

GEOGRAPHICAL ASPECTS OF INVASION: THE ANNUAL BROMES

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ABSTRACT: *Among conservation biologists, there is great interest in developing rules to predict which alien species are most likely to become serious invaders. Invasion is both an ecological and a geographical process, but mostly ecological rules have been proposed. Studies of several weedy genera have found that invasion success correlates with the size of the species' native distribution. A geographical explanation has been offered: species with broader distributions are more likely to be transported overseas. But several ecologists have countered by arguing that the enormous increase in trade and traffic volume in recent times ensures that all species have already been transported to essentially everywhere. This argument is tested by re-analyzing data from one of the above studies, on the annual bromes (*Bromus* spp.) The bromes are native to mediterranean (especially) and temperate climates, and have invaded overseas mediterranean climate regions spectacularly. The number of brome species successfully introduced into the mediterranean regions of California, central Chile, South Africa, and southern Australia corresponds to the number of source regions from which trade and traffic formerly flowed to those territories. Also, for each mediterranean region, the brome species that invaded correspond to the source region(s) that existed in early days. In short, invasion correlates with native distribution size because a larger distribution means that there will be a greater number of potential routes by which a species can reach a given land mass.*

Keywords: *Invasive species, Conservation, Mediterranean ecosystems*

INTRODUCTION

Concern over the negative effects of alien, invasive species is growing steadily (e.g., Elton, 1958; Harris, 1966; Drake et al., 1989; Groves and di Castri, 1991; Blumler, 1992b; 2002; 2003b; 2005; Lodge, 1993; Vitousek et al., 1996; Enserink, 1999). In addition to the economic impacts, there are ecological ones, which concern conservation biologists (Diamond, 1989; Blumler, 1992b; 1998; 2002). Consequently, in recent years many ecologists have turned their research attention to attempting to predict which aliens are likely to become invasive and which are not, i.e., to develop invasion "rules" (Enserink, 1999; Kolar and Lodge, 2001). The idea is that governments could then blacklist those species having the potential to become serious pests. While a number of rules have been proposed, for the most part they are specific to particular regions or ecosystems and there remains considerable doubt as to whether they are sufficiently valid as to be useful.

Thus far, the rules proposed have been almost entirely ecological. While the ecology of invasion is important, by definition invasion is also a geographical process. To invade, an alien species must disperse from its homeland to some new territory, and then spread spatially across that

territory (Blumler, 1995; 2002; 2003a; 2005). Forcella and Wood (1984; Forcella et al., 1986) proposed a geographical rule, that invasion success correlates with the size of a species' native distribution. They offered the geographical explanation that species with broader distributions are more likely to be transported overseas, because their distributions will intersect with a greater number of trade routes. Studies of several weedy genera support the generality of this rule (Roy et al., 1991). But some ecologists doubt Forcella and Wood's explanation, arguing that the enormous increase in trade and traffic volume in recent times ensures that all species have already been transported to essentially everywhere (Jackson, 1985; Noble, 1989; Roy et al., 1991).

Roy et al. (1991) studied the annual species of the weedy grass genus *Bromus* (the annual brome grasses), and found that species with broader native distributions were more likely to successfully invade overseas regions of mediterranean-type climate (California, central Chile, Cape region of South Africa, and southern Australia) than congeners with smaller native ranges. For instance, *B. hordaceus* and *B. japonicus*, which occur in temperate Eurasia as well as parts of the Mediterranean region, have each successfully invaded three of the four overseas regions. In contrast, *B. lanceolatus* and *B. fasciculatus* are almost completely restricted to the

Mediterranean; *lanceolatus* has invaded only Australia, while *fasciculatus* has not invaded overseas. Roy et al. (1991:221) offered an ecological explanation:

We suggest that the same biological traits that enable some species to spread across their native continents also enable them to invade new continents...it is the species which spread across climate barriers in their native continents which invade other continents. Plasticity, ecotypic differentiation, as well as an appropriate phenology, are among the traits allowing a species to occupy different climates.

