rate for each species, which varied for each island according to different biotic and abiotic conditions (Supplementary Material 1, Appendix S1; Lohr et al., 2017).

2.2.1 | Human-mediated dispersal pathways

Recreational dispersal pathways include passive propagule attachment to visitor vehicles (in this case boats), baggage or clothing (Pickering & Mount, 2010). From the 1970s to 1990s, industrial activity in the Pilbara region increased significantly, with concomitant increases in human population and related recreational island visits. The islands vary widely in size, proximity to shore, and popularity, so boat ownership and expert-elicited data were used to estimate the probabilities of visitor-dispersed NNS (see Supplementary Material 1, Appendix S1; Lohr et al., 2017 for full details). Industrial dispersal pathways are generally more controlled, because stricter quarantine protocols tend to apply to industry rather than recreation. Data for employee numbers per site, shift changes per year, and the type (e.g., gas refinery and lighthouse) and phase (active or not, etc.) of industrial activity were combined to give an annual estimate of the probability of transporting NNS to an island (Supplementary Material 1, Appendix S1; Lohr et al., 2017).

2.2.2 | Natural dispersal pathways

First, flood plume and rainfall data were used to calculate the annual probability of floodwater reaching an island, and expert knowledge was elicited to determine whether a species would be caught up in floodwater and survive transport to an island. Second, ocean currents unrelated

to flooding can disperse some species if their propagules fall into the sea (e.g., prickly pear, *Opuntia stricta*). The probability that NNS propagules would disperse via currents to and among islands was based on the Australian ocean connectivity model and web application (CONNIE2) (Condie & Andrewartha, 2008; Condie, Waring, Mansbridge, & Cahill, 2005; CSIRO, 2015), which combines an oceanographic model and a particle-tracking algorithm to predict the source or destination of particles dropped into ocean currents (Supplementary Material 1, Appendix S1). Wind dispersal was the third natural dispersal pathway we considered, and the model estimated the probability of dispersal of non-native propagules based on a species having specific morphological traits, such as lightweight, flat or winged seeds, or tall adult plants (Tackenberg, Poschlod, & Bonn, 2003). Species morphology and weather data were combined to estimate the wind dispersal potential for each NNS. Although animal (e.g., bird) dispersal is also a natural mechanism, this was not modeled for this study.

2.3 | Analyses

To identify islands where legal restrictions or behavioral change could potentially reduce the rate of arrival of non-native weed species, we investigated the arrival patterns of 16 non-native plant species from the Pilbara mainland to the islands. Outputs given by the model were mean annual arrivals for each island/weed species combination, summarized in Table 1 across all islands. Subsequently, we focused on the weed species that arrived along human-mediated pathways to identify islands where legal restrictions or behavioral change could potentially reduce the rate of arrival of NNS. We also identified “weed hotspots”: island source locations responsible for most propagules. We explored the effect on weed spread of removing or eradicating weeds from these islands to compare different types of management and establish which was most effective.

2.4 | Model validation

A fuller validation of the model would require comprehensive new field surveys, which are not feasible in our study area. In lieu of this, we ran the model assuming that none of the NNS were present on the islands, to see how well predictions on the probability of establishment matched current distribution patterns. This approach does not allow for an assessment of how weeds have previously dispersed among islands from already established populations, nor does it take into consideration historic

TABLE 1 Total annual propagules for 14 weed species arriving on Pilbara islands

Common name	Latin name	Propagules
KAPOK	<i>Aerva javanica</i>	494,552
TRIDAX	<i>Tridax procumbens</i>	59,378
RUBBERPLANT	<i>Calotropis procera</i>	23,290
STYLO	<i>Stylosanthes scabra</i>	16,765
PRICKLY_PEAR	<i>Opuntia stricta</i>	3,657
BUFFEL	<i>Cenchrus ciliaris</i>	652
NATAL_RED_TOP	<i>Melinis repens</i>	414
INDIGOFERA	<i>Indigofera oblongifolia</i>	381
PURPLE_BEAN	<i>Macroptilium atropurpureum</i>	349
BELLY_ACHE_BUSH	<i>Jatropha gossipifolia</i>	272
STINKING_PASSIONFLOWER	<i>Passiflora foetida</i>	265
MOTHER_OF_MILLIONS	<i>Bryophyllum delagoense</i>	264
CENCHRUS_SP	<i>Cenchrus sp.</i>	11
RUBY_DOCK	<i>Rumex vesicarius</i>	1

use of the islands, which has been ongoing for over 100 years (Lohr et al., 2016).

