An investigation of the invasion dynamics of *Asparagus asparagoides* (L.) Druce at the habitat level using spatial analytical techniques

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Summary
Questions relating to management and dynamics of the early stages of weed invasion into remnant vegetation were investigated using *Asparagus asparagoides*, a bird-dispersed weed. An extensive data set was collected from fieldwork undertaken at two sites where *A. asparagoides* is a recent invader. These data were used to: develop a predictive model for *A. asparagoides* presence, question the previously accepted rate of dispersal for *A. asparagoides* and suggest that in the early stages of the invasion process, *A. asparagoides* enters the reserves via the track network. The spatial nature of the invasion was investigated using a number of spatial statistics that revealed a non-random occurrence of *A. asparagoides* within the reserves. The results of the spatial analysis also showed that the spatial pattern of *A. asparagoides* within the reserves might be the result of dispersal occurring at two different scales. Finally a number of recommendations regarding the direction of future research are discussed.

Keywords: *Asparagus asparagoides*, remnant vegetation, spatial analysis, weed invasion.

Introduction
Asparagus asparagoides (L.) Druce is a member of the Asparagaceae family and is native to southern Africa (Obermeyer 1984). Originally introduced into Australia as a horticultural specimen, it was first recorded naturalized in Victoria in 1886 (Parsons and Cuthbertson 2001). The plant is a perennial climbing herb with round fruit (5–10 mm in diameter) that is red when ripe and contains an average of six seeds and a maximum up to nine black seeds (Raymond 1999). After flowering and fruiting, the above ground shoots die down in the summer months (Raymond 1999). An extensive mat of rhizomes and tubers beneath the soil surface is implicated in preventing indigenous species from germinating (Fox 1984, Raymond 1995). In many instances, *A. asparagoides* invasion of temperate ecosystems in southern Australia results in a dense monoculture that impacts on biodiversity (Batchelor and Woodburn 2002).

Dispersal of *A. asparagoides* occurs locally through the growth and extension of the underground tuber mass and to new sites through long distance dispersal of seeds primarily by avian frugivores. While there have been no observed cases of birds dispersing *A. asparagoides* seeds in southern Africa (Stansbury 2001), in Australia, a number of bird species have been observed feeding on *A. asparagoides* berries (Stansbury 1996, Raymond 1999). Dispersal by foxes (*Vulpes vulpes* L.) is known to occur and Graham and Mitchell (1996) reported that rabbits (*Oryctolagus cuniculus* L.) and floating fruits being transported downstream by flood events (hydrochory) can act as dispersal vectors. The movement of soil containing tubers also occurs but is of secondary importance. However, it is the factors operating on short and long distance dispersal of *A. asparagoides* into suitable new habitat that require investigation.

This paper presents a summary of the research undertaken for a doctoral thesis as part of the Cooperative Research Centre for Weed Management Systems (Weeds CRC) Landscape Management program, Weed Syndromes Task, Bird-dispersed weeds project. This research examined aspects of bird-dispersed weeds and their invasion of remnant vegetation patches at the spatial scale of habitat. The target species, *A. asparagoides*, a fleshy-fruited bird dispersed weed that is invading remnant vegetation in areas of southern Australia (Stansbury and Scott 1999), is one of the 20 Weeds of National Significance (WoNS) (National Weeds Strategy 1999).

Study site location
The main study site was within the Bass Coast Shire approximately 100 kilometres to the south east of Melbourne. The Shire includes both the Bass Valley and Phillip Island, a rural region covering 865 km^2 with economic activity primarily consisting of grazing, agriculture and tourism.

