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Are invasions episodic?

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To determine if invasions are episodic we examined the age structure (survivorship curves) within populations of Dalmatian toadflax (*Linaria dalmatica*) using herb-chronology. Two separate metapopulations were mapped and sampled in 2007 and 2008, in Yellowstone National Park. Within each metapopulation one large population (patch) was sampled plus 12 smaller "satellite" populations within a 100 m radius of the large patch edge. Analysis of the age structure of the large patches showed clear deviations from a population experiencing constant survivorship. These results indicated external variables are driving the population dynamics causing episodes with increased survivorship or recruitment. Survivorship was positively correlated with higher growing season precipitation years. Survivorship curves in the satellite patches also deviated from populations experiencing constant survivorship but were more variable than the larger populations. The relative importance of mortality or recruitment in shaping the age structure has yet to be determined but the satellite patch data suggests more temporal variation in recruitment or mortality than in the larger patches. In addition, the satellite patches demonstrated a significant ($p=0.017$) negative relationship between maximum age of the satellite populations and distance from the edge of the main patch. This suggests that the older, larger patches were acting as source populations. Comparison between the two metapopulations suggested that both temporal and landscape variability may play important roles in the establishment, survival and spread of new non-indigenous plant populations.



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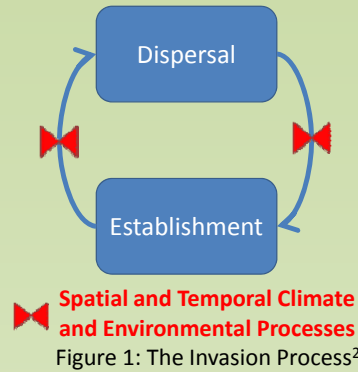
Empirical results from populations of *Linaria dalmatica*

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Introduction: From a practical perspective, the management of all non-indigenous species (NIS) is met with monetary and other logistical constraints. Thus, a system of prioritization and targeted management of high risk populations of NIS has been proposed to improve efficiency and success¹. However, landscape heterogeneity makes this prioritization concept difficult to implement because we do not have a solid understanding of how populations respond in time and space.

Plant invasion can be characterized by two processes: dispersal and establishment². Structure emerges in populations as a result of these two processes (Fig. 1). Examination of the spatial and temporal climate and environmental factors influencing the movement between the two stages could help us better understand how successful a given species will be across a landscape continuum. This improved knowledge could help predict future high expansion years and aid in the prioritization of populations for management.



Objectives: (1) To understand invasion by evaluating the spatial age structure of *Linaria dalmatica* (Dalmatian toadflax) populations. **(2)** Quantify the establishment and spread rates of metapopulations of *L. dalmatica*.



Figure 2: Map individuals and excavate roots.

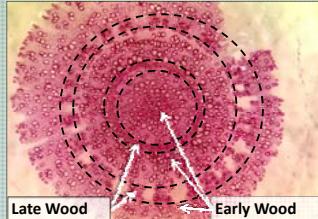


Figure 3: Cross section root and identify annual rings.



Figure 4: Sampling transects from main patch.

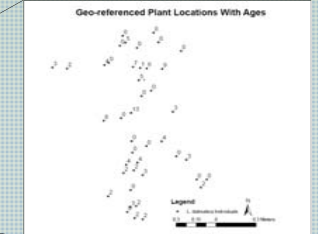
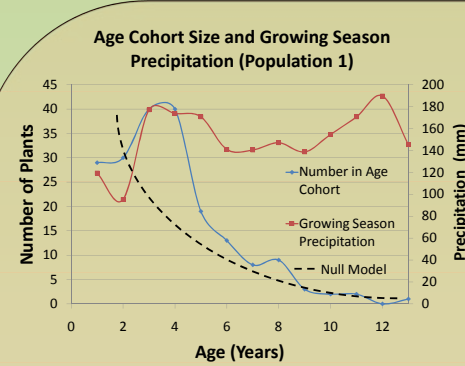
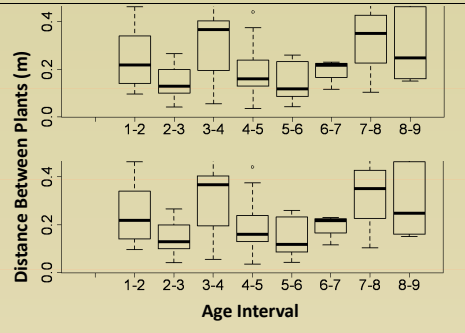


Figure 5: Generate Spatial Age Map

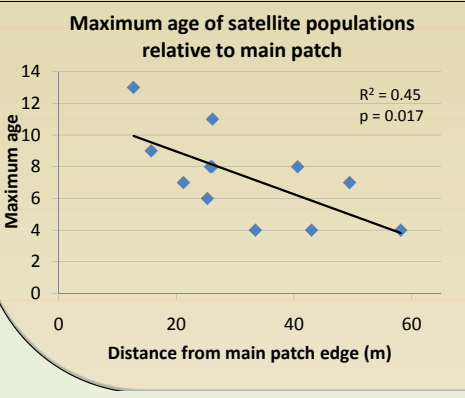
Methods: Two populations of *L. dalmatica* were sampled in Yellowstone National Park, WY. The plants were mapped in the main patch as in Figure 4 and roots excavated (Fig. 2). Roots were cross sectioned and annual rings identified (Fig. 3) through herb-chronology techniques³. Plant positions and associated ages were used for analysis (Fig. 5). Satellite populations within ~100m of the main population were mapped and sampled in the same way.



The survivorship curves showed a decrease in age cohort size with increasing age as we would expect with age-dependent mortality. However, there were deviations from a population experiencing constant survivorship (dashed line). When incorporated into a quasi-Poisson model, growing season precipitation showed a significant association to cohort size after accounting for age in populations 1 and 2 ($p = 0.006$ and $p = 0.026$ respectively).



To look at temporal variation in growth, the distance to the nearest neighbor in the next greater age cohort was measured. Some variation between cohorts was seen indicating some years may have been more favorable for growth. These differences were not significant ($p = 0.08$). Genetic analysis may improve the calculation of annual growth by allowing for differentiation between seed and vegetative propagation.



The maximum age of each satellite population was quantified to determine establishment year. There was a significant negative relationship ($p = 0.017$) between maximum age and distance to main patch. A number of spatial or temporal processes could cause this pattern to be observed (e.g. decreasing environmental suitability spatially or temporal variation in the conditions favorable to dispersal, establishment, and survival).

Summary

- The pattern of the age distribution showed variation from the null model (constant survivorship) which could be related to precipitation.
- The median distance between adjacent age cohorts was X, and the mean X. There was some variation between years suggesting temporal influences on annual spread.
- The negative relationship between maximum age and distance from the main patch may indicate population expansion originating at the main patch or increased mortality rates in the satellite colonies due to less suitable microenvironments.