# Invasive species control: Incorporating demographic data and seed dispersal into a management model for *Rhododendron ponticum*

C.M. Harris [a,b,*], K.J. Park [a], R. Atkinson [a,c], C. Edwards [d], J.M.J. Travis [e]

[a] *Centre for Conservation Science, School of Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, Scotland, UK*
[b] *Centre for Research into Ecological and Environmental Modelling, The Observatory, University of St Andrews, St Andrews, Fife, Scotland, KY16 9LZ, UK*
[c] *Charles Darwin Foundation, Puerto Ayora, Santa Cruz Island, Galapagos, Ecuador*
[d] *Forest Research, Northern Station, Roslin, Midlothian EH25 9SY, UK*
[e] *Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, AB24 2TZ, Scotland, UK*

## ARTICLE INFO

## ABSTRACT

*Rhododendron ponticum* is a serious invasive alien plant in the British Isles and is of significant conservation and economic concern. Here, we integrate information on both the demographics and spatial dynamics of this species within an individual-based, spatially-explicit model and investigate the effectiveness of different control strategies. Importantly, we simulate seed movement and dispersal using a mechanistic seed dispersal model. We investigate the effectiveness of initiating control at the edge versus the core of the infestation, with and without returning each year to remove seedlings. We compare these results to an age-dependent strategy whereby the oldest plants are removed each year. Age-dependent control, in which the oldest plants were removed first, was the most effective strategy investigated, both in terms of the probability of successful eradication and the number of years taken to control. We demonstrate that this is because the older (and taller) plants towards the core produce more seeds that, on average, travel further. Indeed, our results suggest that the expansion of the invading front is actually driven as much by seeds that disperse long distances from these larger plants as by the seed rain from recently matured plants located much closer to the front. Finally, we investigate the potential use of 'quarantine lines' — corridors of unsuitable habitat that are sufficiently wide to contain an infestation, preventing spread to vulnerable areas. This study has provided generic insights into best practice for management based on the current understanding of the biology and ecology of this pernicious, invasive plant.

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## 1. Introduction

Invasive alien plant species are increasingly being recognised as important drivers of ecological change, with consequences for ecosystem processes, biological diversity, economics and human health (Earth Summit, Rio Convention, 1992 http://www.cbd.int/; Vitousek et al., 1996; IUCN Council, 2000; Le Maitre et al., 2000). Vast sums are spent on control programs. For example, up to 6 million dollars is spent annually on controlling the tree *Melaleuca quinquenervia* in the United States, and 100 million dollars on controlling invasive aquatic weeds (Pimentel et al., 2000 and refs within). Given that evidence suggests that impacts of invasive plants are likely to be exacerbated by future increases in large-scale habitat modification and by climate change (e.g. Mooney and Hobbs, 2000) the demand for more efficient and effective control strategies is likely to grow.

Despite often very considerable expenditure, examples of successful eradication of invasive plants are relatively few. If control is implemented very early in an invasion process and all individuals are detected and removed before they set seed then complete extirpation can be achieved (Mack and Lonsdale, 2002). However, if an infestation is given the chance to become established then eradication, and even containment, becomes increasingly difficult. Invasions are inherently spatial, and while we may often know how best to remove individual plants we lack an understanding of how we should optimally target our control efforts to achieve local eradication or containment at the landscape scale. An important management question, therefore, is how a finite resource for control should be used to achieve management objectives over a particular time horizon. Spatially explicit models of invasion dynamics offer a powerful framework for exploring this question.

A range of different types of spatial model have been used to describe invasion processes. Reaction diffusion equations (e.g. Skellam, 1951; Okubo and Levin, 2001), integrodifference equations (e.g. Kot and Schaffer, 1986; Neubert et al., 1995; Shigesada and Kawasaki, 2002) and spatially-explicit simulations all continue to be used (e.g. Higgins et al., 2000; Wadsworth et al., 2000). There are clear

* Corresponding author. Centre for Research into Ecological and Environmental Modelling, The Observatory, University of St Andrews, St Andrews, Fife, Scotland, KY16 9LZ, UK. Fax: +44 1334 461800.
*E-mail address:* catriona@mcs.st-and.ac.uk (C.M. Harris).

benefits of the more mathematical methods in that they permit a rapid exploration of parameter space and, in many cases, provide exact solutions. However, while these models can now incorporate considerable ecological realism such as age/stage structure (e.g. Caswell et al., 2003; Neubert and Caswell, 2000), Allee effects (Veit and Lewis, 1996) and long-lasting transients (Hastings and Higgins, 1994), questions still remain as to whether they capture the dynamics adequately when demographic stochasticity is important (eg. Snyder, 2003; Clark et al., 2001; Kot et al., 2004). Individual-based spatially explicit models are relatively straightforward to implement and computing power now imposes far less of a constraint than it used to; simulations are now feasible even when they involve many millions of individuals. The simulation approach allows stochasticity to be introduced and also offers the potential to explore a wide-range of control scenarios. Additionally, both the specification of a rule-based model and the graphical results that emerge from it are quite readily interpreted by non-modellers within a community of stakeholders. Clearly, both mathematical and simulation based approaches can play an important role in the development of more effective control strategies and here we seek to develop an individual-based model for the spatial spread of a plant species.

