

## **Cooperative Research Centre for National** Plant Biosecurity

# **Final Report**

# CRC 10124

# **Forecasting Spread for Rapid Response**

## Authors

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#### **1. Executive Summary**

This final report for project CRC 10124 - Forecasting Spread for Rapid Response describes the original aims, objectives and rationale for the project, and how these aims and objectives have been met during the course of the project. The key findings of our research are summarised in this report and the reader is directed to relevant scientific publications for further details. In summary, we developed a characterisation system that can be used to quickly collect and synthesise relevant biological information about an Emergency Plant Pest (EPP) in the event of a new incursion and provide parameter values for simulation models. We found that no simulation model of biological spread of sufficient generality existed to be used with our characterisation system, so we developed a new simulation model that met these requirements. We called this model the General Model of Biological Invasion (GMBI) and the whole integrated system for quickly characterising and simulating a new EPP was called the GMBI framework. As required, this GMBI framework contains enough biological detail of relevant processes to facilitate parameterisation by biological experts, but is abstract enough to represent a wide range of different types of organisms. The framework was tested and successfully used to represent and simulate the spread of three particular organisms: an insect, a fungal pathogen and a weed.

The report also presents the implications of our research for stakeholders and finishes with a number of recommendations based on this study. We suggest that the GMBI framework should be considered as a valuable tool for predicting spread of biological organisms and, in particular, synthesising available information and informing rapid response to new incursions in a biosecurity context. In its present form the framework should be able to be used by non-expert users with some training or assistance, but we provide a series of suggestions for software developments to improve the usability of the current system in future. We also give a series of recommendations for future research that has the potential to further improve the power and applicability of the GMBI framework.

### 2. Aims and objectives

The overall aim of this project was to develop a characterisation and modelling system that allows all available scientific information that will influence the rate of build-up and spread of an organism to be quickly and effectively synthesised to inform rapid response to a new biological incursion.

The objectives of the project were to:

- 1. Meet CRC deliverables:
  - Development of generic precision surveillance simulation tools for selected emergency plant pest (EPP) groups.
  - Develop a terrestrial observation predictive simulation system.
- 2. Develop a system for characterisation of EPPs that:
  - rapidly characterises invading organisms with respect to behaviours affecting spread in a particular environment,



- has direct biological relevance, so that existing biological knowledge can be used to quickly generate useful parameterisations for simulating spread,
- can be used directly by managers to make quick tactical decisions,
- is applicable across a range of environmental types including urban, peri-urban, rural and natural environments,
- can handle uncertainty and allow for iterative improvements as surveillance and experimental data are acquired, and
- is designed for the future, for expansion to evaluate surveillance and management strategies.
- 3. Validate the use of the EPP characterisation system by characterising a number of 'key' pest/disease organisms, parameterising existing simulation models to predict spread, and assessing the results using available surveillance data.
- 4. Use planned releases of biological control agents to predict and monitor the spread of invading organisms in landscapes, allowing us to validate the trait characterisation approach and its application to parameterising existing spread models.

#### Rationale

In the event of an incursion of an invading pest/disease organism, rapid response is crucial to minimising the cost of the incursion. An essential part of a rapid response is an effective surveillance strategy and central to effective surveillance is knowing where to look. Knowing where to look requires a rapid assessment of the potential of the organism to spread in the environment where it has been found. This project will help managers to quickly marshal all available biological information to forecast spread of a new pest or disease.

In the past, surveillance and containment programs have been performed in an ad-hoc manner, on a case-by-case basis when incursions have occurred. The effectiveness of these programs is often constrained by lack of information about both the extent of the invasion and the biology of the invading organism influencing its spread, and by the inability to capture this required information in an accurate and cost-effective manner. When biosecurity managers are unable to quickly gather information about the ways that an invading organism spreads, the results of containment programs can be disappointing. An example is the lupin anthracnose incursion that occurred in Western Australia in 1996. Before the full extent of the 1996 outbreak was known a containment program was implemented, with a potential view to eradication. An initial judgement was made that the disease was potentially eradicable and a decision was taken to destroy infected lupin crop on 133 properties. In March 1997, a decision was made that eradication was not feasible because wild lupins outside the crop area were acting as a reservoir for the disease. Had it been possible at the time to rapidly marshal all of the spread related information for lupin anthracnose, it is likely that the decision to destroy crops would not have been made and substantial losses in production could have been averted.

