

*Research review*

# The Neolithic Plant Invasion Hypothesis: the role of preadaptation and disturbance in grassland invasion

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## Summary

A long-standing hypothesis is that many European plants invade temperate grasslands globally because they are introduced simultaneously with pastoralism and cultivation, to which they are 'preadapted' after millennia of exposure dating to the Neolithic era ('Neolithic Plant Invasion Hypothesis' (NPIH)). These 'preadaptations' are predicted to maximize their performance relative to native species lacking this adaptive history. Here, we discuss the explanatory relevance of the NPIH, clarifying the importance of evolutionary context vs other mechanisms driving invasion. The NPIH makes intuitive sense given established connections between invasion and agricultural-based perturbation. However, tests are often incomplete given the need for performance contrasts between home and away ranges, while controlling for other mechanisms. We emphasize six NPIH-based predictions, centring on trait similarity of invaders between home vs away populations, and differing perturbation responses by invading and native plants. Although no research has integrated all six predictions, we highlight studies suggesting preadaptation influences on invasion. Given that many European grasslands are creations of human activity from the past, current invasions by these flora may represent the continuation of processes dating to the Neolithic. Ironically, European Neolithic-derived grasslands are becoming rarer, reflecting changes in management and illustrating the importance of human influences on these species.

'...as western and northern Europe became agricultural and pastoral, these plants came with the husbandmen and the flocks, or followed them, from the woodless or sparsely wooded regions farther east where they originated.'

Gray (1879)

'...without these plants, what would have – what could have – replaced the native species disappearing under the hooves of the exotic herds?'

Crosby (1986)

## Introduction

The success of grassland plant species from Europe in invading temperate grasslands around the world is well-known (La Sorte & Pysek, 2009; Firn *et al.*, 2011; Kalusová *et al.*, 2017). Like all invasions, the challenge is to understand what factors contribute to their success. There are a number of possible invasion pathways that undoubtedly interact (Fig. 1), relating to trait differences, propagule pressure, the influence of human perturbation, and whether perturbations complement the traits of the invaders, weaken biotic

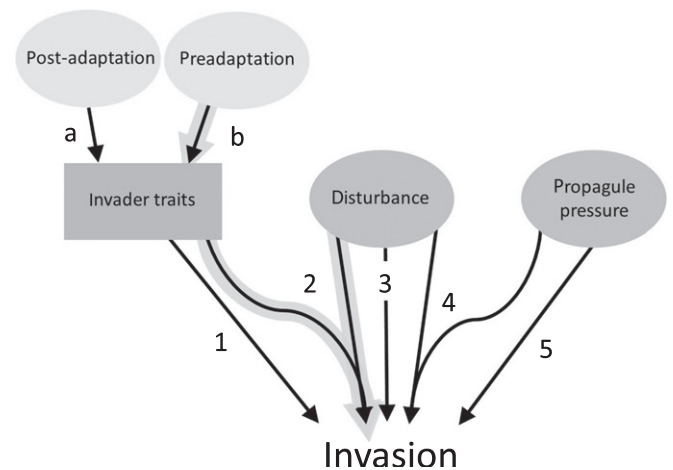
resistance by the native community, or both (Sax & Brown, 2000; Hierro *et al.*, 2005; Fridley *et al.*, 2007; Fridley, 2008; Rout & Callaway, 2009; Ellis *et al.*, 2010; Davis *et al.*, 2011; MacDougall *et al.*, 2014). The multivariate nature of invasions, reflecting one or combinations of these various factors (Fig. 1), is consistent with the diverse array of hypotheses proposed to explain why and how species invasions have become one of the more transformative processes in biological systems globally (Rejmanek & Richardson, 1996; Blumenthal, 2005; Sax *et al.*, 2005; Fridley *et al.*, 2007; Catford *et al.*, 2009; Gurevitch *et al.*, 2011; Visser *et al.*, 2016).