Many models that consider optimal control strategies for invasive plants are spatially implicit (e.g. Parker, 2000; Buckley et al., 2003b; Taylor and Hastings, 2004; Hall & Hastings, 2007), and, of these, many are deterministic. However, a number of studies using spatially explicit simulation models have now clearly demonstrated that where control effort is initially targeted can have a considerable bearing on the likelihood of success (Moody & Mack, 1988; Higgins et al., 2000; Wadsworth et al., 2000; Hulme, 2003). In many cases the optimal control strategy is very dependent on the assumptions of the authors as to which individuals are responsible for the majority of seed production and long distance dispersal events. For example, Wadsworth et al. (2000) suggest that control of satellite populations could be a useful strategy where the spread of a species was dominated by relatively short range dispersal events, but not for species with long distance dispersal, and particularly those whose seeds disperse along waterways. More recently, the results of invasion models incorporating metapopulation dynamics have led to a strategy of first controlling larger core populations. This approach rapidly reduces the propagule supply that contributes most to long-distance dispersal and therefore the generation of satellite populations (Hulme, 2003).

Whether it is best to start control at the expanding front, or at the core, has been of interest not only to theoreticians, and there are numerous examples where one or the other strategy has been adopted in programs aimed at eradicating different invasive plants. The campaign against witchweed, *Striga asiatica*, originally introduced to the United States in 1956 pursued a removal strategy starting at the periphery of infestation and working towards the centre (Eplee, 1979). By 1999, this approach had eradicated 97% of the maximum known infested area, although this species is still recorded as a weed in the Carolinas (Eplee, 1992; Westbrooks and Eplee, 1999). This strategy of removing outlying small populations and systematically reducing the size of the main infestation from the edge inwards has become the rule of thumb for many agricultural weeds and other invasive plants including leafy spurge, *Euphorbia esula*, in the U.S. (Watson, 1985), the woody shrubs *Hakea sericea* and *H. gibbosa* in South Africa and *Mimosa pigra* in Australia (Fugler, 1982; Cook et al., 1996), and the trees *Casuarina* sp. and *M. quinquenervia* in the Florida Everglades (Doren and Jones, 1997). There have, however, also been some promising results using the opposite approach: control of several alien plant species on Raoul island off the north coast of New Zealand initially focused on mature individuals in dense infestations before searching for seedlings (West, 2002).

In this study we develop a spatially-explicit, individual-based model to investigate the effectiveness of a range of control strategies for containment or eradication of *Rhododendron ponticum*, one of the most problematic invasive weed species in Britain and Ireland (Cross, 1982, Colak et al., 1998, Rotherham, 2001). *R. ponticum* was introduced into Britain in 1763 (Elton, 1958) and has since become well-established throughout the British Isles (Cross, 1981, 1982; Gritten, 1995; Rotherham, 1986; Thomson et al., 1993). It thrives in moist, temperate climates and acidic soils and has established itself in natural and semi-natural oak and mixed woodlands, heaths, upland acid *Nardus* grassland and occasionally dune heaths and bogs (Cross, 1975, 1982). It is an evergreen shrub, the shape and size of which varies with habitat but it is usually found between 2 and 8 m tall (Cross, 1975). It flowers each summer, and seeds are released and dispersed, primarily by wind, during February and March the following year (Cross, 1975). Large numbers of seeds are produced each year and germination occurs during spring and summer. There is little evidence for a seed bank and it is believed that only the current source of seed in a given year is important in terms of annual recruitment (Cross, 1975; Shaw, 1984). Within woodland, *R. ponticum* has a number of competitive advantages over other understorey species (Cross, 1973) and the dense shade it casts and its allelopathic effect may prevent successful germination and establishment of native tree seedlings so that as canopy trees die there is no regeneration (Cross, 1982; Rotherham and Read, 1988). The reduction in native species in a woodland leads to a reduction in the fauna that rely upon native plants for resources such as food or breeding habitat (Cross, 1982; Colak et al., 1998). Therefore, *R. ponticum* invasion of a habitat can result in reduced overall biodiversity (eg. Colak et al., 1998).

*R. ponticum* can also present considerable logistical and economic challenges to forestry operations as infestations under woodland canopies can become extremely dense, interfering with stand development, and limiting the capacity of a woodland to regenerate naturally (Edwards et al., 2000). Controlling *R. ponticum* can cost between £150 and £10,000 per hectare depending on bush size and density, habitat and site accessibility (Dehnen-Schmutz et al., 2004), although restoration costs may also have to be considered. Control can be successful if recommended removal and herbicide regimes are employed (eg Barron, 2000; Edwards et al., 2000; Edwards, 2006; Eşen and Zedaker, 2004). The main problem with widespread control of this species is expense, and lack of funds can be a major factor limiting *R. ponticum* control efforts and allowing re-invasion from uncleared areas. Thus, it is important that, where eradication requires sustained effort over a prolonged period of time, work is targeted so that the control strategy is as efficient and cost-effective as possible.

The model presented in this study examines the relative success of different spatial and age-structured control strategies in achieving complete eradication from an infested area, and the efficacy of quarantine lines as a containment, rather than eradication, strategy. Buckley et al. (2001; 2003a,b) have emphasised that the ecology and biology of invasive plant species will influence the effectiveness of different control strategies. Although there are still gaps in our knowledge about this species for which we have to make assumptions, we are fortunate that we now have a comparatively detailed knowledge of this species' life-history through both empirical and modelling studies (e.g. Stephenson et al., 2006; Stephenson et al., 2007; data presented in this paper), and by building this information into a stochastic simulation model we aim to provide some sound generic management recommendations for control.

## 2. Methods

### 2.1. Field study

A range of empirical data was collected from three different field sites in the region of Argyll, in Scotland (UK) where *R. ponticum* was established; an open landscape located near Kinlochleven, (56°43′23″N, 4°57′55″W), a mixed woodland near Lochgilphead