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Science **342**, 364 (2013);

DOI: 10.1126/science.1242121

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Rapid Adaptation to Climate Facilitates Range Expansion of an Invasive Plant

Robert I. Colautti*† and Spencer C. H. Barrett

Adaptation to climate, evolving over contemporary time scales, could facilitate rapid range expansion across environmental gradients. Here, we examine local adaptation along a climatic gradient in the North American invasive plant *Lythrum salicaria*. We show that the evolution of earlier flowering is adaptive at the northern invasion front where it increases fitness as much as, or more than, the effects of enemy release and the evolution of increased competitive ability. However, early flowering decreases investment in vegetative growth, which reduces fitness by a factor of 3 in southern environments where the North American invasion commenced. Our results demonstrate that local adaptation can evolve quickly during range expansion, overcoming environmental constraints on propagule production.

The contribution of rapid evolution to range expansion and invasion into novel climatic regimes is poorly understood. Several common garden studies of introduced species have demonstrated the reestablishment of latitudinal or altitudinal clines in life-history traits similar to those observed in the native range, im-

plicating a role for adaptive evolution in response to local climate (1–3). However, linking geographical clines in candidate traits to range expansion requires additional lines of evidence. First, fitness trade-offs among life-history traits should be investigated to distinguish adaptive evolution from nonadaptive responses to selection on cor-

related traits (4, 5). Second, reciprocal transplants across environmental gradients must demonstrate crossing reaction norms—the signature of local adaptation—in which locally adapted “home” populations have higher fitness than the non-adapted “away” populations at each site. Third, measurements of natural selection on candidate traits are needed to identify ecologically divergent selection—a geographically shifting optimum—responsible for adaptive clines. Finally, the fitness effect of local adaptation should be compared with other factors thought to facilitate range expansion. We used each of these criteria to link adaptive evolution to the spread of an invasive wetland plant.

We measured natural selection and tested for local adaptation in introduced populations of *Lythrum salicaria* (purple loosestrife—Lythraceae) from eastern North America. This species is one of the world’s most serious wetland invaders and

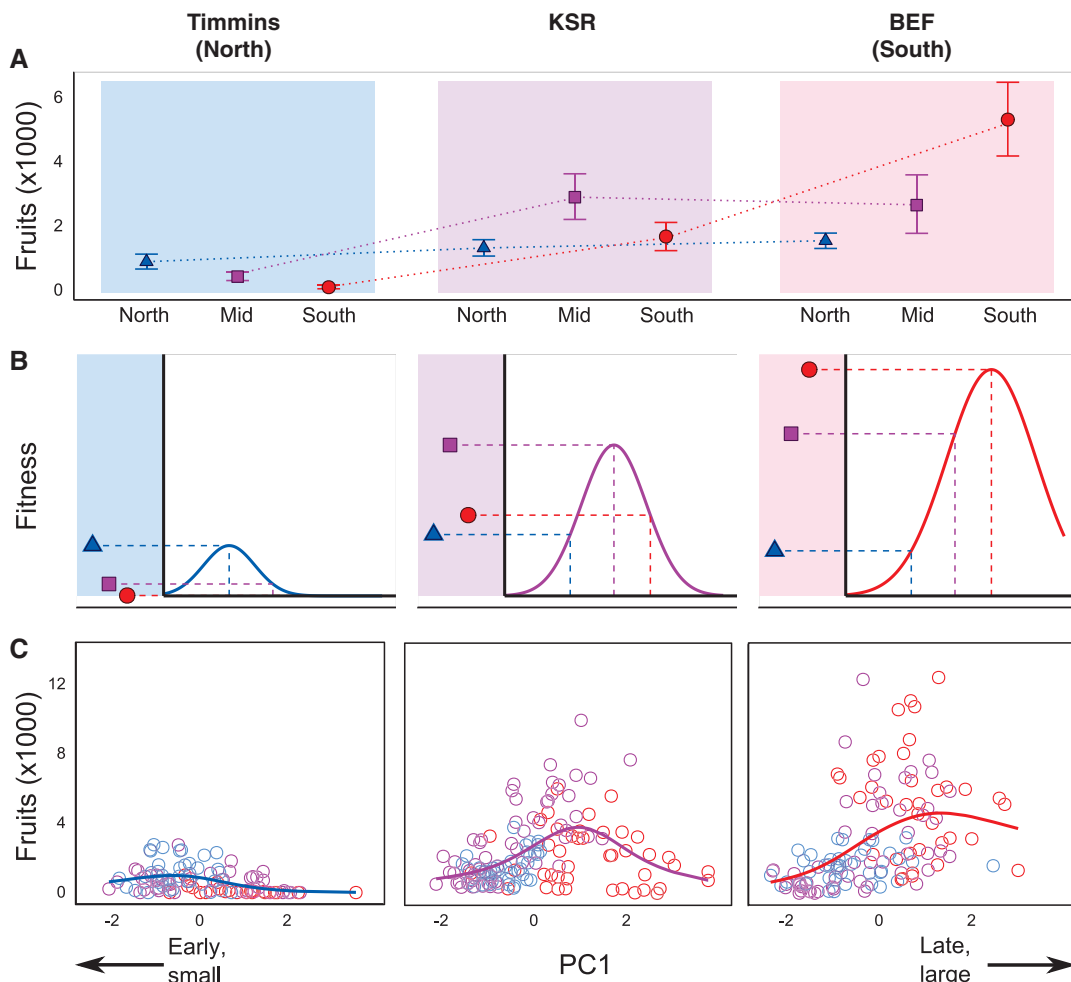
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Fig. 1. Rapid evolution of local adaptation to climate among invasive populations of *L. salicaria* resulting from a latitudinal shift in the adaptive landscape. (A) Evidence for local adaptation based on survival and fruit production data over 4 years (2007–2010) at each of three sites spanning a latitudinal gradient of 10° (~1000 km). Each point is the mean of a pair of populations [$\pm 95\%$ confidence interval (CI)] grown from seeds collected from northern (blue triangles), southern (red circles), and mid-latitude sites (purple squares).