Thus, both a geographical and an ecological explanation have been offered to explain the pattern that Forcella and Wood (1984) first documented. In this paper, the data on the annual bromes are re-examined, to test whether the ecological or geographical explanation is more likely.

continuing to invade, often at an ever-increasing rate (Cohen and Carlton, 1998; Ruiz and Carlton, 2003). On the other hand, if the pattern of annual brome invasion of alien regions is due to transport, than it should correlate with the number of routes and source regions, trade volume, the frequency of intentional introductions, and perhaps with the area of suitable environment in the receiving region. Also, under the geographical explanation, the species introduced will reflect trade routes, that is, will tend to be native to the regions whence trade originated. In contrast, if Roy et al. (1991) are correct, there should be no correlation between the species introduced and the species native near the origination points for early trade with the overseas Mediterranean-climate regions. Careful attention to the routes and to nativity in the source regions might therefore be able to discriminate between these competing explanations.

TESTING THE HYPOTHESIS

Although Roy et al. (1991) argued for an ecological rather than a geographical explanation, they did not actually test their hypothesis. Rather, they simply dismissed the geographical hypothesis on the above-mentioned grounds, that all species must already have been transported almost everywhere – without offering any supporting empirical evidence for this claim. One can discriminate between the two competing hypotheses, since they lead to different predictions (Table 1). Roy et al.’s (1991) argument asserts in effect that alien species have achieved equilibrium or near equilibrium with overseas environments, hence transport is no longer relevant. If Roy et al. (1991) are correct, the current pattern of invasion will remain as it is, unless environmental conditions change. Clearly, this seems dubious given that most authorities report that species are

THE ANNUAL BROMES

Native annual bromes are found on every continent except Antarctica, but most are indigenous to the Mediterranean region, adjacent Middle East, and to a lesser extent, temperate Europe (Smith, 1986; Roy et al., 1991). These Old World species have invaded overseas regions with mediterranean-type climate. Roy et al. (1991) examined floras to determine which species had invaded which mediterranean-type region(s). I have adopted their data, with some revisions.

In some cases, these floras misidentified species because of the problem of unfamiliarity with the taxonomy of alien species, or because lumping or splitting of taxa has confused matters. Specifically, “*Bromus rigidus*” of several floras may be *B. diandrus*, as has been demonstrated for California

Table 1. Predictions of the Ecological and Geographical Explanations for the Overseas Success of Species with Large Native Range

Explanation	Prediction(s)
Ecological	No future change in the introduced species present, unless there are environmental changes (e.g., global warming) No correlation of introduced species with those native to the source region(s) of early trade routes
Geographical	Correlation of number of introduced species present with: a) number of different early trade routes b) frequency of intentional introductions c) trade volume (particularly of unprocessed agricultural products) d) size of region receiving introductions? Introduced species will mostly be native to source region(s) of early trade routes

(Munz and Keck, 1973; Hickman, 1993; Blumler, unpublished data). Both *rigidus* and *diandrus* are definitely present in Australia (Kleemann and Gill, 2006), but the similarity in the two species leaves considerable doubt whether both are also present in South Africa and Chile. Also, the *B. hordaceus* complex is today generally treated as a single species, but was split into several variants, themselves sometimes misidentified, in some of the floras that Roy et al. (1991) consulted. Wilken and Painter, who treated *Bromus* for Hickman (1993), concluded that the variants of *B. hordaceus* formerly known as *B. racemosus* and *B. scoparius* are not in California, contrary to the conclusions of Munz and Keck (1973). But their knowledge of California was comparatively limited at the time they worked up the genus for Hickman. It is likely that Munz and Keck were correct, but that appropriate specimens of these relatively uncommon taxa were not available to Wilken and Painter. *B. racemosus* is certainly present in California (Blumler, 1992a). Finally, *B. commutatus* is now subsumed under *B. japonicus*, and *B. rubens* is treated as *B. madritensis* ssp. *rubens*. Where different morphotypes formerly classified as separate species are now lumped as a single entity, they are treated as different taxa for purposes of this analysis. After all, each morphotype does represent a separate introduction. None of the questionable taxa are crucial to the analysis, as they tend to be so

broadly distributed that they could have dispersed by any of the early routes.

The annual bromes were characterized according to the region(s) to which they are native, largely following Tutin et al. (1980). The results are summarized below (see Table 2).