The speed and efficacy of our response to invasions can be improved by developing general strategies that avoid the ad-hoc nature of historical efforts. The aim of this project was therefore to produce a general system for rapidly summarising and synthesising the spread-related characteristics of any new invading organism. The purpose of this system



was to quickly gather biological information that could readily be estimated by scientists to characterise invading species according to their spread-related functions, to facilitate fast qualitative and quantitative prediction of spread. The idea was that these predictions could be used to inform the development of timely effective surveillance strategies at the time they are most needed, to take immediate and appropriate action to limit damage in newly discovered incursions.

## 3. Key findings

The main aim of this project was originally to develop a system for characterisation of EPPs to allow rapid response to new incursions and the first part of the project focussed on this aim. Our strategy for developing this EPP characterisation system was based on what we called 'multi-layered functional grouping'. Using this strategy, we identified the key traits of organisms that are important in establishment and spread processes. These included the number of life stages involved in the organism's life-cycle; the duration of each lifestage; the chance of mortality within each life-stage; the age(s) at which dispersal and reproduction occur; the fecundity of the organism; and the dispersal characteristics of the organism. We developed a system based on these functional traits to allow an invading organism to be characterised in the event of an incursion. We ensured that the traits were defined with as much direct biological relevance as possible, so that the process of characterising each organism for each trait would be straight-forward and fast. The resulting combination of trait values forms a functional characterisation of the organism that is biologically detailed and thus most likely unique to that organism. However, the overall system is general enough that it can be used to characterise a wide range of EPPs, including vertebrate and invertebrate animals, plants (weeds), fungal and bacterial pathogens, and even viruses spread by insect vectors.

We also determined that interactions between these key functional traits and the landscape in which the incursion was occurring was likely to be a key determinant of the spread and establishment of the organism. We therefore developed a system for characterising the suitability of landscape for a particular organism based on GIS data, or aerial or satellite photographs, or on more general statistics of proportion and connectivity of suitable landscape areas. This was to allow the dynamics of spread to be represented in a spatially-explicit way, which is essential to capture the realities of a biological incursion into a spatially heterogeneous landscape.

The system that we developed for characterising new organisms was then tested for two key EPPs: lupin anthracnose and Asian gypsy moth. This involved working with experts on those species to identify appropriate values for all required parameters. We found that the characterisation process itself was extremely useful for all involved; it helped identify knowledge gaps and areas of uncertainty and disagreement between experts, as well as facilitate sharing and synthesis of available knowledge. The discussion and the resulting characterisation was seen to be of direct and immediate use to biosecurity managers, because it would provide timely biological information about the invading organism that would give a preliminary indication of spread and guide initial decision-making even without additional simulation modelling.

A key objective of this project was that the system for characterisation of EPPs we developed could be used to parameterise existing simulation models to predict spread. The CRCNPB project *Simulation platform technology for predicting spread of Emergency Plant Pests* was to develop a generic simulation platform for predicting the spread of invading organisms, and this project was to develop a system for quickly parameterising that



simulation platform or other suitable general simulation platforms. However, it became apparent that this generic simulation platform was unlikely to be finished by the end of our project and extensive literature review and investigation did not find any other suitable general simulation platforms capable of representing the whole range of EPP organisms as intended. Thus, one important finding of the project was that no suitable general simulation platform existed. Therefore, we decided that, in order to meet the objectives of this project, we would expand its scope to include the development of a generic simulation platform that we called the General Model of Biological Invasion (GMBI).

The development and testing of the GMBI, together with its integration with the characterisation system, became the main focus of the second part of this project. We found that it was eventually possible to design a simulation model that was general enough that it can be used to simulate the spread and establishment of a wide range of EPPs, including vertebrate and invertebrate animals, plants (weeds), fungal and bacterial pathogens and even viruses spread by insect vectors, and yet include enough biological detail to capture the suite of important functional traits of each unique organism and landscape combination. This was achieved by putting the model through an ongoing process of testing and refinement: testing its ability to represent a series of different types of organism and changing the framework as required to address any revealed limitations. This process also involved refining the characterisation system itself so that finally it consists of a set of biologically relevant parameters that can be estimated based on expert knowledge and directly link with the GMBI simulation framework. The final GMBI simulation model consists of three main interlinked components: a spatially-explicit representation of a heterogeneous landscape consisting of many cells, each with a defined level of suitability for the organism; simulation of the age-structured population dynamics within each cell; and dispersal of propagules between cells (Figure 1).