The sensitivity of the estimated number of arrivals to continuous nodes was measured iteratively by independently varying the inputs of each node, both doubling and quadrupling the modeled inputs. This generated multiple sets of results with uncertainty in one parameter. We evaluated the rate of change across the three input levels and provide an average propagule arrival rate for each continuous node (See Supplementary Materials 2, Appendix S2). We assessed the relationship between number of arrivals and likelihood of establishment using outputs generated from the arrivals sensitivity analysis.

2.5 | Management decision assessment

Quarantine, surveillance and control, and eradication will each be appropriate only in specific situations. To determine which islands and weeds should be the focus of different management interventions, we examined three scenarios. The first considered weeds that would arrive only by human mediation and islands where these species had >10% chance of establishment, for which suggested management actions would be education campaigns to inform visitors about the risk of accidental introduction, quarantine programs, and eradication. The second scenario considered weeds arriving via all pathways and islands where these species had >50% chance of establishment, for which appropriate actions to implement would be surveillance and control of new arrivals. The third scenario considered weeds arriving via all pathways and islands where the eradication of propagule

source populations would reduce the probability of establishment by 50% or more. For this final scenario, we examined weed species with at least 10% chance of establishment on islands in the study area when island hotspots were included, and calculated the proportional change in establishment rates when weed hotspots were excluded from the model.

3 | RESULTS

3.1 | Model validation and sensitivity analysis

Model validation results (Supplemental Information 2, Appendix S2, Table S1) suggest that, when applied to the Pilbara Islands, our model has a high degree of accuracy: $\geq 97.6\%$ of predictions (combinations of weed species and islands) on the probability of establishment matched current weed distribution patterns on the islands. Some 97.1% of predictions were correct negatives (model results suggested the weed would not invade, and the weed was not present on the island), and 0.5% of predictions were correct positives (weed identified as NNS and was currently present on the island). In contrast, only 2.4% of model results were incorrect: 1.4% were weakly false positive (model results suggested <50% chance of weed establishing, but weed was not present), 0.3% cases were strongly false positive (model results suggested >50% chance of weed establishing, but weed was not present), and 0.7% cases were false negatives (model results suggested weed will not establish but weed was present on the island). The worst performing weed

in regards to model accuracy was buffel grass with only 90.7% of invasion events being correctly identified and 8.8% of events being false negatives.

Our sensitivity analysis indicated that almost all of the continuous parameters had a linear relationship with the number of arrivals (only current carry drop rate and threat attachment rate had non-linear relationships with propagule arrival.) The relationship between arrival of propagules and probability of establishment was weak, indicating that probability of establishment was more strongly influenced by the other parameters in the model at the propagule arrival loads tested (see Supplementary Material 2, Appendix S2; Table S2 and Figure S11).

3.2 | Overall patterns of modeled weed arrival

Across the 556 islands, 16 non-native plants were already present on 87 islands. Kapok (*Aerva javanica*) accounted for most arrivals (Table 1). Of all the arrival events of each weed species onto the islands (8,896), kapok accounted for the top 406 arrival events in terms of the number of propagules, predominately driven by wind dispersal. Human-mediated arrival pathways were solely responsible for bringing propagules of thirteen weed species (of a total of 16 modeled) to 411 Pilbara Islands: belly ache bush (*Jatropha gossypifolia*), buffel grass (*Cenchrus ciliaris*), kapok (*Aerva javanica*), indigofera (*Indigofera oblongifolia*), mother of millions (*Bryophyllum delagoense*), Natal red top (*Melinis repens*), prickly pear (*Opuntia stricta*), purple bean (*Macroptilium atropurpureum*), ruby dock (*Rumex vesicarius*), stinking passionflower (*Passiflora foetida*), shrubby stylo (*Stylosanthes scabra*), and *Tridax procumbens* (Supplementary Information 2, Appendix S2; Table 1). Of these species, the five most prevalent, by propagule number were belly ache bush, stinking passionflower, buffel grass, stylo, and Natal red-top (Figure 2). Based on the dataset, the most successful already-established species overall in terms of numbers of islands were: buffel grass, stinking passionflower, prickly pear, Natal red top, and shrubby stylo (Figure 2).