ROUTES AND SOURCE REGIONS

At least during the initial phases of European colonization and settlement of the mediterranean climate regions, trade and transport routes were relatively limited. They are shown in Figure 1. For instance, there were three main routes by which Mediterranean species could reach California, up to at least the period of the Gold Rush (Blumler, 1995; 2001; and unpublished). The earliest was from Spain by way of the Mexican highlands. (During the period of Spanish rule, no ships sailed all the way from Spain to California, except for those of the Malaspina scientific expedition.) Since this route required establishment in the Mexican highlands prior to dispersal on to California, few if any Mediterranean endemics could come this way. The second route was from Spain via Chile. Central Chile, including its major port of Valparaiso, has a mediterranean-type climate, and Chilean agricultural

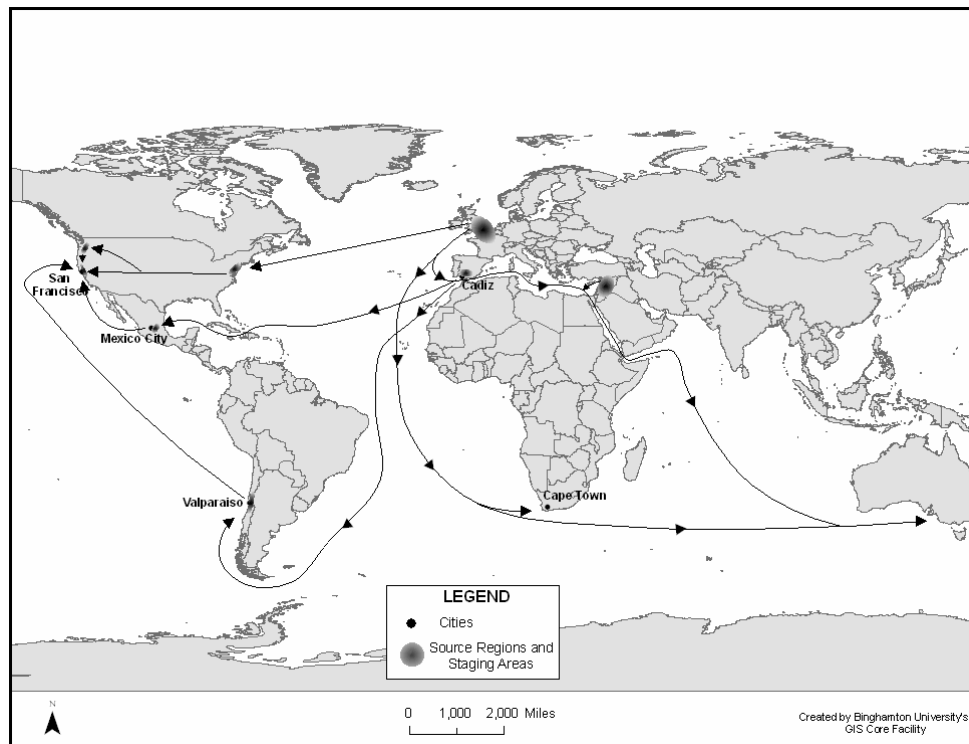


Figure 1. Early trade routes from European colonial powers to their colonies with Mediterranean-type climate.

goods, livestock, and miners all were shipped to California in large quantities during the Gold Rush era. On the other hand, return trade tended to involve processed goods that were much less likely to disperse alien species, and in any case there were few alien species in California at the time. Thus, Spanish species established in Chile might have gone on to California. The third main route was from northwestern Europe to the eastern US, and then either overland or by ship to the Pacific Coast. *Bromus* spp. native to or naturalized in northwestern Europe could have reached California along this trajectory.

The picture for Chile and South Africa is simpler. Both were supplied mainly by their colonial rulers, Spain for Chile, and England and Holland for South Africa. Australia also had strong trade relations with its colonizer during the nineteenth century, and at least at times British ships would have stopped at Capetown en route. With the opening of the Suez Canal, British shipping often would have taken a Mediterranean route, increasing the possibility that Mediterranean species, not necessarily Spanish, would have reached Australia. Perhaps more important, Australia's unusually poor soils led to an early and massive intentional importation of Mediterranean species for pasture improvement. Probably the best known of these species in southern Australia today is subclover (*Trifolium subterraneum*), a species particularly

abundant in the eastern part of the Mediterranean region. It is well known that many weedy species were unintentionally introduced when species such as subclover were brought to Australia and tried out. One might predict then, that southern Australia would have received a greater percentage of eastern Mediterranean species than the other three overseas Mediterranean-type regions, while Chile would be expected to have received only western Mediterranean species, at least in early times.