(B) Adaptive landscapes modeled for a single quantitative trait representing a trade-off between reproductive timing versus size at maturity (PC1, x axis) in three environments: short (Timmins), long (BEF), and intermediate growing seasons (KSR). Solid curves in each graph show the predicted adaptive landscape, and dotted lines show the consequences for fitness of populations collected from northern (blue triangles), southern (red circles), and intermediate latitudes (purple squares). (C) Observed cumulative reproductive output (circles) over 4 years (2007–2010) and nonlinear fitness splines (solid curves) of 450 plants from three pairs of populations collected from northern (blue), southern (red), and intermediate latitudes (purple), reciprocally transplanted into the three common garden sites.



is the target of numerous control programs (6, 7). Previous studies have shown the reestablishment of latitudinal clines in growth and phenology in this region (8, 9), with northern populations flowering an average of ~20 days earlier, but at half the size of southern populations, when both are grown in a common environment (4, 5, 9, 10). To determine whether these genetic differences in flowering time and size are locally adaptive, we transplanted seedlings in 2007 from three pairs of populations originating from northern, mid-latitude, and southern populations into each of three common garden sites with contrasting growing seasons and spanning most of the introduced range in eastern North America [Timmins, 48.47°N; Koffler Scientific Reserve (KSR), 44.03°N; Blandly Experimental Farm (BEF), 39.06°N] (11).

Measurements of survival and fruit production over four field seasons (2007–2011) showed the characteristic “home site advantage” predicted by the local adaptation hypothesis—on average, populations from latitudes closest to each garden location had higher fitness than populations from more distant latitudes (Fig. 1A). Local adaptation is frequently observed in native plant populations (12, 13), but in this case historical evidence indicates a relatively recent (<100 years) northward migration of *L. salicaria* into Ontario, Canada, following multiple introductions from Europe to the eastern seaboard of the United States (6). Evidence from neutral markers (14, 15), historical records (6), and patterns of quantitative genetic variation (4) do not support parallel introductions of preadapted populations from Europe to areas of similar climate in North America (11).

Rather, adaptive latitudinal clines in *L. salicaria* have evolved rapidly. We tested for divergent selection among populations responsible for the rapid evolution of local adaptation.

We modeled the adaptive landscape for each point along a latitudinal transect as a Gaussian function defined by three parameters: (i) the phenotypic optimum, (ii) the strength of stabilizing selection, and (iii) the mean fitness at the optimum phenotype. Previous studies showed that natural selection at the mid-latitude site (KSR) favored both early flowering and larger size, but early-flowering plants were constrained to be small, resulting in stabilizing selection along the primary axis of genetic covariance for these traits (PC1) (4, 10). Parameter values for each of our three study sites were inferred from latitudinal clines observed in both common garden (4) and field (9) studies of 20 populations spanning our experimental garden sites (11). Evolution of adaptive clines through ecologically divergent selection is predicted in the parameterized model, because the phenotypic optimum shifts from flowering early at a small size, to flowering later at a large size, as the length of the growing season increases and relaxes selection for early flowering (Fig. 1B). We tested this model by measuring natural selection at each of our common garden locations.