3.3 | Overall patterns of establishment

Although there were 8,896 weed arrival events onto the islands, only 1,661 of those events, and fourteen of the weed species, had >10% chance of establishment (Table 2). The probability of establishment and the number of islands where the weed species could establish varied widely across species. For instance, ruby dock had a



FIGURE 2 The top five Pilbara Island NNS: bellyache bush; stinking passionflower; buffel grass; shrubby stylo; Natal red top, and establishers: buffel grass; stinking passionflower; prickly pear; Natal red top; shrubby stylo. (All images from Wikimedia Commons, attributions as given.) NNS, non-native species

very low chance of establishment (0.1% chance) on only one island (Dolphin), whereas kapok, rubberplant (*Calatropis procera*), and tridax could potentially establish on 443, 449, and 406 islands, respectively, although the probability of establishment varied, with kapok having >90% chance of establishing on 71 islands. In comparison, the highest probabilities of establishment for rubberplant and tridax were 29% and 65%, respectively. These differences were reflected in the prevalence of already-

TABLE 2 Overall annual establishment rates for 14 weed species on Pilbara islands

Common name	Latin name	Islands established	Establishment >10%
RUBBERPLANT	<i>C. procera</i>	449	53
KAPOK	<i>A. javanica</i>	509	359
TRIDAX	<i>T. procumbens</i>	406	105
PRICKLY_PEAR	<i>O. stricta</i>	61	28
STYLO	<i>S. scabra</i>	55	21
BUFFEL	<i>C. ciliaris</i>	28	3
CENCHRUS_SP	<i>Cenchrus sp.</i>	23	0
NATAL_RED_TOP	<i>M. repens</i>	19	0
INDIGOFERA	<i>I. oblongifolia</i>	9	2
STINKING_PASSIONFLOWER	<i>P. foetida</i>	9	3
PURPLE_BEAN	<i>M. atropurpureum</i>	7	2
MOTHER_OF_MILLIONS	<i>B. delagoense</i>	6	2
BELLY_ACHE_BUSH	<i>J. gossipiifolia</i>	6	2
RUBY_DOCK	<i>R. vesicarius</i>	1	0

established populations on the islands: kapok was established on at least 66 islands, whereas rubberplant was not established on any island and tridax was established on only one. Many islands were likely to have several weeds establish on them, with Barrow, East Mid Intercourse, Mistaken, and Preston each at risk of having ten or more species establish.

3.4 | Propagule source hotspots

We identified 10 islands as weed source hotspots for >1% of naturally dispersed propagules (Table 3). Two islands—Enderby and West Lewis South—were hotspots for both wind- and current-dispersed propagules; Thevenard and West Lewis North were sources for current-dispersed propagules, and Angel, Delambre, Dolphin, East Lewis, Malus Large, and Rosemary were sources of wind-dispersed propagules (Supplementary Information 2, Appendix S2; Table 3). Enderby Island was by far the largest source of current-dispersed propagules, with more than 80% of all such propagules across the study islands. Enderby and West Lewis South were both sources of for around one quarter of wind-dispersed propagules.

3.5 | Management decision assessment

Our first scenario determined how many weed species arrived onto islands only via human dispersal, and with >10% chance of establishment, and identified key islands

TABLE 3 Island weed source hotspots for naturally dispersed propagules, by dispersal method. Figures are percentages of all weed propagules

	Dispersal by wind	Dispersal by current
Angel	10.2%	
Delambre	8.7%	
Dolphin	1.2%	
East Lewis	10.3%	
Enderby	25.1%	82.9%
Malus large	3.7%	
Rosemary	2.5%	
Thevenard		2.3%
West Lewis north		1.4%
West Lewis south	24%	12.4%

where education campaigns, quarantine, and consideration of eradication feasibility would be most effective. Of the 411 islands with arrival events via human pathways, only five islands and eight weed species met the criteria set by this scenario (Table 4).