If trait differences between invaders and native species are a driver of invasion, a central question is how have these differences developed? The traits exhibited by successful invaders, relating to growth and fecundity in particular, could result from plasticity or rapid adaptation to being released from co-evolved herbivores or pathogens, or greater resource availability in the introduced range (Fig. 1a – Blair & Wolfe, 2004; Maron *et al.*, 2004; Blumenthal, 2005; Bock *et al.*, 2015; Flory *et al.*, 2011; Guo *et al.*, 2014). Alternatively, some introduced species could arrive with traits already adapted to the conditions of the new environment (Fig. 1b; Bock *et al.*, 2015; Fridley, 2013; Fridley & Sax, 2014; Mack, 2003). A species that has evolved in a particular set of environmental conditions, and is introduced to a new region with similar conditions, may possess adaptations superior to the resident native species, especially if adaptation by the natives has somehow been constrained by evolutionary history (i.e. phylogenetic constraint; Mack, 2003; Fridley & Sax, 2014). For example, native South American tree species can struggle to survive the moisture-limited conditions of the grasslands there, but introduced pines adapted to drought elsewhere have been able to invade (Mack, 2003). This phenomenon is often termed ‘preadaptation’ in the invasion literature, even though it does not exactly match the traditional evolutionary definition where a trait developed in one context results in fitness advantages in a new context (Bock, 1959). Although we use the term ‘preadaptation’ here, others have used ‘prior adaptation’ where adaptations to a set of environmental conditions in the home range allow an invader to succeed when faced with the same conditions in a new range (Hufbauer *et al.*, 2011).

The potential importance of preadaptation for invasion may be greatest for pastoral and cultivated grassland species of Europe – an idea that has long been suggested (e.g. Gray, 1879; di Castri, 1989; La Sorte & Pyšek, 2009). In the grasslands of central, western, and northern Europe (hereafter ‘Europe’), there may have been long-term intense selection pressure on plants via practices relating to grazing, cultivation and haying, possibly dating as far back as the Neolithic era *c.* 6000 yr BP (Childe, 1925; Prins, 1998; Cousins & Eriksson, 2002; Pyšek *et al.*, 2005; Pärtel *et al.*, 2007; La Sorte & Pyšek, 2009; Eriksson, 2013; Hejman *et al.*, 2013; Eriksson & Cousins, 2014). For example, many grassland plants in Europe have evolved adaptations to tolerate or avoid damage by repeated grazing or mowing (Grime, 2006). Large numbers of grass and forb species from these systems, with possible evolved affinities for human perturbations, have subsequently become naturalized or invasive in many temperate grasslands outside of Europe (Seastedt & Pyšek, 2011; Kalusová *et al.*, 2013, 2015, 2017). The success of these

species may be explained by the combined effects of long-term selection and their simultaneous introduction with European-based pastoralism and cultivation, a process we refer to as the ‘Neolithic Plant Invasion Hypothesis’ (NPIH). The NPIH is thus a particular case of preadaptation in which species have evolved traits adapted to environmental conditions created and maintained by human activities (Fig. 1). If true, the NPIH suggests that present-day invasion by these species represents an extension of processes initiated by humans in the distant past. Furthermore, it predicts that invasion derives mechanistically from the combination of trait advantages and agriculture-based (here defined as grazing, haying, cultivation and related practices) land use, rather than one or the other in isolation (La Sorte & Pyšek, 2009; Eriksson, 2013). It also posits that these two factors alone (preadaptation and introduction of pastoralism) are sufficient to enable invasion, with no requirement for post-introduction adaptation or high propagule pressure (Fig. 1).

The NPIH makes several direct or implicit assumptions about the trait- and disturbance-based mechanisms driving invasion by these species. Although these mechanisms may make intuitive sense, they have not always been systematically examined. In the present paper, we discuss the potential explanatory power of this hypothesis by highlighting six predictions that derive from the NPIH (Table 1). For example, one of the key challenges for demonstrating NPIH-based preadaptation is showing the correlations between trait differences and disturbance (Mack, 2003; Fridley, 2008; Parker *et al.*, 2013), given that one or the other could drive invasion in isolation (and thus not support the NPIH).



**Fig. 1** Potential pathways of invasion. Traits of the invader relative to the resident community can allow a competitive advantage and subsequent invasion in the absence of a novel disturbance (1), or can combine with a novel disturbance regime to which native species are poorly adapted (2). Alternatively, disturbance alone can facilitate invasion by killing natives and preventing biotic resistance (3), or can combine with increased propagule pressure of introduced species (4). Propagule pressure alone may also permit invasion in some cases (5). Trait advantages for invaders can arise from rapid adaptation post-introduction (a), or can be preadapted due to a long evolutionary history in similar environmental conditions (b). The Neolithic Plant Invasion Hypothesis (NPIH) is a potential mechanism for grassland invasion whereby European species preadapted to grassland management successfully invade temperate grasslands outside of Europe subjected to the same type of management (grey highlighted path). It is important to note that post-adaptation and preadaptation can also combine to shape invader traits.