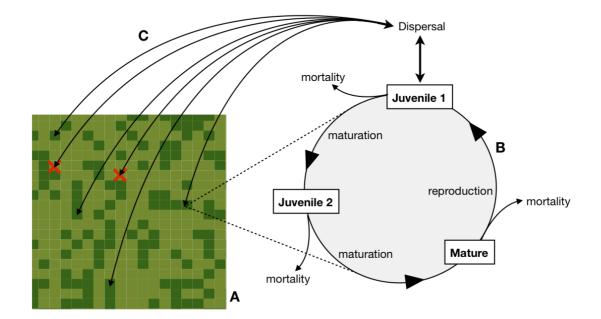


Figure 1. Overview of GMBI structure, showing three main components of the model, a spatially-explicit representation of landscape suitability (A), within-cell population dynamics (B), dispersal (C), and the relationship between them.

A final series of tests of the GMBI framework was conducted on three very different organisms in very different environments, each of particular interest in terms of their



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potential spread and establishment for three different reasons: a lupin anthracnose incursion within a rural cropping system; an invasion of the perennial weed veldt grass into an urban parkland; and a release of a beetle popularly known as 'Nessie' as a biocontrol agent for the invasive weed mimosa along water bodies in remote wilderness areas. These tests resulted in successful characterisations of the three organisms and their respective environments and showed that, once characterised, with the click of a button the GMBI then produces detailed predictions of the areas to which the organism is most likely to spread and thus an indication of what surveillance and management strategies would be most useful in a particular incursion scenario. These tests showed that our characterisation system was general enough to capture the main biological characteristics of a wide range of organisms, which was the main original aim of the project. They also showed that the GMBI simulation model we developed to meet the project requirements was able to synthesise the information provided by the biological characterisation process and provide predictions of how the organism might spread over time in its particular landscape.

The patterns of spread predicted by the GMBI are different each time the model is run, because the underlying processes represented are stochastic. This mirrors the reality of a real invasion, where the course of the invasion is likely to depend on a series of chance events, such as whether a particular far-dispersing propagule happens to land in a suitable environment, or whether an isolated juvenile happens to reach reproductive maturity and found a viable satellite population. This stochasticity makes it impossible to predict the actual course of any particular invasion, which in turn makes it difficult to quantitatively 'validate' model predictions against data for a particular historical invasion or spread event. Moreover, detailed data on the spatial spread of our three test organisms was not available, since Nessie failed to establish at the two sites where detailed monitoring was conducted. Nonetheless, qualitative observations of the spread of our three test organisms were available (since the weed and the pathogen had actually already invaded the relevant landscapes and Nessie had successfully established at one particular release site where general surveillance had been conducted), so we were able to qualitatively validate the model by confirming with the relevant experts that predicted patterns of spread and establishment were reasonable both temporally and spatially.

Uncertainty is a key problem in predicting biological spread. Spread is driven by highly stochastic processes, as explained above, meaning that invasions by the same organism in very similar conditions may potentially unfold in very different ways. The GMBI highlights and accounts for this aspect of uncertainty by showing that a range of outcomes are possible for a given invasion scenario. It can also illustrate this uncertainty by simulating a large number of possible outcomes for a single invasion scenarios, and then integrating the results into a probabilistic 'risk map' (Figure 2). Uncertainty in predictions is also greatly increased by uncertainty in characterisation of the landscape and even more particularly in characterisation of the organism. This can similarly be accounted for by conducting a large number of simulations across a range of values for the uncertain parameters and then constructing integrated risk maps such as those shown in Figure 2.



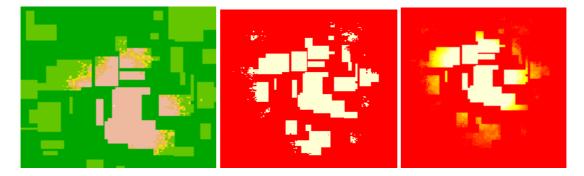


Figure 2. Example model outputs, including population densities from a particular model run after a certain time (A), the union of all cells occupied after the same time in any of a large number of model runs (B), the expected probability of each cell being occupied after the same time, based on the same set of model runs (C). (A) shows how a particular possibility of how an incursion might unfold, whereas (B) and (C) represent risk maps integrating over all possibilities of how an incursion might unfold.