Our second scenario identified islands where weeds arriving via all pathways had >50% chance of establishment. There were many more islands than for scenario one, with 121 islands where at least one of four weed species (kapok, prickly pear, stylo, and tridax) had >50% chance of establishment. For these islands and weed species, the indicated course of action would be surveillance and control of new arrivals. Only 23 of those islands had

TABLE 4 Islands with human-dispersed weeds with >10% probability of establishment

Island name	Weed name	Propagule arrivals (mean)	Propagule arrivals (SD)	Probability of establishment (%)
Barrow	Belly_ache_bush	45.3	87.0	13.5
Barrow	Mother_of_millions	45.9	102.2	14.2
Barrow	Prickly_pear	44.5	89.6	11.9
Barrow	Stylo	44.7	89.5	23
East_mid_intercourse	Buffel	25.1	51.6	23.1
East_mid_intercourse	Stinking_passionflower	22.6	44.1	17.2
Finucane	Indigofera	100.8	203.5	15.8
Finucane	Purple_bean	96.7	198.4	18.6
Mistaken	Belly_ache_bush	65.3	131.8	19.2
Mistaken	Buffel	63.2	126.8	16.8
Mistaken	Indigofera	62.7	126.5	12.8
Mistaken	Mother_of_millions	63.2	132.6	11
Mistaken	Purple_bean	67.5	134.0	23.9
Mistaken	Stinking_passionflower	68.6	133.7	23.3
Preston	Stinking_passionflower	115.0	240.1	16.4

Island	Kapok	Prickly_pear	Stylo	Tridax
East_mid_intercourse	99.9	58.7	96.8	57.6
East_intercourse	0	66.6	97.5	50.5
Intercourse	97.5	51.4	84	0
Mistaken	0	60.2	97.9	64.5
West_mid_intercourse	96.6	51.2	86.6	0
Birthday	99.7	0	0	53.2
Boodie	99.9	0	0	54.3
Brigadier	99.8	0	0	52.4
Conzinc	0	0	97.2	55.6
East_goodwyn	99.5	0	0	54.3
East_lewis	0	0	97	51.6
Elphick_nob	99.8	0	0	54.4
Gossypium	99.7	0	0	52.3
Hauy	99.9	0	0	55.5
Island_n	99.8	0	0	55.2
Kendrew	99.8	0	0	53.8
Kingcup	99.9	0	0	56.3
Lady_nora	99.8	0	0	54.8
North_west	99.9	0	0	51.8
Parakeelya	99.9	0	0	53
South_east	99.9	0	0	55.1
West_intercourse	96.7	0	85.4	0
West_lewis_south	0	0	97	55.3

TABLE 5 Islands with two or more weed species with >50% probability of establishment. Figures give % probabilities of establishment

two or more weed species arriving with >50% chance of establishing (Table 5), which is likely to be a much more tractable number of islands for routine surveillance and control.

Our third scenario considered the decrease (by at least 50%) of establishment probability of weeds if the propagule source populations, that is, “hotspots,” were removed. Of the 11 weed species with >10% chance of establishing on islands, the removal of the source populations would substantially reduce the chance of establishment only of kapok on eight islands. However, our scenario identified that there were 26 islands acting as source populations for kapok on those eight islands.

4 | DISCUSSION

Resources for biodiversity conservation everywhere are limited and often inadequate (McCarthy et al., 2012), and it is therefore imperative that NNS management targets areas with the best chance of success (Forsyth, le Maitre, O'Farrell, & van Wilgen, 2012). Understanding how NNS disperse and establish can inform more effective conservation planning (Perry, Moloney, & Etherington, 2017). Using a novel BBN model, we were able to identify a small subset of islands and non-native weeds for which invasive species management would be most effective, narrowing down the possible options from 8,896 island \times weed combinations (16 species \times 556 islands) to 171 possible interactions. This illustrates both the power of the model as a tool for guiding effective targeted action, derived from an explicit decision-making framework, and its broad flexibility in application: it can be used for island systems (including landscape or topographic islands) anywhere. The model used general rules to inform managers when and where to carry out quarantine, surveillance, or control. Its inherent flexibility means that different objectives can be analyzed in a transparent way, and more information relevant to different aspects of the objectives can be added, such as data on species of concern on particular islands. Thresholds (e.g., establishment probability) applied within the tool can also be manipulated. In addition to the model's spatial adaptability, time components can be included to explore different establishment probabilities over time, and new information can be added at different time steps.

For weed species that arrive only, or predominantly, with humans, we recommend consideration of eradication feasibility followed by quarantine and education programs to reduce reintroduction, and then periodic monitoring. Surveillance and control are indicated for islands where establishment probabilities are high but arrival rates might be lower. This approach includes sites

where quarantine is already in place but could be ineffective on its own. Our analysis also identified two islands (East Mid-Intercourse and Mistaken) where there were both weeds that only arrived only via human dispersal and weeds that arrived via all pathways and had a high chance of establishment (see Tables 4 and 5). These islands represent an opportunity for multiple NNS management outcomes to occur simultaneously and should thus be targeted for further exploration in relation to taking action.