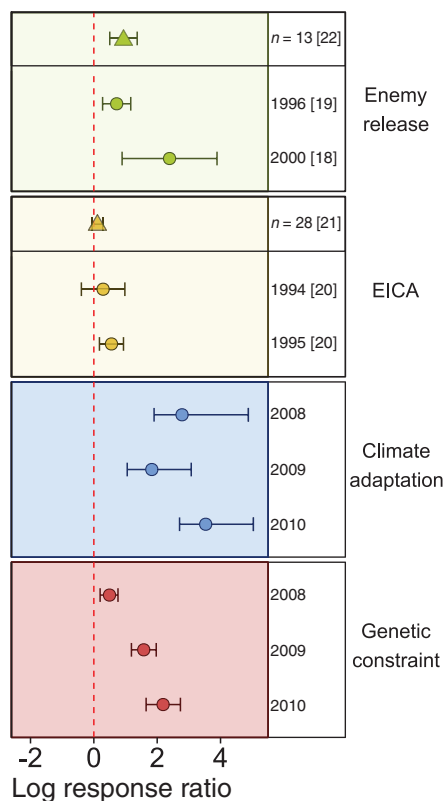
Selection analysis confirmed a geographical shift in the adaptive landscape, from an optimum of early flowering at a small size in the northern common garden to later flowering at a larger size in the south (Fig. 1C). This difference persisted after controlling for region of origin in the selection analysis, ruling out among-population

genetic correlations with other traits, such as frost tolerance or growth rate (11). We cannot rule out within-population genetic correlations with unmeasured traits, but the specific signature of local adaptation provides additional evidence for ecologically divergent selection on PC1 per se. As predicted by the parameterized model, transplanting northern populations to sites with progressively longer growing seasons had little effect on reproductive fitness because fruit production is limited by size in these small plants, resulting in a relatively flat reaction norm (compare blue triangles in Fig. 1, A and B). In contrast, large southern plants acquired ample resources, but their delayed reproduction sharply reduced fitness when transplanted into sites with shorter growing seasons, as predicted by the model (compare red circles in Fig. 1, A and B). Thus, divergent selection favored earlier reproduction in the north but larger size in the south, resulting in an adaptive latitudinal cline in flowering time and size.

Given that clines in eastern North America have established quickly as a result of local adaptation, what are the ecological consequences of rapid adaptation to climate compared with other proposed selective factors? *Lythrum salicaria* has played an important role in the development of two key hypotheses in invasion biology: the enemy release hypothesis (ERH) (16) and the evolution of increased competitive ability (EICA) (17). Escape from two specialist herbivores that dramatically reduce seed production is thought to have facilitated the North American invasion of *L. salicaria*, consistent with the ERH (18, 19). The EICA hypothesis additionally predicts relaxed selection for costly defensive traits, allowing reallocation of resources to growth and reproduction (17). Consistent with this idea, introduced populations of *L. salicaria* have higher reproductive output relative to native conspecifics when grown in a common environment (20). We compare these fitness effects (11) and two recent meta-analyses (21, 22) with our reciprocal transplant results to assess the ecological consequences of local adaptation to climate among invasive populations.

Rapid evolution of earlier flowering is adaptive under short growing seasons (Fig. 1, Timmins site) and increased fitness of northern versus southern populations by as much as 37 times at the northern site (183 versus 5 fruits in 2010) (Fig. 2, Climate adaptation). However, local adaptation of northern populations comes at a cost of reduced vegetative growth, which is maladaptive under longer growing seasons (Fig. 1, BEF site) and reduced reproductive fitness by as much as 90% at the southern site (1433 versus 161 fruits in 2010) (Fig. 2, Genetic constraint). In most years of our study, the magnitude of these fitness effects were significantly higher than the putative fitness increase inferred from EICA studies, and as high as or higher than effects of specialist herbivores (Fig. 2). This indicates that both climate adaptation and genetic constraint strongly affect survival and propagule production in *L. salicaria* populations.

Fig. 2. Comparison of fitness effects (log-response ratio ± 95% CI) among potential drivers of invasive spread in two meta-analyses of introduced plants (triangles), and three studies of the same factors in *L. salicaria* (circles). Number of species or years of study are shown to the right of each study, along with reference numbers in brackets. Effects of specialist herbivores (enemy release) and evolution of increased competitive ability (EICA) measured in previous studies are compared to the fitness benefit of local adaptation to shorter growing seasons near the northern invasion front at the Timmins site (Climate adaptation), and the fitness cost of early reproduction at the BEF site (Genetic constraint), the region where the North American invasion likely commenced.



We have shown that contemporary evolution of local adaptation to climatic conditions strongly influences seed production of a globally important invasive species—as much as or more so than biotic factors such as enemy release or the evolution of increased competitive ability, which have up to now dominated the literature on plant invasions. Local adaptation can evolve rapidly in outbreeding invaders like *L. salicaria* if multiple introductions from diverse native sources (6, 14, 15) contribute substantial standing genetic variation (5). In such cases, higher recombination rates increase the efficiency of natural selection in invasive populations of outcrossing relative to selfing species. Management efforts and comparative studies of native and introduced populations could be improved by explicitly considering that invasive species are not static entities, but can evolve rapidly, with important implications for future spread.