#### **Publications**

Details of the work conducted in this project and the findings obtained can be found within a number of already published or forthcoming peer-reviewed scientific publications. In the list below, paper 1 presents the concept of the GMBI framework with its rationale and a prototype design of the simulation model; paper 2 presents details of the design and implementation of the GMBI simulation model; and paper 3 discusses testing of the overall framework for the three final applications mentioned above (anthracnose, veldt grass and nessie), with a focus on the characterisation system and the resulting simulations rather than the model details. Papers 4-11 describe results arising from other tests of the characterisation system and modelling for various applications and organisms that were carried out as part of this project and helped refine the framework to its final form. All of these papers are available on request to Michael Renton (as yet unpublished papers on condition of confidentiality). These publications are in addition to the publications arising from related CRCNPB PhD projects that also helped inform this research.

- Renton M, Savage D and Chopard J. 2011. A general spatially-explicit model to inform rapid response to new biological invasions: why do we need one and what should it look like? In: Chan, F., Marinova, D. and Anderssen, R.S. (eds) MODSIM2011, 19th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, December 2011, pp. 2542-2548, ISBN: 978-0-9872143-1-7. <u>http://www.mssanz.org.au/modsim2011/E16/renton.pdf</u>
- 2. Savage D, Renton M, and Chopard J. (prepared for submission to *Mathematical Biosciences*). Design and implementation of a general model of biological invasion.
- **3.** Renton M, Savage D, Shackelford N and Schellhorn N. (prepared for submission to *Biological Invasions*). Testing the applicability of a general model of biological invasion to a weed, an insect and a fungal pathogen.
- 4. Bennett JC, Diggle AJ, Evans FH and Renton, M. 2011. Towards measures of the eradicability of rain-splashed crop diseases. In: Chan, F., Marinova, D. and Anderssen, R.S. (eds) MODSIM2011, 19th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, December 2011, pp. 2486-2492, ISBN: 978-0-9872143-1-7. http://www.mssanz.org.au/modsim2011/E16/bennett.pdf
- 5. Bennett JC, Diggle AJ, Evans FH and Renton, M. (under review by *Plant Pathology*). The eradicability of rain-splashed crop diseases: Case study of the 1996 Western Australian lupin anthracnose incursion



- 6. **Borger C, Renton M, Riethmuller G and Hashem A. 2012.** Seed abscission increases with more upward oriented and faster winds, but sensitivity to speed and orientation declines with increasing age of the seed head. (*Functional Ecology*, Accepted, In Press)
- 7. Savage D, Borger C and Renton M. (prepared for submission to *Ecology*). The preferential release of wind-dispersed *Conyza bonariensis* seeds into strong upward gusts leads to dispersal over greater distances than for random release
- Shackelford N, Renton M, Perring MP and Hobbs RJ. 2011. Management implications of modeling invasion by *Allocasuarina huegeliana* in kwongan heathland. In: Chan, F., Marinova, D. and Anderssen, R.S. (eds) MODSIM2011, 19th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, December 2011, pp. 2563-2569, ISBN: 978-0-9872143-1-7. <u>http://www.mssanz.org.au/modsim2011/E16/shackelford.pdf</u>
- 9. **Renton M. 2012.** Shifting focus from the population to the individual as a way forward in understanding, predicting and managing the complexities of evolution of resistance to pesticides. *Pest Management Science*: doi: 10.1002/ps.3341
- Renton M, Shackelford N, Standish RJ. 2012. Habitat restoration will help some functional plant types persist under climate change in fragmented landscapes. *Global Change Biology*. doi: 10.1111/j.1365-2486.2012.02677.x
- 11. **Renton M, Childs S, Shackelford N, Standish RJ.** (Provisionally Accepted). Plant migration and persistence under climate change in fragmented landscapes: does it depend on the key point of vulnerability within the lifecycle? *Ecological Modelling*.

#### 4. Implications for stakeholders

When a new Emergency Plant Pest/disease (EPP) is discovered, a rapid and accurate response is needed. The cost of management escalates and the feasibility of eradication quickly declines as the organism spreads.

Historically, surveillance programs have been developed in an ad-hoc manner, on a caseby-case basis. Biosecurity managers have needed to make quick decisions about surveillance and containment programs, despite having little information about the potential size of an infestation.

With recent advances in spread simulation modelling, fast predictions can be made of which areas are most likely to be inhabited by an invading species at various times as an incursion unfolds. However, most existing simulation models are either species-specific and not easily modified to predict spread of a new species, or achieve generality at the cost of a high level of abstraction, thus neglecting important aspects of the biological processes involved.

