Traits influencing the invasion success of annual plant species

Outline of PhD thesis

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BACKGROUNDS AND QUESTIONS

Globalization has become the primary driver of one of the most devastating form of environmental decline: biological invasions (Vitousek et al. 1996, 1997). The outcome of the spread of a species beyond its natural range might vary substantially, from failing to establish in the new habitat to showing high invasiveness, and causing ecological and economic damage (Kolar and Lodge 2001). Traits that make an alien species invasive, characteristics of invasible communities and the impact of range-expanding species are the central topics of invasion ecology. Among these studies, those that are dealing with the causes of invasiveness are continuously increasing in number. Traits such as height, vigorous vegetative growth, early and extended flowering, high fecundity, efficient dispersal of seeds, easy germination and a long-term persistent seed bank have been found to predispose plant species to be invasive, however, only a few traits have been proved to be generally associated with invasiveness (reviewed in Pyšek and Richardson 2007). The difficulty of robust generalizations can be attributed, on the one hand, to the heterogeneity of taxa and invaded ecosystems and, on the other hand, to the preponderant effect of variation in propagule pressure among case studies. Therefore, use of circumscribed subsets might provide a better chance to reveal the mechanisms behind the invasion process.

Based on fundamentally different ecological strategies between long and short-lived species, one can expect that different traits are associated with invasiveness of short-lived and long-lived herbaceous aliens. That is why I have chosen life span as a "key feature" in distinguishing species groups and focused exclusively on short-lived invasive plants and on their traits associated with invasiveness. I formulated several questions:

1. Can we distinguish the short and long-lived invasive species according to their traits associated with invasiveness?
2. Which are the soft traits (easily quantified, general traits which can be found in plant trait databases) associated with invasiveness of annual plant species?
3. Which are the hard traits (attributes that are rarely quantified due to its difficulty to measure, however obviously linked to invasive success) associated with invasive

success of annual plant species: phenotypic plasticity, competitive ability or generalist-specialist character?

4. Is there a germination strategy that helps an annual species to become successful in invasion process?
5. Can the invasive annual species' seeds accelerate or delay the time of their germination with the environment becoming more and more competitive?
6. Is there empirical evidence for phenotypic divergence (trait evolution) along the historical spreading route of an annual invasive species?
7. Which traits are likely to be under selection during the invasion process?

METHODS

I planned and carried out four independent studies to answer the questions:

1. I compared some selected biological traits of successful range-expanding (invasive species in natural areas) and less successful (non-invasive naturalized species) alien species of the United States that originate from Central Europe. I split the dataset into short-lived species and long-lived species (herbaceous perennials). The final database consisted of 116 (34 invasive species in natural areas) short-lived and 296 (81 invasive species in natural areas) long-lived herbaceous species. I chose traits related to competitive ability (dominance pattern, ecological strategy, plant height), reproduction (e.g., timing of flowering, compatibility, pollination), dispersal (vegetative dispersal, specialized and unspecialized dispersal agents, range of dispersal types), size of the native range and relation to human disturbances (e.g., tolerance to human disturbance, affinity of plant species towards urban areas, use by humans). I used the source-area approach, the analysis of biological traits of species introduced to a region from a defined geographical 'source' area. Since attributes often covary due to phylogenetic constraints, I applied a method that accounts for the degree of relationship between species during the statistical analysis.

2. I compared three *Bromus* species which can be ranked according to how successful they are in their American introduced range: Cheatgrass (*Bromus tectorum*) is "the quintessential invader" of

North America occurring throughout the United States and Canada. Poverty brome (*Bromus sterilis*) has a narrower distributional range and it is an exotic species with moderate invasion success, while corn brome (*Bromus squarrosus*) is even less widespread and it is not considered an invasive species in North America. I performed a series of experiments and observational studies. First, I tested whether the species differed in biomass production and reproduction in a growth experiment in outdoor plots with and without added fertilizer and water; second, I examined whether intraspecific competition is different in the three *Bromus* species in a common-garden experiment; third, I ascertained how the composition and abundance of vegetation influence the performance and fitness of the species with a community-scale survey; fourth, I tried to place the three species along a generalist-specialist gradient using a landscape scale study. I used the still overlooked approach of studying the aspects of invasions, namely the source area approach.

3. The germination response of an annual invasive species in increasingly competitive environments was studied on the common ragweed (*Ambrosia artemisiifolia*) by modifying the competitive environment of the seeds. Seeds were germinated in adequate conditions without competition at one extreme of the competition gradient. Towards the other extreme of the gradient we chose the competitive environments to be as various as possible by manipulating life stages (seed, seedling or adult plant), density (low, high) and also identity (4 species) of neighbours. We also followed the fate of non-germinating seeds by recovering them after the germination period and checked their viability.

