

## NEWS AND VIEWS

## PERSPECTIVE

**Unearthing the impact of human disturbance on a notorious weed**

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Large-scale anthropogenic changes in the environment are reshaping global biodiversity and the evolutionary trajectory of many species. Evolutionary mechanisms that allow organisms to thrive in this rapidly changing environment are just beginning to be investigated (Hoffmann & Sgrò 2011; Colautti & Barrett 2013). Weedy and invasive species represent 'success stories' for how species can cope with human modified environments. As introduced species have spread within recent times, they provide the unique opportunity to track the genetic consequences of rapid range expansion through time and space using historic DNA samples. Using modern collections and herbarium specimens dating back to 1873, Martin *et al.* (2014) have provided a more complete understanding of the population history of the invasive, agricultural weed, common ragweed (*Ambrosia artemisiifolia*; Fig. 1) in its native range with surprising results. They find that the recent population explosion of common ragweed in North America coincided with substantial shifts in population genetic structure with implications for invasion.

**Keywords:** *Ambrosia artemisiifolia*, historic DNA, invasive species, population structure

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The history of common ragweed invasion is a fascinating tale, as shifts in demography and range size are closely tied to human activities. The North American landscape was dramatically transformed during the nineteenth and twentieth centuries, opening new opportunities for select species, such as common ragweed, in modern agricultural and disturbed environments. The impact of this conversion is clearly stamped into the pollen cores and is commonly known as the '*Ambrosia* horizon'. Although introduced into France by 1863, prior to the first historic specimens of Martin *et al.* (2014) study, the population explosion in Western Europe did not occur until several decades later and has

been tied to the repeated introduction of contaminated horse fodder during the First World War (Chauvel *et al.* 2006). The population boom that Eastern Europe is now experiencing was propelled by the fall of communism, which led to the large-scale abandonment of agricultural fields and poor management of disturbed areas (Kiss & Beres 2006). This opened up abundant habitat for ragweed. Each summer common ragweed (Fig. 1) blankets Eastern North America and Europe with pollen, spawning annual bouts of runny noses and itchy rashes in its wake. It is the primary cause of hayfever (Bagarozzi & Travis 1998) with medical costs upwards of \$3.5 billion per year in the US alone (Storms *et al.* 1997). With climate change, the outlook is bleak, as delayed frosts, particularly in northern areas, means a lengthening flowering period and allergy season (Ziska & Knowlton 2011; Chapman *et al.* 2014). The ragweed menace has spread to all continents except Antarctica. It is unknown whether, or when the populations in Asia, Australia and South America will explode to the levels seen in Eastern North America and Europe.

One of the major questions in invasion biology is when and how multiple introductions can fuel invasion (Prentis *et al.* 2008). Multiple introductions can mitigate demographic and environmental stochasticity through propagule pressure. Diverse source populations can increase the chances of introducing advantageous alleles or result in the formation of beneficial allele combinations that can drive adaptation and spread (Simberloff 2009). In Martin *et al.* (2014), clustering analysis of historic and modern North American samples suggests admixture occurred primarily in the native range perhaps even before its introduction into Europe. This suggests that human activities in North America may have primed ragweed for invasion elsewhere. It will be interesting to compare these findings with an analysis of historic and modern samples in Europe to examine shifts in population structure and admixture during invasion. A cryptic invasion of North American *Phragmites* by a foreign genotype has been detected using a similar data set (Saltonstall 2002). Such data could help determine whether there has been a cryptic spread of European ragweed in North America. Large changes in population structure between historic and modern samples (Martin *et al.* 2014) that coincide with ragweed's invasion of Europe, as well as the presence of 'invasive' phenotypes in Ontario (Hodgins & Rieseberg 2011), are suggestive of this possibility. Future analyses of historic genetic data might benefit from the advent of new methods that explicitly incorporate temporal sampling, to make full use of the information provided by heterochronous DNA samples.

Plant reproductive systems are thought to play an important role in governing introduction success (Barrett *et al.* 2008). Reproductive mode has substantial

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**Fig. 1** Male inflorescences of common ragweed. Photo credit: Will Kirk, Homewood Photographic Services.

consequences for the structuring of genetic variation, which can impact the likelihood of adaptive response during invasion (Barrett *et al.* 2008). Baker (1955) predicted that many annual colonizers should be self-compatible to overcome mate limitation experienced during severe bottleneck associated with colonization. For many years common ragweed was assumed to be self-compatible, in part because of this reasoning. However, careful manual crosses and estimates of selfing rates using allozyme markers by Friedman and Barrett (2008) clearly showed that common ragweed was self-incompatible (SI), although leakiness in the SI system was also detected. The spatial pattern in the inbreeding coefficient found in Martin *et al.* (2014) study could be explained by geographical variation in selfing rates and the potential breakdown of self-incompatibility in the western portion of the range. Microsatellites are often plagued with null alleles and clines in the frequency of these alleles could mimic this pattern, as could hidden population structure. Geographical surveys of self-fertilization are needed to settle this debate and assess the role of mating system, if any, in ragweed's recent demographic explosion and continental range expansion.

Reconstructing invasion history is often a critical first step before adaptive evolution occurring during invasion can be inferred. Identification of genetic source populations in the native range can be essential to ensure that any genetic differences observed in common gardens coincide with introduction. Martin *et al.* (2014) proposed that the 'invasive phenotype' observed in previous studies (Hodgins & Rieseberg 2011; Hodgins *et al.* 2013) may have evolved in Eastern North America perhaps during the recent human mediated population expansion in this

region and may pre-date invasion into Europe. If this hypothesis is correct, it suggests that studies interested in the genetic changes contributing to invasion should contrast wild and weedy populations in the native range rather than focus on transcontinental comparisons alone. This may be particularly true in cases of disturbance loving species, such as ragweed, where large-scale changes in population density and range size occurred in the native range before invasion. Future studies of local adaptation and population structure in common ragweed should be sure to include samples from the Great Plains, where pollen records indicate ragweed has been relatively abundant for thousands of years (Williams *et al.* 2004), and wild populations in remnant grasslands still exist today.

Modern advances in genomics are enabling researchers to move beyond the analysis of a few anonymous genetic markers in nonmodel species. Now, there is the opportunity to assess genetic variation across hundreds or even millions of markers. This will allow the identification of variants, genes and genomic regions important for adaptation in invasive species. Historic samples will provide a window into the past by making direct observation of changes in adaptive allele frequency over time possible (Wandeler *et al.* 2007). These data will shed light on the tempo of evolution during invasion, and the role adaptation plays at different stages of the process. Such studies will provide new and exciting opportunities to illuminate how natural selection shapes evolution on contemporary timescales.

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