To be of real use in informing rapid response to a new biological incursion, a simulation platform must be quickly tuned to handle the particular invading species, which will be one of very wide range of potential organisms. However, biological information about the spread-related characteristics of the new organism must be translated into quantitative parameters suitable for use in the simulator; because of the wide variety of mechanisms for dispersal and establishment that can be employed by invading organisms, variable types of environment (including urban, peri-urban, rural and natural environments) and complex interactions with life-cycle, this tuning process has typically been time consuming and labour intensive.

The GMBI framework developed in this project, which includes the characterisation process and the GMBI simulation model itself, provides a system for rapidly summarising the spread-related characteristics of any new invading organism and substantially facilitates use of the underlying simulation platform. The system links new simulation technology with a biologically meaningful 'front-end' in a system that combines computationally



efficiency, generality and detail of relevant biological processes. The system can be used to gather biological information that can readily be estimated by scientists, use that information to generate quantitative parameters required for simulating spread, and produce predictions of spread based on this biological information. It provides a valuable tool for managing organisms that are known to be high risk, that have just arrived and that need to be dealt with as quickly and effectively as possible.

#### 5. **Recommendations**

Based on the findings from the research project, we recommend that the GMBI be considered as a valuable tool for predicting spread of biological organisms and, in particular, informing rapid response to new incursions in a biosecurity context. In its present form the model should be able to be used by non-expert users with a small amount of training or assistance.

We recommend that further testing of the GMBI framework should be carried out to:

- evaluate its ability to represent a wider range of organisms in a wider range of situations and a wider range of applications,
- compare its usage and predictions with more detailed species-specific models, to determine to what extent it is able to emulate the predictions of such models, and
- evaluate the accuracy of the predictions of the GMBI framework in situations where actual spread and establishment data is available.

The ease-of-use of the GMBI framework could be further improved by:

- building an interactive graphical-user-interface for guiding users through the process of entering the required model parameters,
- integrating the framework with GIS software to facilitate the creation and use of landscape suitability files,
- developing simple tools to facilitate the creation and use of landscape suitability files based on available aerial or satellite photographs, and
- □ improving the output from simulations and further automating the process of generating such output to meet user requirements.

The overall GMBI framework could also be further improved by further methodological research. We recommend that an extensive sensitivity analysis be conducted on the GMBI parameterised for several key organism types. This would provide a clear indication of which parameters are most important in predicting the speed and extent of biological spread for each type, in turn allowing the characterisation system to be further refined to concentrate the time and effort of experts on the most critical biological processes. We also recommend that 'meta-modelling' of the GMBI should be investigated, with the aim of creating simpler statistical models that closely emulate the GMBI simulation, yet are faster to run, more transparent, and thus easier and faster to analyse. Uncertainty and risk are important considerations in any biosecurity context, especially when important decisions must be based on expert opinion; while the GMBI is already capable of accounting for uncertainty and risk using computationally intensive 'brute-force' approaches, more sophisticated and efficient approaches based on sensitivity analyses and meta-modelling should be developed. Furthermore, the current version of the GMBI is a pure 'bottom-up' model, with predictions emerging from simulation of the underlying processes; the usefulness of the model would be increased by the development of methods for ongoing automatic calibration or updating of underlying model parameters based on any discrepancies between current model predictions and new observations of spread and establishment as they become available.



Finally, we recommend that extensions to the GMBI and its application should be developed. The current version of the GMBI is focussed on predicting the spread and establishment of biological organisms dispersing primarily through 'natural' means through landscapes. We recommend that similar approaches should be used to develop an equivalent framework for predicting the spread and establishment of biological organisms dispersing primarily with human-mediated transport and storage networks. Moreover, in addition to its current aim of predicting the initial stages of a new incursion to inform rapid response, we believe that the GMBI framework can provide a valuable tool for investigating and evaluating different surveillance and management strategies for a wide range of organisms and applications. This potential use of the GMBI should be explored.