Indeed, the strong predicted linkage with disturbance raises questions of whether the global spread of Neolithic invaders actually constitutes ‘invasion’, given that these species may have trouble establishing and spreading without human assistance. We do not provide an extensive review of temperate grassland invasion as this topic has been examined numerous times (e.g. Seabloom *et al.*, 2015); instead we highlight studies that have tested some of the NPIH-derived predictions. Our aim is to help clarify how trait differences, evolutionary context both present and past, and human-based perturbations (defined as disruptions to natural disturbance regimes) may combine to influence the invasion process in contemporary anthropogenic landscapes (Thebault *et al.*, 2014).

## Background factors of the NPIH

There are several interacting factors that may explain why some European grassland species are likely to possess preadaptive

advantages to agricultural management. Foremost, the grasslands of many areas of Europe themselves were a creation of human management, replacing forests and woodlands of varying stand densities that covered the region in the early to mid-Holocene (Eriksson, 2013; Noble, 2017). Agriculture, in the form of both pastoralism and crop production, spread in several waves from the east, reaching western and northern Europe *c.* 5500–800 BCE depending on location (Eriksson & Cousins, 2014). Overall, these herbaceous systems – occurring as managed heathlands, grasslands and patchy woodland – have persisted in many parts of Europe for several millennia (Eriksson *et al.*, 2002; Eriksson & Cousins, 2014).

Second, a sizeable portion of plants found in these constructed grasslands are not ‘native’ to Europe, with ancestral ranges to the east (e.g. Asia Minor). Some of these species arrived several thousand years ago (i.e. European archaeophytes); others possibly within the past several centuries (i.e. neophytes) (Pavord, 2005; La Sorte & Pyšek, 2009; Pyšek *et al.*, 2012). All share long-term

**Table 1** The Neolithic Invasion Hypothesis (NPIH) predicts that invasion of temperate grasslands by introduced European species derives mechanistically from the combination of preadapted trait advantages and agriculture-based land use, with no requirement for increased propagule pressure or post-introduction adaptation

Prediction	Required tests	Key points	Example references
1. European invader plant genotypes from native and invasive range perform similarly	Common garden trials with seed sources from both ranges	Rule out post-introduction adaptation	Blair & Wolfe (2004); Flory <i>et al.</i> (2011); Guo <i>et al.</i> (2014); Kinter & Mack (2004); Leifso <i>et al.</i> (2012); Maron <i>et al.</i> (2004); Williams <i>et al.</i> (2008)
2. European invaders reach higher abundances in ‘away’ range compared to ‘home’ range (where both under pastoral management)	Field observations/experiments in native and introduced range*	When competing with a community of natives not adapted to grassland management, European invaders should be more successful than when competing with a suite of fellow European species	Beckmann <i>et al.</i> (2014); Finn <i>et al.</i> (2011); Moroney & Rundel (2013); Seabloom <i>et al.</i> (2015)
3. European invaders respond more positively than native species to pastoral management (grazing, trampling, mowing)	Field or glasshouse trials with and without simulated disturbance*	NPIH requires European-style pastoral environment	Callaway <i>et al.</i> (2011a); Hierro <i>et al.</i> (2006); Seabloom <i>et al.</i> (2015)
4. European invaders require pastoral grassland management to invade (or reverse: native grassland species can outcompete European invaders in the absence of pastoral management)	Manipulative field experiments*	NPIH requires European-style pastoral environment	Corbin & D’Antonio (2004); Faithful <i>et al.</i> (2010); Harnden <i>et al.</i> (2011)
5. European invaders are better at colonizing pastorally-managed grasslands than natives, even when natives are not seed-limited	Field experiments simulating colonization process with equal amounts of seed*	Rule out role of seed limitation of natives/high propagule pressure of non-native (NPIH requires superior adaptation of invaders, not just more seeds than natives)	Seabloom <i>et al.</i> (2003)
6. Temperate grasslands outside of Europe should be more invaded by European species than European grasslands are by species not native to Europe	Biogeographical studies that study global invasion patterns by habitat type	NPIH posits that grassland species from outside Europe are poorly adapted to European grassland disturbance regimes	Kalusová <i>et al.</i> (2015)

Here we present six key predictions, required experimental tests and examples of studies that have investigated aspects of the NPIH for explaining the success of European grassland plant species abroad.