RESULTS

Table 2 lists the *Bromus* taxa introduced into each region, as well as the region of nativity. All species introduced into Chile are common in Spain. All South African species are common in Europe, with the possible exception of *B. rigidus*. Even the latter occurs along the Atlantic coast of Europe as far as Holland, so it could have reached South Africa from Europe. But it seems more likely, if it really is present, that it dispersed to South Africa from Australia.

All species introduced into Chile are also present in California, with the possible exception of *B. scoparius*, and also *B. rigidus* if indeed that species actually is in Chile. In addition, California

Table 2. Alien Annual Bromes, by Region, with their Source Regions

Species	Source	Regions to which Introduced				
<i>B. diandrus</i>	EU-Med	Chile?	CA	S Afr	AU	
<i>B. hordaceus</i>	EU-Med	Chile	CA	S Afr	AU	
<i>B. madritensis</i>	EU-Med	Chile	CA	S Afr	AU	
<i>B. scoparius</i>	Med	Chile	CA?			
<i>B. sterilis</i>	EU-Med	Chile	CA		AU	
<i>B. rigidus</i>	Med-ish	Chile?		S Afr?	AU	
<i>B. trinii</i>	Chile		CA			
<i>B. commutatus</i>	EU-ish		CA	S Afr	AU	
<i>B. japonicus</i>	EU		CA	S Afr	AU	
<i>B. tectorum</i>	EU-Med		CA	S Afr	AU	
<i>B. arvensis</i>	EU-Med		CA			
<i>B. briziformis</i>	EU		CA			
<i>B. secalinus</i>	EU-ish		CA			
<i>B. racemosus</i>	EU-Med		CA			
<i>B. arenarius</i>	AU		CA			
<i>B. carinatus</i>	CA				AU	
<i>B. alopecuroides</i>	e. Med		CA		AU	
<i>B. madritensis</i> <i>ssp. rubens</i>	Med		CA		AU	
<i>B. lanceolatus</i>	Med				AU	

EU = European, not Mediterranean; EU-Med = European and Mediterranean; EU-ish = more European than Mediterranean (either more abundant in Europe, or with a distribution that spills over only slightly into the Mediterranean); Med = Mediterranean; Med-ish = more Mediterranean than European (either more abundant in the Mediterranean, or with a distribution that spills over only slightly into non-Mediterranean Europe); AU = Australian; CA = Californian

Sources: Munz and Keck, 1973; Tutin et al., 1980; Roy et al., 1991; Hickman, 1993; Kleemann and Gill, 2006.

has the native Chilean annual, *B. trinii*, and *B. arizonicus*, which is a polyploid derivative of a cross between *B. trinii* and the California native, *B. carinatus*. California has all species that are in South Africa, except again for the doubtful case of *B. rigidus*. California has four additional European or European-Mediterranean species that are likely to have come by a European route, not from Spain. One of these, *B. briziformis* (rattlesnake chess), was introduced intentionally through the ornamental seed trade (Mack, 1991). Finally, California has the only native Australian *Bromus*, and two Mediterranean species, not found in Spain, that may have come to California via Australia. The European-Mediterranean species *B. racemosus* also could have reached California from Australia.

Australia has all species that are found in South Africa, plus two species that are European-Mediterranean in distribution, a California native, and three Mediterranean taxa (*alopecuros*, *lanceolatus*, and *madritensis* ssp. *rubens*), that are rare or absent in Spain.

DISCUSSION

The evidence presented here demonstrates clearly the major role of early dispersal routes in determining the number of annual bromes successfully introduced to the different mediterranean climate regions. With the exception of some evidence for a California-Australia connection, the species present in each region reflect faithfully the source regions that were identified in Table 2. Since Australians participated in the Gold Rush, and the country continued to trade with California subsequently, it is probably not terribly surprising that there may have been additional *Bromus* introductions to California by this route, and at least one return introduction to Australia.

It seems likely that there are additional factors. The British, and later their American descendents, were much more active in intentionally introducing species to their colonies than were the Spanish. This reflected in part Britain's ornamental gardening tradition, in contrast to the need in semi-arid southern Spain to landscape with relatively few, drought tolerant species. It also reflected Britain's much greater involvement in and adherence to the values of the Enlightenment. For instance, while British and American governments sponsored legions of scientific exploring expeditions, the Spanish sponsored only the Malaspina expedition. Only in recent decades, under the influence of globalization and development theory, has Chile begun to

intentionally introduce large numbers of foreign plant species; in contrast, California began doing so as soon as it became a part of the US, as any perusal of mid-nineteenth century state agricultural journals will attest. Most of these were crops initially, and pasture and fodder species began to be introduced somewhat later. As discussed above, Australia was even more active in introducing such species than was California.