Phillip Island (Latitude 38.5°S, Longitude 145.26°E) covers an area of 100 km^2. Tertiary and Quaternary sedimentary deposits form the main geological units on Phillip Island with outcrops of volcanic rocks (Douglas and Ferguson 1988 p. 413-14). The Island has a strong tourist focus along with cattle and sheep grazing. Interspersed among the agricultural and urban areas are patches of fragmented native vegetation and natural reserves. The site used for this study was the Oswin Roberts Koala Reserve, located in the northeast corner of Phillip Island (Figure 1); referred to as ORR hereafter. In addition, data were collected from sections of

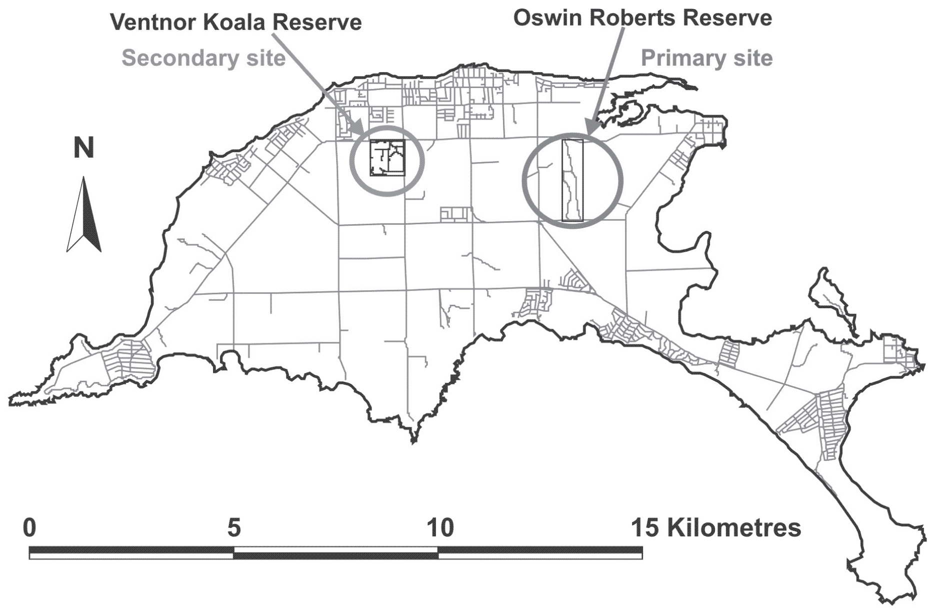

Figure 1. Primary and secondary study sites on Phillip Island.

Rhyll Swamp that are adjacent to the south eastern boundary of ORR as well as the pasture on the remaining eastern boundary and on the adjacent western boundary. Ventnor Koala Reserve (VKR) served as an independent site and data collected there were used for validation.

Research questions

Before any examination of dispersal can begin the question of appropriate scale needs to be addressed. Table 1 shows how spatial scale determines the dispersal processes being examined. The research presented in this paper is at the habitat and landscape scale as defined in Table 1.

The project addressed the broad question 'what new insights can be gained from the study of an active invasion front using both qualitative and quantitative spatial methods?' This broad question was broken up into a number of specific areas of investigation.

The initial stage of the research identified landscape and vegetative factors that could potentially influence early stage invasion in a habitat. The second stage examined the utility of a geographic information system (GIS) in visualizing the process of invasion and providing an avenue for development of hypotheses. Visual examination of the mapped data revealed a pattern in the distribution of *A. asparagoides* that appeared to be associated with the network of foot and vehicular tracks within the habitat. Subsequent statistical analysis quantified this pattern and addressed two questions that arose from the apparent pattern.

The first question asked 'Do tracks and paths within the habitat provide a conduit for *A. asparagoides* in the early stages of invasion?' The second question asked, 'Can a quantitative spatial approach provide an indirect measure of dispersal distance for *A. asparagoides* within the habitat?' The results of the exploratory and statistical analyses confirmed the non-stochastic nature of the invasion process. This then lead to development of a model using the variables previously identified as influential during the early stage of *A. asparagoides* invasion. Model validation was then performed using data from an independent second site. Spatial analysis techniques were used to investigation these questions.

Research objectives

The problem was broken down into five manageable objectives:

1. Determine how A. asparagoides invasion proceeds within a habitat

Data were collected on the density and location of *A. asparagoides* from a recently invaded vegetation reserve. The data were then used to map the distribution of *A. asparagoides*. During the initial stages of invasion, *A. asparagoides* begins to enter a habitat from the edges. Once the weed becomes established, it appears that dispersal may proceed along the track network within the habitat and along the edges of the habitat before entering the body of the reserve (Figure 2).

