The ecology of native and introduced thistles

by

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The dissertation of Daniel A. Gluesenkamp is approved:

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Abstract

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I examined the factors controlling the abundance and distribution of a native thistle, *C. brevistylum*, an introduced European thistle, *C. vulgare*, and their insect herbivores in a northern California redwood forest. Experiments and observational studies focused on 37 thistle populations occupying disturbance patches over more than 100 km^2 of forest. This research explored differences in patterns of abundance of native and alien thistle species; addressed how habitat productivity affects the intensity and importance of competition versus herbivory experienced by the two thistle species; and investigated the degree to which abundance of insect seed predators on the native thistle varied among scales and with regard to plant and habitat characteristics.

Greater abundance of the alien *C. vulgare* on the scale of the forest was chiefly a result of longer population persistence. Ability of *C. vulgare* to persist at patches from which *C. brevistylum* had vanished was attributable chiefly to plant characteristics: greater seed production, larger seeds, and higher survival rates. The two species did not differ in ability to tolerate competition with background vegetation, and differential impact of natural enemies on the native thistle did not explain patterns of abundance.

Both experimental and pattern data showed that competition with background vegetation had strong negative effects on germination, survival, and reproduction of thistles. Absolute and relative intensity of competition increased with habitat productivity, though vegetation actually had a facilitative effect on thistles under low productivity conditions. Impact of herbivores was quite variable overall. Intensity of herbivory was positively related to habitat productivity about half of the time. Overall, competition was much more important than herbivory. Increases in the density of vegetation with increasing productivity led to very strong negative indirect effects on thistle survival and reproduction. The negative effects of increases in herbivore abundance with increasing productivity were weaker than the positive effects of productivity on thistle growth and survival.

The three species of insect seed predator displayed rather different patterns of occurrence and abundance. For all three species, variation in abundance was greatest among seedheads, but variation among sites was very high for the introduced weevil *Rhinocyllus conicus*. Variation at the seedhead level was very well explained by seedhead characteristics, but explanatory ability was lower at plant and site scales. Overall, occurrence and abundance were best explained by plant and soil nitrogen and by plant phenology, but differences among species responses were stronger than were similarities.

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Chair Date

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Chapter 3 **Distribution of insect seed predators on a native thistle.**

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GENERAL INTRODUCTION

The modern science of ecology began when North American botanists applied Darwinian theories to the study of natural history, and is essentially 100 years old (Kingsland 1991). In this century, ecologists have made significant progress in describing how biotic and abiotic factors can shape the abundance and distribution of species and the structure and function of communities and ecosystems. Much of this progress has been made in the last 50 years, particularly the last three decades, and is largely due to the revolutionary application of experimental approaches, statistical rigor, and hypothetical-deductive prediction testing that is the legacy of Robert MacArthur, G.C. Varley, and Joe Connell (Peet 1991, Hairston 1989).

Research has substantially proven that factors and interactions such as resource availability, physical environment, species diversity, disturbance frequency, competition, herbivory, and predation are capable of structuring ecological systems. In spite of this body of knowledge, however, the degree to which ecologists can explain the structure of natural communities is still limited. This is partly due to the fact that, though the hypothetical-deductive approach has revolutionized the manner in which ecologists establish the occurrence of ecological relationships, we still evaluate the importance of these relationships the same way: by comparing the number of studies showing a significant effect against the number showing other relationships to be important or showing no effect. Several recent advances promise to improve this deficiency, including use of meta-analysis to determine effect strength (Gurevitch et al. 1992), and assessing the role of context-dependency in determining relative importance (Berlow 1997, Bonser and Reader 1995, Hunter and Price 1992).