## 6. Abbreviations/glossary

ABBREVIATION	FULL TITLE
CRCNPB	Cooperative Research Centre for National Plant Biosecurity
EPP	Emergency plant pest
GMBI	General Model of Biological Invasion

## 7. Plain English website summary

CRC project no:	CRC10124
Project title:	Forecasting Spread for Rapid Response
Project leader:	Michael Renton
Project team:	Michael Renton, David Savage, James Bennett, Art Diggle, Nancy Schellhorn, Nancy Shackelford, Fiona Evans, Jerome Chopard, Susanne Casanova, Tash Burrows, Tim Heard, Andy Hulthen, Lynita Howie, Anna Marcora
Research outcomes:	This project developed a framework that will improve our ability to successfully respond to new incursions of emergency plant pests. Spread predictions are made by integrating information provided by experts into a General Model of Biological Invasion (GMBI). We have shown that the framework is general enough to characterise, simulate and make reasonable predictions for a wide range of organisms (including vertebrate and invertebrate animals, plants, fungal and bacterial pathogens, and even viruses spread by insect vectors) in a wide range of landscapes (including urban, peri- urban, rural and natural environments).



Research implications:	The General Model of Biological Invasions (GMBI) framework developed in this project provides a valuable tool for managing organisms that are known to be high risk, that have just arrived and that need to be dealt with as quickly and effectively as possible.
Research publications:	<ol> <li>Renton M, Savage D and Chopard J. 2011. A general spatially-explicit model to inform rapid response to new biological invasions: why do we need one and what should it look like? In: Chan, F., Marinova, D. and Anderssen, R.S. (eds) MODSIM2011, 19th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, December 2011, pp. 2542-2548, ISBN: 978-0-9872143-1-7.</li> </ol>
	<ul> <li>December 2011, pp. 2542-2548, ISBN: 978-0-9872143-1-7. <u>http://www.mssanz.org.au/modsim2011/E16/renton.pdf</u></li> <li>2. Savage D, Renton M, and Chopard J. (prepared for submission to <i>Mathematical Biosciences</i>). Design and implementation of a general model of biological invasion.</li> </ul>
	<ul> <li>3. Renton M, Savage D, Shackelford N and Schellhorn N. (prepared for submission to <i>Biological Invasions</i>). Testing the applicability of a general model of biological invasion to a weed, an insect and a fungal pathogen.</li> </ul>
	4. Bennett JC, Diggle AJ, Evans FH and Renton, M. 2011. Towards measures of the eradicability of rain-splashed crop diseases. In: Chan, F., Marinova, D. and Anderssen, R.S. (eds) MODSIM2011, 19th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, December 2011, pp. 2486-2492, ISBN: 978-0- 9872143-1-7. <u>http://www.mssanz.org.au/modsim2011/E16/bennett.pdf</u>
	<ol> <li>Bennett JC, Diggle AJ, Evans FH and Renton, M. (under review by <i>Plant Pathology</i>). The eradicability of rain-splashed crop diseases: Case study of the 1996 Western Australian lupin anthracnose incursion</li> </ol>
	6. <b>Borger C, Renton M, Riethmuller G and Hashem A. 2012.</b> Seed abscission increases with more upward oriented and faster winds, but sensitivity to speed and orientation declines with increasing age of the seed head. ( <i>Functional Ecology</i> , Accepted, In Press)
	7. Savage D, Borger C and Renton M. (prepared for submission to <i>Ecology</i> ). The preferential release of wind-dispersed <i>Conyza bonariensis</i> seeds into strong upward gusts leads to dispersal over greater distances than for random release
	<ol> <li>Shackelford N, Renton M, Perring MP and Hobbs RJ. 2011. Management implications of modeling invasion by <i>Allocasuarina huegeliana</i> in kwongan heathland. In: Chan, F., Marinova, D. and Anderssen, R.S. (eds) MODSIM2011, 19th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, December 2011, pp. 2563-2569, ISBN: 978-0-9872143-1-7. http://www.mssanz.org.au/modsim2011/E16/shackelford.pdf</li> </ol>
	<ol> <li>Renton M. 2012. Shifting focus from the population to the individual as a way forward in understanding, predicting and managing the complexities of evolution of resistance to pesticides. <i>Pest Management Science</i>: doi: 10.1002/ps.3341</li> </ol>
	<ol> <li>Renton M, Shackelford N, Standish RJ. 2012. Habitat restoration will help some functional plant types persist under climate change in fragmented landscapes. <i>Global Change Biology</i>. doi: 10.1111/j.1365-2486.2012.02677.x</li> </ol>
	11. Renton M, Childs S, Shackelford N, Standish RJ. (Provisionally Accepted). Plant migration and persistence under climate change in fragmented landscapes: does it depend on the key point of vulnerability within the lifecycle? <i>Ecological Modelling</i> .
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