Table 1. Definitions of spatial scale and associated dispersal processes (Kollmann 2000).

Scale	Area	Vegetation traits	Dispersal process
Microhabitat	0.01–10(100) m^2	Individual plant	Seed bank dynamics, germination, establishment
Habitat	10–10 000 m^2	Plant community	Seed rain, seed predation, succession
Landscape	0.01–1000 km^2	Community mosaic	Genetic population structure, species dispersal
Region	>10^3 km^2	Regional vegetation	Site-specific distribution, phenological patterns
Biome	>10^4 km^2	Biome, floristic province	Climatic limits of distribution, phylogenetic history

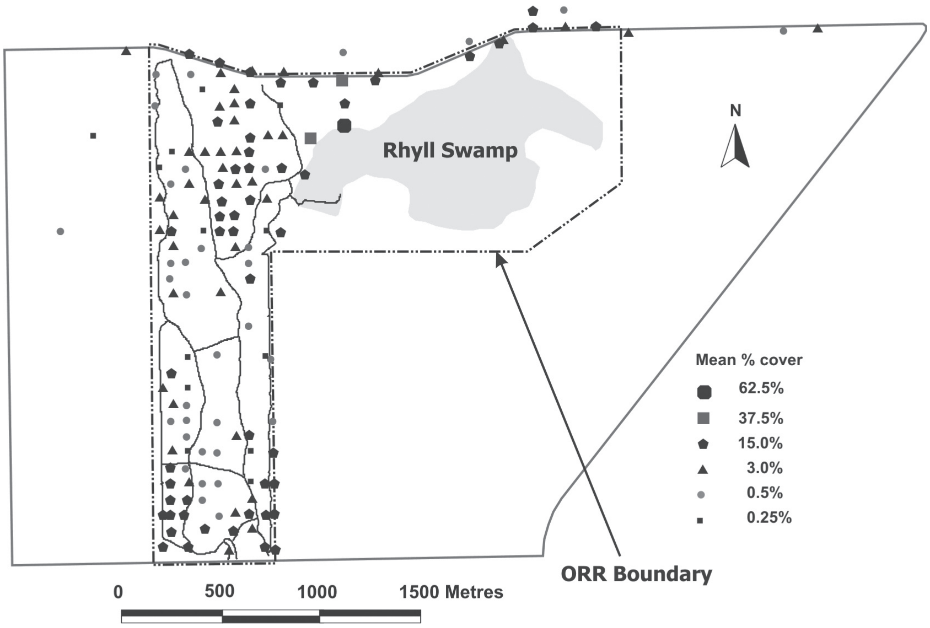

Figure 2. Mean per cent cover of *Asparagus asparagoides* per 20 × 20 m quadrat across Oswin Roberts Reserve and adjacent pasture in 2002.

2. Identify the factors that determine where A. asparagoides is found

This objective was achieved by constructing an extensive dataset on key vegetative and landscape attributes from a systematic survey of ORR. Preliminary analysis of the field data resulted in the identification of 22 vegetative and landscape elements. A more detailed description of the data collection has been reported elsewhere (Siderov and Ainsworth 2004). The vegetative attributes (Table 2) included ground understorey and overstorey mean cover density, the number of vegetation layers, percentage crown cover and the plant habit of the tallest vegetation layer. The landscape attributes (Table 3) included disturbance levels, perch type and perch

Table 2. Description of the vegetation attributes recorded. Attributes marked * are from the Australian Soil and Land Survey field handbook (McDonald *et al.* 1990).

Vegetative attribute	Metric
Vegetation structure*	Number of layers
Height of the tallest layer	Metres
Habit* of the tallest layer	Category
Native species: total	Percentage cover
Overstorey	Percentage cover
Understorey	Percentage cover
Ground	Percentage cover
Crown type*	Category
Crown type*	Percentage cover
Foliage Cover*	Percentage cover
Weed species: all	Percentage cover
A. asparagoides	Percentage cover

number and distance from the track network. Subsequent analysis during the model development in Objective 4 found that only five of the 22 variables (Table 4) were statistically significant.