However, the ability of ecologists to understand the structure of ecological systems, and to predict the consequences of alterations to these systems, may also be limited by the fact that a majority of ecological research has been conducted in comparatively simple systems. Selection of more simple systems for investigation is partly a logical element of conducting reductionist science and is partly due to human behavior: ecologists are motivated to understand patterns, and the patterns that entice investigation are more apparent in simple systems; we are motivated to obtain clear and strong results, which are obtained by minimizing external variability. This differential investigation of less complex systems may be important, if complex and simple systems differ; for example, simple systems may be reach equilibrial states more quickly or may be more susceptible to perturbation-induced changes. More importantly, ecological systems in which patterns are shaped by high levels of variability and numerous interacting or counteracting processes may not be easily understood using theories and frameworks derived under less variable conditions. Thus, there exists a need for studies that evaluate the degree to which our current understanding of ecological systems is capable of explaining the function of more complex and variable natural systems.

The decision to focus my dissertation research on the population and community ecology of thistles was based not on any clear patterns suggesting *a priori* importance of specific processes, not on the amenability of the system to analysis and understanding, but rather due to the aesthetic appeal of a very complex system. Variability in this system is driven by the inherent complexity in plant life history. Populations are stagestructured, and soil seedbanks, rosette banks of juvenile plants, and reproductive adults all independently influence pattern. Plant are extremely plastic, with adult plant height ranging from 10 to 300 cm, reproductive output ranging from 0 to 100,000 seeds per plant, and plants can take as little as 4 months or as long as 12 years to reach reproductive maturity. These plants are also very strongly influenced by highly variable physical and biotic environments. Within a site, patch-initiating disturbances create significant heterogeneity, with bulldozers excavating pits and mixing together topsoil, undeveloped mineral soil, and woody debris into mounds of variable sizes. This heterogeneity affects the environment experienced by plants; for example, soil nitrogen ranges from nearly 0 to almost 20 ppm, and there is similar variability in light and moisture. Plants are affected by competition with background vegetation and by a diverse assemblage of herbivores; significant variability in density of vegetation and the occurrence and abundance of two guilds herbivores adds further complexity to the system. In addition, physical and biotic factors operate on a diversity of physical and temporal scales. Spatial scales range from individual seedheads, to whole plants, populations, and patches across the landscape. Changes over the course of patch succession mean that subsequent generations experience different environments, and also mean that seeds germinating in the bare soil of a large disturbance will be in competition with background vegetation when they reach reproductive maturity. Finally, both the thistles and their herbivores include native and non-native elements, and this diversity of biogeographic and evolutionary histories can result in a complementary diversity in interactions.

In one sense, this system may seem unrepresentative of many natural communities, since much of the variation in this system is due to a novel and very dynamic disturbance regime (logging disturbance), and the presence of aggressive alien species. To the contrary, however, these traits are actually rather characteristic of the landscape that humans are creating and that ecologists should be concerned with managing. The chief difference between this thistle-herbivore system and most other modified semi-natural systems is that previous research on thistles and their herbivores has provided background natural history information for these species that is unavailable for most other systems. This system is therefore appropriate for testing the explanatory power of current ecological theory.

I evaluated the degree to which natural variation is explicable based on ecological theory alone, the degree to which knowledge of life-histories of the organisms is required to explain patterns, and the degree to which variation remains unexplained without additional research. In each of the papers comprising this dissertation, I used correlative and experimental approaches to evaluate hypotheses generated by the ecological literature and natural history intuition. In each case, I evaluated the degree to which support for hypotheses varied among species or among investigative approaches. In addition, I examined multiple hypotheses simultaneously, in order to assess relative importance of each hypothesized factor and the total explanatory power of all hypothesized factors together.

The work presented in this dissertation addresses the following specific questions:

1. What ecological factors influence patterns of abundance of the two thistle species, and how does this lead to greater abundance of the invasive alien?

2. How does habitat productivity affect the intensity of competition and of herbivory, and what are the net consequences of variation in productivity for plant populations?

3. How do occurrence and abundance of phytophagous insects vary among spatial scales, to what degree is variation explained by ecological factors at each scale, and are answers to these questions the same for different herbivore species?

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