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Acknowledgments: We thank D. Carr and A. Weis for assistance at BEF and KSR, respectively, and K. Pols (Millson Forestry Service) and G. Paquette for assistance in Timmins. We also thank S. Yakimowski, M. Johnson, J. Alexander, J. Stinchcombe, K. Rice, K. Dlugosch, and L. Riesberg for helpful comments. This work was supported by Ontario Government and University of Toronto graduate scholarships (to R.I.C.), the Canada Research Chair's program and an Ontario Premier's Discovery Award for funding (to S.C.H.B.), and the Natural Sciences and Engineering Research Council of Canada for graduate and postdoctoral funding to R.I.C. and Discovery Grants to S.C.H.B. The Original data and analysis are available from the Dryad Data Repository (DOI:10.5061/dryad.878m3).

Supplementary Materials

www.sciencemag.org/content/342/6156/364/suppl/DC1
Materials and Methods
Figs. S1 to S3
References (23–36)

19 June 2013; accepted 16 September 2013
10.1126/science.1242121

The Invasive Chytrid Fungus of Amphibians Paralyzes Lymphocyte Responses

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The chytrid fungus, *Batrachochytrium dendrobatidis*, causes chytridiomycosis and is a major contributor to global amphibian declines. Although amphibians have robust immune defenses, clearance of this pathogen is impaired. Because inhibition of host immunity is a common survival strategy of pathogenic fungi, we hypothesized that *B. dendrobatidis* evades clearance by inhibiting immune functions. We found that *B. dendrobatidis* cells and supernatants impaired lymphocyte proliferation and induced apoptosis; however, fungal recognition and phagocytosis by macrophages and neutrophils was not impaired. Fungal inhibitory factors were resistant to heat, acid, and protease. Their production was absent in zoospores and reduced by nikkomycin Z, suggesting that they may be components of the cell wall. Evasion of host immunity may explain why this pathogen has devastated amphibian populations worldwide.

Although causes of global amphibian declines are complex (1), the chytrid fungus, *Batrachochytrium dendrobatidis* (2, 3), is now recognized as a leading contributor (1, 4).

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Previous studies in *Xenopus laevis* suggest that both innate immune defenses, such as antimicrobial peptides in the mucus, and adaptive immunity contribute to resistance against *B. dendrobatidis* infection (5). However, lack of extensive lymphocyte infiltration in diseased skin (2, 6) suggests an impaired immune response (7–9). Because evasion of host immunity is a common strategy employed by pathogenic fungi (10, 11), we hypothesized that *B. dendrobatidis* avoids clearance by inhibiting critical immune functions. To test this hypothesis, we examined the effects of *B. dendrobatidis* on peritoneal leukocytes enriched for macrophages, and we cultured *X. laevis* splenocytes stimulated with T lymphocyte-specific

activators (12) or heat-killed bacteria to stimulate B lymphocytes (13) in the presence of *B. dendrobatidis* [see materials and methods in supplementary materials (14)]. Viability and functions of peritoneal phagocytes were not impaired by *B. dendrobatidis* (figs. S1 and S2). However, when splenic lymphocytes were cultured with either live or heat-killed *B. dendrobatidis*, T cell proliferation was reduced (Fig. 1, A and B, and fig. S3, C and E). Live *B. dendrobatidis* cells also inhibited B cell proliferation (fig. S3A). When lymphocytes were separated from *B. dendrobatidis* by a cell-impermeable membrane in a transwell culture system, the fungal cells inhibited lymphocyte proliferation, but less effectively than in coculture (Fig. 1C). The inhibitory effects of *B. dendrobatidis* were replicated in *X. laevis* T and B cell populations enriched by magnetic sorting (fig. S4). Inhibition of T and B lymphocyte proliferation by *B. dendrobatidis* was also observed when the splenocytes were isolated from another frog, *Rana pipiens* (fig. S5). Induced T and B cell proliferation was inhibited in a dose-dependent manner by 24-hour supernatants derived from *B. dendrobatidis* incubated in water (Fig. 1D and fig. S3, B, D, and F). Proliferation of mouse and human lymphocytes was also inhibited by *B. dendrobatidis* supernatants (fig. S6). Frog splenocytes pretreated with *B. dendrobatidis* supernatants for 48 hours had reduced proliferative capacity in response to phytohemagglutinin (PHA), and delayed addition of supernatants at 24 hours after PHA stimulation still inhibited proliferation (fig. S7). Thus, *B. dendrobatidis* can prevent activation and interfere with proliferation after lymphocyte activation has been induced. Further, *B. dendrobatidis* supernatants derived from killed cells inhibited proliferation