Our hotspot analysis indicated that removing weeds from key propagule source islands would not make much difference in terms of reducing arrivals on other islands (~5% on average), and therefore would not be cost-effective, given the conditions we set for this assessment. In our case, it is likely more effective to control populations that receive propagules from hotspots than to attempt to manage the hotspots in the scenario presented here. However, because there are a couple of islands that are key sources (Enderby and West Lewis South), it might be worthwhile to control these to limit increase in propagule numbers and potential to disperse. Given that the continuing existence of multiple sources will lead to continuing invasions and reinvasions, further research on the role of controlling source populations is indicated here, and the Biosecurity BBN tool can be used to assess at what point, and where, action should be taken in this scenario.

All models have inherent assumptions and uncertainty and our model is no exception. Model users need to be aware that the accuracy of the results depends on the accuracy of the inputs, and many of the assumptions made about the data inputs are detailed in the supplementary material. Scientific data on the dispersal of weeds species are limited, so in the absence of empirical data, we had to rely on expert-elicited data to parameterize the model. The use of expert knowledge in conservation science and decision-making has been growing due to limited resources available to collect direct field data and the urgent need to plan and implement conservation actions (Caley et al., 2014; Drescher et al., 2013; Martin et al., 2012). In our study, we used as much empirical data as possible and relied on expert knowledge only to help parameterize the model when no other data existed. BBNs can accommodate uncertainty and are particularly useful for combining expert-derived information with empirical data. Furthermore, the model validation indicates that, when applied to the Pilbara Islands, our model had a high degree of accuracy, with $\geq 97.6\%$ of predictions on the probability of establishment matching weed distribution patterns on the islands. The model validation results suggest that, using relative establishment probability across the island system, our BBN can identify the

most at-risk islands, and the weeds most likely to establish on each island, and will reduce the exposure of investment in surveillance to uncertainty in species- or site-specific parameters. Still, users are advised that pre-eradication surveillance and planning are necessary early steps in any eradication campaign (Wenger et al., 2018).

Non-native plants increase the extinction risk of native plant species (Richardson & Ricciardi, 2013), as well as affecting animal populations. For example, spreading root systems may make it difficult for some species to dig burrows or nests (Cook, McCluskey, & Chambers, 2018; Leslie & Spotila, 2001), and where non-native plant species replace native vegetation, nesting birds lose suitable nesting space (Feare, Gill, Carty, Carty, & Ayrton, 1997; Lamb, Hall, Kress, & Griffin, 2014). The Pilbara Islands are important for Australian fauna: 33 vertebrate species have been recorded on 14 of the 19 islands, in the Dampier Archipelago, Montebello and Onslow groups (Figure 1). Of these, 14 species are listed as threatened by the International Union for Conservation of Nature (www.iucnredlist.org), Australia's Environmental Protection and Biodiversity Conservation (EPBC) Act List (www.environment.gov.au/epbc), or both (10 species: Table 6). The Montebello Islands and nearby Barrow Island provide important habitat for three threatened or priority mammal species, three species of threatened marine turtles, and three birds (Table 6). The Dampier Archipelago islands are also important sites for nesting turtles and the endangered northern quoll (*Dasyurus hallucatus*) (Table 6; Figure 3). In addition, the Lewis Islands provide important habitat for Rothschild's rock-wallaby (*Petrogale rothschildi*), translocated there to protect populations (Carwardine et al., 2014; Lohr, Passeretto, Lohr, & Keighery, 2015). Given

that endangered species are of “national environmental significance” (www.environment.gov.au/epbc), weed management on the Pilbara Islands is critical.

Our explicit, tractable approach to NNS management allowed us to determine where and how to act. Management action should focus on five islands for quarantine + education (where there is human dispersal and a high probability of establishment), and 23 islands for surveillance and low-level control (where two or more weed species arriving along all dispersal pathways have a > 50% chance of establishment). There are islands where two goals—eradication and management—can be met simultaneously (e.g., East Mid Intercourse and Mistaken, in this analysis), which improves cost-effectiveness and can aid prioritization where management on all islands is not possible.