3. Examine the spatial nature of dispersal within a habitat and throughout a landscape.
This objective was achieved by using spatial statistical methods to indirectly determine long distance dispersal instead of using time consuming and laborious seed collection methods. Analysis of the data found that dispersal is not a random event. The spatial nature of the dispersal process was examined by mapping the number of times *A. asparagoides* was found to be present per unit area i.e. spatial intensity and the identification of hot spots indicating presence of developing satellite colonies within the habitat. Analysis of the data using Ripley's *K*-function (Haase 1995) helped to identify distinct distances within the habitat at which clustering of *A. asparagoides* was apparent. The analysis showed that the longest distance at which this occurred was approximately 200 m. However, this may not be representative of a true long distance dispersal event as evidence of dispersal distances of 360 m to 380 m was also found.

4. Develop a presence/absence model for A. asparagoides invasion.
This was achieved by developing a logistic regression model using five of the factors identified in the preliminary field data (Table 4). The model is given by the following:

$$g(\mathrm{Bc}) = 0.317 - 0.022\mathrm{Crown} - 0.016\mathrm{Under} - 1.38\mathrm{Habit} - 0.043\mathrm{Drds{:}lod1} - 0.048\mathrm{Drds{:}lod2} + 0.036\mathrm{Drds{:}lod3} + 0.001\mathrm{Drds{:}crown}$$

$g(\mathrm{Bc})$ represents the logarithm of the odds ratio, $\frac{P_x}{1 - P_x}$ the ratio of the probability of success and the probability of failure, for a predictor variable with a value of *x*. See Hosmer and Lemeshow (2000) for a description and further details of multiple logistic regression analysis.

The logistic model was able to correctly predict 67% of responses overall. Within this overall result locations where *A. asparagoides* was actually present were successfully identified 74% of the time, whilst locations where *A. asparagoides* was absent were correctly identified only 60% of the time. Thus when the weed is present the model is very likely to predict correctly, but when it is absent there is a reasonably high rate of error. The model development and validation procedures have been previously reported in more detail elsewhere (Siderov *et al*. 2005).

Table 3. Description of the landscape attributes recorded. Attributes marked * are from the Australian Soil and Land Survey field handbook (McDonald *et al*. 1990).

Landscape attribute	Metric
*Aspect/bearing	To the nearest 10°
*Slope: Class:	Level to cliffed
*Slope: Form:	Crest to closed depression
*Disturbance	Natural through highly disturbed
Perching element: Number:	None, single, multiple
Perching element: Type:	Tree, fence, power line
Soil	pH
Litter depth	Centimetres
*Ground surface	Percentage cover of: bare ground, litter, rocks
Distance from nearest path/road	Metres

Table 4. Description of the five variables used in the logistic regression model. Bc is the dependent variable.

Variable	Description
Bc	Response to the question: 'Is *A. asparagoides* present in a particular location?' Yes = 1, No = 0.
Lod	Level of disturbance. Three categories: 1 = Natural, no disturbance, 2 = Past grazing, 3 = Disturbed.
Drds	Distance from quadrat to nearest path/track/road in metres.
Habit	Habit of the tallest vegetation level. Two categories: 1 = Tree, 2 = Not a tree.
Crown	Percentage cover of the quadrat by tree/shrub crown.
Under	Understorey cover (all species) as a median percentage value based on the Braun-Blanquet cover class.

5. Determine the general applicability of the developed model.
This objective was achieved by testing the model developed in Objective 4 at a second independent site (VKR) in order to determine if it is generally applicable. The model was shown to be valid at VKR achieving an overall percent correct rate of 67%, the same rate as in Objective 4. However, the percent correct rate for *A. asparagoides* presence was higher at 87%.

Discussion

This research established a comprehensive data set for an extensively surveyed remnant vegetation patch to investigate the early stage invasion by and dispersal of *A. asparagoides*. Although not an objective of this study it would be possible for the field sites to be resurveyed, thus providing a direct record of the invasion progress.