4. I chose the common ragweed as model species to study the divergence of phenotypic traits between older and recently introduced populations. The common ragweed is one of the rare cases of successful invaders with well documented spreading history in Hungary, owing to the regular weed surveys during the 20th century. I sampled individuals to compare their offspring's phenotypic traits from eight populations belonging to four residence time categories, as follows: # 1: populations established less than 30 years ago, #2: established more than 30 years ago, #3: established more than 40 years ago and #4:established more than 60 years ago. Seeds were separately collected from eight individual mother plants from each site; thus, a total of 64 individuals were sampled. We selected four large (among the tallest individuals) and four small (among the shortest individuals, which had at least 50 matured seeds) individual plants in each population to control for maternal effects. Seeds were put to germinate and eight seedling of each seed family was reared in a common garden. At the end of the experiments, five vegetative life

history traits were measured: plant height, aboveground biomass, the longest secondary axis, number of secondary axes and basal diameter.

NEW SCIENTIFIC RESULTS

(1) Our results verify that the role of traits in the success of naturalized alien species differs between groups of short-lived and long-lived herbaceous species.

(2) Short-lived invasive species benefited from having greater competitive ability than other potential aliens, because I proved that annual invasive species were taller than non-invasive naturalized species. Consequently, it seems that effective light competition or dispersal-vector competition (e.g., releasing height is important for wind and animal dispersal) helps determine the success of short-lived alien species becoming a successful alien species. Besides, annual species are good colonizers with effective reproduction and dispersal, as the results show that intermediate compatibility contributes to the invasiveness of short-lived alien species. Moreover, our results suggest that dispersal traits are of overriding importance in the case of short-lived invasive species in natural areas, as the number of possible dispersal types was also higher in the case of invasive species.

(3) According to the results, the three bromes are unequally equipped with trait that could enhance invasiveness. B. tectorum (the highly invasive species) possesses several traits that may be especially relevant: it has uniquely high phenotypic plasticity, as demonstrated in a nitrogen addition experiment, and it is a habitat generalist, thriving in a wide range of habitats, from semi-natural to degraded ones, and having the widest co-occurrence based niche-breadth. The other two species were less equipped with benefic traits. For example, B. squarrosus is a habitat specialist with low competitive ability, always occurring with low coverage. Therefore, this ranking of the species' abilities can explain the current spreading success of the three bromes on the North American continent.

(4) – (5) Common ragweed seeds proved to have keen abilities to perceive cues which might predict future competitive conditions and respond to it by modifying germination rate, but not by accelerating emergence. Plastic environmental cueing in common ragweed seeds is a precise mechanism for detecting ephemeral bare ground surfaces. The selection of the suitable habitats without possible competitive neighbours is achieved by accurately

perceiving the identity, density, but most importantly the life stage of competitors. The presence of seeds and seedlings of other species as only neighbours indicates a 'safe site' for common ragweed, because it has a high suppressive effect upon same-sized competitors. However, the presence of conspecific seedlings in high density has detrimental consequences on the development, thus final biomass of *Ambrosia* seedlings, and seeds do not have strategies to avoid the intraspecific competition among seedlings. In contrary, *Ambrosia* seeds developed keen abilities to accurately predict crowded or competitive conditions, where establishing individuals may have low chances of survival or reduced final biomass, using biotically influenced decrease in germination rate by induction of secondary dormancy as a competition avoiding strategy. As common ragweed seeds have the same viability after several induced secondary dormancy events (Fumanal et al 2007), this strategy might help its persistence despite high population fluctuations between years. Earlier studies have linked the large and long-persistent soil seed bank to invasiveness (Moravcová et al. 2007 and literature therein). Therefore, we can add the fine-tuned ability to predict future competitive environment and adequate dormancy release mechanisms in seeds to the list of traits (large number of pollen and seed production, high phenotypic plasticity, generalist character) that make *Ambrosia* one of the most successful invasive species of disturbed habitats in Europe.

(6) – (7) All five measured vegetative traits (plant height, aboveground biomass, the longest secondary axis, number of secondary axes and basal diameter) gradually decrease from populations with the longest residence time (introduced more than 65 years ago) towards the most recently established populations (established less than 30 years ago). These differences might reflect the invasion history of the populations: the longer the residence time the higher the chance to develop relevant traits beneficial in invasion process. Therefore, our results provide support for the existence of phenotypically distinct populations along the Hungarian spreading route of *A. artemisiifolia*. However, we cannot rule out the possibility that the results are the effects of adaptation to local environment or stochastic events. Nevertheless, all options suggest a great potential of adaptive differentiation of common ragweed populations that can assure present and future range expansion and local persistence of this highly invasive and harmful species.

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