Even though recreational island users responsible for transporting weed propagules might have limited ability to recognize NNS (Campbell, Bryant, & Hewitt, 2017), targeting human behavior could be the most effective and cost-efficient method of limiting the spread of weed propagules. Education programs combined with legislation have been effective in similar situations elsewhere. Community-based social marketing is used in New South Wales, Australia, to implement behavioral change for weed management (Verbeek, van Oosterhout, & Gibney, 2018). Building community norms has been shown to be effective when combined with educative and other approaches (Niemic, Ardoin, Wharton, & Asner, 2016), and encouraging weed-responsible behavior could be highly achievable. Similarly, Barrow Island uses the observational power of the site's large workforce to increase the effectiveness of its biosecurity surveillance programs (Barrett, Whittle, Mengersen, & Stoklosa, 2010).

TABLE 6 Threatened vertebrate species by island group

Latin name	Common name	IUCN	EPBC	Montebello	Onslow	Dampier
<i>Bettongia lesueur</i>	Boodie/burrowing bettong	Near threatened	Vulnerable	✓		
<i>Isoodon auratus</i>	Golden bandicoot	Vulnerable	Vulnerable	✓		
<i>Lagorchestes conspicillatus</i>	Spectacled hare wallaby	Vulnerable	Vulnerable	✓		
<i>Numenius madagascariensis</i>	Far eastern curlew	Endangered	Crit.Endangered	✓		
<i>Calidris tenuirostris</i>	Great knot	Vulnerable	Crit. Endangered	✓		
<i>Dasyurus hallucatus</i>	Northern quoll	Endangered	Endangered			✓
<i>Sternula nereis</i>	Fairy tern	Vulnerable	Vulnerable	✓	✓	✓
<i>Chelonia mydas</i>	Green turtle	Endangered	Vulnerable	✓	✓	✓
<i>Eretmochelys imbricata</i>	Hawksbill turtle	Crit. Endangered	Vulnerable	✓	✓	✓
<i>Natator depressus</i>	Flatback turtle	Data deficient	Vulnerable	✓	✓	✓

Abbreviation: EPBC, Environmental Protection and Biodiversity Conservation.