The project also highlighted difficulties in finding suitable remnant vegetation in which to carry out this investigation. Many remnants are linear with high edge/interior ratios. Those vegetation remnants that were large enough to enable edge effects to be discounted contained extensive path networks. Similarly such networks did not allow for large enough areas between the paths to discount any influence that adjacent paths may have had on invasion dynamics. Finally in remnants where edge and path effects could be reduced, *A. asparagoides* had been present for a considerable time. This late stage invasion may have already masked any spatial patterns present during the early stage of invasion.

Weed invasion into native vegetation presents a challenge from a management perspective. Management is all the more critical as urbanization and agricultural practices within Australia have led to a highly fragmented and heterogeneous landscape. The development and validation of a logistic regression model provides a tool that can be used for on-ground management of *A. asparagoides* invasion. The high rate of correctly predicted *A. asparagoides* presence provides a high degree of confidence that most infestations will be located and can be targeted for removal, either manually or by herbicide use. This information would provide a method of targeting weed control in order to maximize limited resources.

This project has demonstrated that an inverse relationship exists between *A. asparagoides* presence and distance from paths during the early stages of the invasion process. This inverse relationship had only previously been noted from anecdotal evidence. The role that paths and tracks play during the early stages of invasion within remnant vegetation has implications for management. If tracks within the remnant act as conduit for invasion, these areas should be a priority for control programs. Another approach would be to reduce the number of tracks within an area of remnant vegetation, particularly if the area is ecologically sensitive and/or relatively small. An alternative approach would be to change the spatial arrangement of a track network so as to minimize the impact it would have in the dispersal of propagules into the area.

A more controversial measure would be continuation of controlled grazing in areas that are currently being fenced off and revegetated. Grazing is a very effective control measure for *A. asparagoides* as seen from the pasture quadrats and may be more feasible for some land managers than ongoing searching and chemical control of new seedlings.

One of the project outcomes is that the previously accepted velocity of spread of *A. asparagoides* (190 m year^{-1} (Stansbury and Scott 1999) compared to 380 m year^{-1}) is possibly an underestimate. In a largely cleared and grazed landscape, spread of *A. asparagoides* by avian frugivores along roadsides and wildlife corridors potentially has large effects on the rate at which remnant native vegetation patches are invaded. By connecting disparate habitat, seed dispersal and establishment in widely separated vegetation remnants is no longer dependent upon rare long distance dispersal events. Any strategy for management of *A. asparagoides* invasion along corridors will need to double the previously estimated rate of dispersal in estimating where new satellite colonies could become established and then monitor these areas to prevent establishment.

Finally this project highlighted the utility of GIS to visualize the temporal and spatial dynamics of the invasion process during the early stages. It was also effective in visualizing new satellite colonies and regions with little or no *A. asparagoides* as a three dimensional surface. The association of *A. asparagoides* with the track network could be clearly seen when the tracks were overlaid onto the three dimensional surface.

Future directions for research

An investigation into factors that would result in a lower false positive rate would be an important benefit in increasing the precision of the developed logistic regression model. This would have flow-on effects with respect to management of *A. asparagoides* invasion. Far more effective use could be made of limited resources by reducing the time spent searching locations where the weed is not present. Understanding the influence of different landscape elements on the spread of *A. asparagoides* should ultimately allow construction of a spatial model in which the implications of different land management options can be tested, thus allowing more informed decision making.

In its current form the model developed in this project is specific to one weed, *A. asparagoides* and one location, Phillip Island. Further work could test the validity of the model at sites other than Phillip Island in order to determine if it is a general model for *A. asparagoides* invasion. A model of this type could then, in principle, be extended to any bird-dispersed weed for which an adequate data set existed. The identification of *A. scandens* Thunb. at eleven locations in Oswin Roberts Reserve represents an ideal opportunity to follow this new invasion and apply the model to a different bird-dispersed weed.

Finally, the application of spatial statistics, particularly Ripley's *K*-function may provide a measure of dispersal distance and possibly a value for velocity of spread. Dispersal distance and velocity of spread can provide an approximate indication of a weed's potential extent over a given length of time. This would be useful for new weed species where dispersal distance and velocity of spread are unknown, giving land managers some idea of where searches need to be conducted for potential satellite colonies.

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