Roy et al. (1991) noted, with some surprise, the unusually low number of bromes established in Chile, despite its very early colonization (1540) compared to the other mediterranean regions (18th-19th centuries). But the present analysis can explain this result as due to the single major dispersal route in colonial times, as well as because of the comparative lack of intentional introduction of European or Mediterranean plants. Roy et al. (1991) performed factorial correspondence analysis on presence or absence of *Bromus* spp. in the different regions, including the Mediterranean itself, expecting to find a grouping of South Africa with Australia, and of Chile, California, and the Mediterranean. Ecologists generally separate the mediterranean regions in this manner because of the Gondwanan origins and poor soils in South Africa and Australia, in contrast to the comparative fertility of the other three regions. But the factorial correspondence analysis did not so group them. South Africa was reasonably close to Australia, but the latter was also close to the Mediterranean (South Africa was not). California was close to Chile, but neither were close to the Mediterranean. This probably reflects that Australia received taxa from the eastern Mediterranean that had no way of reaching the other regions, except for those that went on from Australia to California. Roy et al.'s (1991) own analysis, then, provides evidence against their ecological explanation and for the importance of dispersal routes.

Today, it is possible to track introductions not only of species but even of genotypes using DNA evidence. A relevant example is Novak and Mack's (2001) research on cheatgrass (*Bromus tectorum*). Cheatgrass has massively invaded the Intermountain West, and is widespread and frequently abundant also in California. Novak and Mack sampled populations from its native range, which includes the Mediterranean, Europe, and especially, the Middle East and adjacent central Asia. The Middle East/central Asia are ecologically most similar to that portion of the western US where cheatgrass is most dominant today. To their surprise, Novak and Mack found that no Middle Eastern/central Asian genotypes had been introduced abroad. Instead, the main spread of the species in the western US was of European genotypes. In addition to these genotypes,

a genotype is present in California that is from Spain or thereabouts, and that was also the only genotype Novak and Mack found in Chile. Thus, in this species there is evidence for a Spain-Chile-California route, as well as a route from Europe to California and the rest of the western US, but not to Chile. But Middle Eastern/central Asian genotypes, which one suspects may be best adapted to the Intermountain West, have never dispersed there.

CONCLUSIONS

Although trade and transport are undeniably becoming increasingly globalized, the pattern of *Bromus* invasion into the Mediterranean analogue regions reflects the much more limited trade routes and bottlenecks of their early colonial history. This rather surprising result suggests several possibilities. One is what I have called the "first spreads most" hypothesis (Blumler, 1995). Aliens that are introduced early to a region, if adapted, may spread over the entire territory relatively readily. But as the number of alien invasive species increases, they themselves block the progress of subsequent invaders. If so, new brome invaders may be reaching the mediterranean regions under the impact of globalization, but spreading so slowly that they have not yet come to the attention of taxonomists.

It is also likely that increasing urbanization/suburbanization of ports of entry, and shifting of traffic from ships to airplanes, are altering the possibilities for successful introduction, in complicated ways. Since trade routes are proliferating, analysis becomes increasingly difficult as one considers more recent time periods. On the other hand, with DNA evidence it becomes increasingly possible to pinpoint sources and routes of introduction, as Novak and Mack (2001) have done for cheatgrass. There is a need to do so for a representative sample of recent invaders, to determine whether trade routes are as overwhelmingly important today as they have been in the past.

On present evidence, at any rate, it appears that trade routes remain crucial determinants of overseas introduction (though at some time in the future this may cease to be so). But without introduction, successful invasion is not possible. Consequently, analysis of invasion and invasion success must focus on sources and routes, not simply on generalized distribution patterns as Roy et al. (1991) did. That is, analysis must reflect geographical considerations, without the assumption of equilibrium which is so dear to the hearts of

ecologists because it is so much easier to generate scientific laws about equilibrium processes than non-equilibrium ones. Another implication of the analysis reported here is that invasion rules, to the extent that they can be formulated at all, must for the time being rest at least as much upon geographical as on ecological considerations.

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