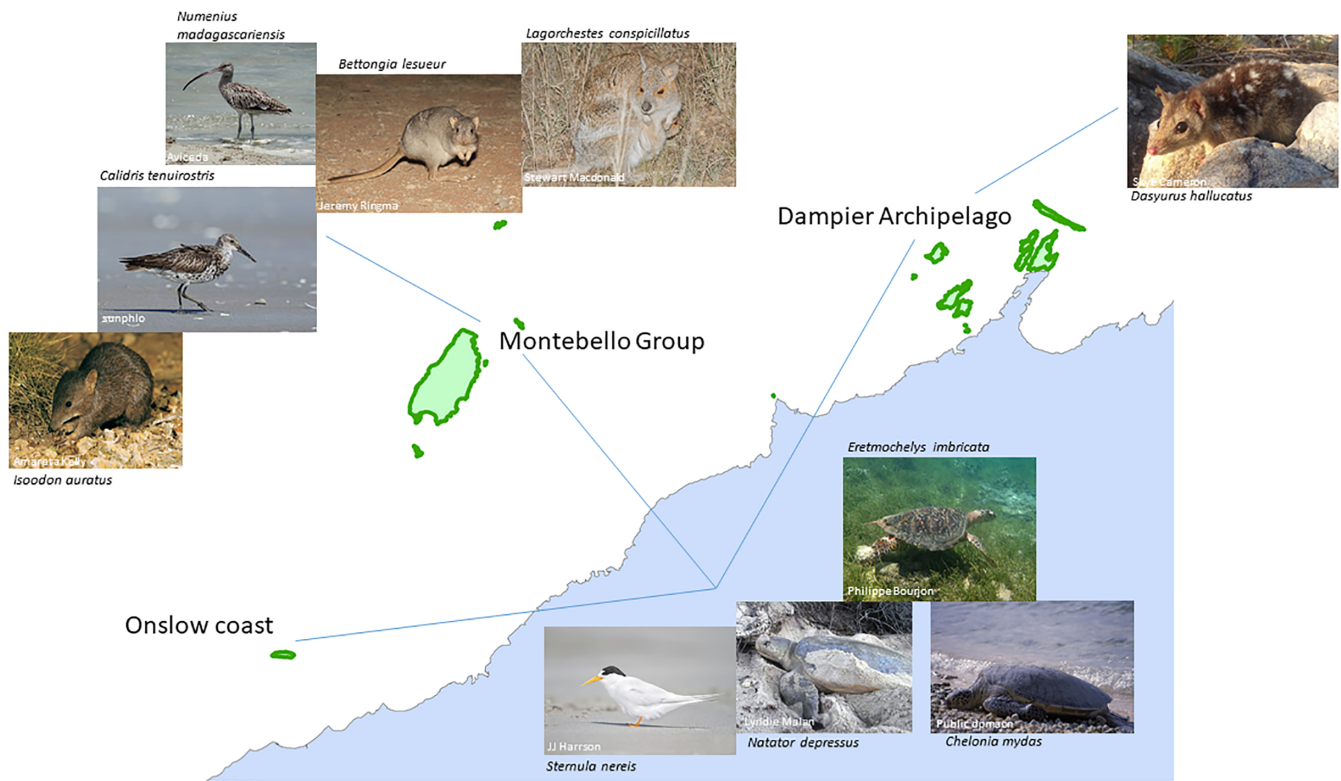


FIGURE 3 Threatened fauna species in the Dampier Archipelago, Montebello Group, and Onslow Coast islands. (Images as attributed, sources as listed and from Wikimedia Commons and Flickr Creative Commons)

Finucane and Preston Islands are both accessible from the mainland by road, and information checkpoints and equipment for removing propagules from vehicles, clothing, and equipment could be economical and easily implemented solutions. Clothing is especially important for the transport of regional weed seeds, particularly perennial forbs and grasses (Ansong & Pickering, 2014).

Eradication costs are determined by the area and density of a weed invasion, and the terrain of the island in question, and by costs associated with labor, travel, equipment, and temporal variability. Estimates for eradication of buffel grass and belly ache bush in the Pilbara Islands ranged from hundreds of thousands to millions of dollars (AUD\$) (Wenger et al., 2018). In our analysis, the cost of managing weeds on hotspot islands, to reduce propagule dispersal, outweighed the cost of managing NNS where they arrive (26 kapok island propagule source hotspots vs. direct kapok management on eight islands). With a more conservative 10% threshold applied for hotspot removal (i.e., a 10% reduction in probability of establishment on target islands), the utility of hotspot management might increase. The flexibility of the tool allows multiple thresholds to be assessed.

Islands are often managed independently, but the efficiency of management would be maximized if islands were managed together (Wenger et al., 2018). For

example, transport costs can be reduced by making single trips to multiple islands (the “travelling salesman” problem approach; Bektas, 2006), and simultaneous eradication and control of different species can result in significant savings (Glen, Pech, & Byrom, 2013). The group of islands in the Dampier Archipelago effectively makes up a single network through which non-native weed species can spread unchecked. Targeted actions, taking into account the spatial relationships between the islands, will thus be many times more effective and cost-efficient than implementing management actions on each island individually. The Biosecurity BBN enables us to identify sources of potential invader propagules in a spatially explicit way, and thus allows us to identify islands where it is worth acting, and those where it is not, and guide actions specific to species and locations.

5 | CONCLUSION

Weeds will arrive naturally at some islands, regardless of any management action or intervention, including islands that have been neglected, unmanaged and are in “disrepair”. It might not be cost-effective to invest in management on these islands, but rather, investment should be made in places where action is most likely to

be effective and conservation gains are the greatest, depending on management objectives. Human-mediated transport of NNS propagules is important to target, and our novel BBN model allows us to identify which islands should be prioritized for action. The model also enabled the identification of weed dispersal hotspot islands and allowed us to assess whether eradication on these islands would affect the spread of NNS to further islands. In the case of the Pilbara Islands, weed removal from propagule source hotspots would be ineffective, due to the proximity of the mainland as a perpetual propagule source. The Biosecurity BBN software is generically applicable to any archipelago, and to any non-parasitic NNS of flora or fauna, and is thus a valuable tool in planning invasive species management.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

A.W. and C.L. contributed to data acquisition; A.W., C.L., K.M., and B.P. all conceived the study and the design; C.L., K.M., and B.P. revised drafted manuscript; O.W. contributed to study design and data analysis; A.W. and N.B. contributed to data analysis, interpretation, and manuscript drafting.

DATA AVAILABILITY STATEMENT

Data used in the current paper are available in the Supporting Information.

ETHICS STATEMENT

Our analysis is based on data collected for other studies. No ethical approval was required for this research.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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