\*Experiments should include European seed sources (i.e. genotypes) to control for post-introduction adaptation (see 1).

associations with humans, and many are known only from anthropogenic habitats in Europe (La Sorte & Pysek, 2009).

Third, the creation and maintenance of open managed habitats are presumed to have acted as a selection filter on traits maintaining persistence in these habitats (Eriksson, 2013). Preadaptation may have played a role here too, as the 'European archaeophytes' arriving from grasslands to the east already may have experienced long-term exposure to pastoralism or cultivation. The selectively favoured traits appear to represent the spectrum of life history strategies associated with plant invasions more broadly (Baker, 1965), including high fecundity, rapid uptake of resource pulses, tolerance or avoidance of perturbation via clonality or seed banks, and plasticity in response to environmental changes associated with agriculture such as higher soil nutrients, increased availability of light, and repeated removal of leaf tissue and biomass via grazing or haying (Fenesi *et al.*, 2011; Eriksson, 2013). These species include both perennial pasture grasses and forbs ubiquitous to the world's temperate grasslands and associated with domesticated herbivores (e.g. *Anthoxanthum odoratum*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Ranunculus repens*, *Plantago lanceolata*), and annual species associated with cultivated habitats (e.g. *Bromus tectorum* and *B. sterilis*; see Fenesi *et al.*, 2011; Leifso *et al.*, 2012; Hejda *et al.*, 2015). Much of our discussion focuses on the former group, although Neolithic-based land management involved both pastoralism and cultivation of crops.

Fourth, starting as early as the 1600s, these European grassland species were introduced globally in association with European colonization (Crosby, 1986). By the late 19<sup>th</sup> and early 20<sup>th</sup> centuries, planted pastures covered large areas of the planet's temperate regions. For example, in New Zealand ~25% of the country's area supported European pasture species by the early 1900s (Cook & Dias, 2006). The history of these introductions varied regionally. Settlers typically brought seed, to facilitate immediate forage production for domestic livestock (e.g., MacDougall *et al.*, 2004). In some regions, pasture species were introduced because native grasses lacked nutritional value or regenerative capabilities with intensive grazing (Leifso *et al.*, 2012). Local breeding programs for agronomic grasses often were started as early as the 19<sup>th</sup> century, with agricultural research stations producing varieties including hybrids best suited to local conditions (Cook & Dias, 2006; Leifso *et al.*, 2012). These introduction programmes in New Zealand and Australia, for example, were organized systematically by 'acclimatization societies', which included global scale plant exchange programs covering the trade routes of European empires (Cook & Dias, 2006). Australian acclimatization societies were more focused on increasing agricultural production for the prosperity of the British Empire than on promoting British species, providing further evidence of the simultaneous introduction of agricultural practices with the introduction of species (Low, 1997; Cook & Dias, 2006). An important caveat, certainly for many regions of North and South America, is to recognize that long-term plant cultivation existed in Native American societies before European colonization (e.g. corns, beans, squash, tobacco, potato –Anderson, 2005; Nabhan, 2016). The NPIH thus rests not on agricultural land use *per se*, but the specific combination of domesticated grazers, plants and management styles introduced simultaneously by Europeans following colonization. This

triumvirate of introductions was repeated in every major temperate grassland region of the planet outside of Europe.

Given that the global spread of these species was facilitated by human intervention, one may again question whether they are truly 'invasive' in the typical usage of the term (MacDougall & Turkington, 2005). It is unresolved, for example, whether some or most of these species would have been able to establish so successfully without the repeated introduction of large amounts of seed in tandem with the colonial-based spread of pastoralism and cultivation. The weakening of biotic resistance by factors such as overgrazing, 'sod-busting' and high propagule pressure could influence establishment without the necessity of substantial trait differences between invaders and the native species they often replaced (England & Devos, 1969). This reiterates the necessity of testing for preadaptation by species associated with human land use.

## Six testable predictions of the NPIH

A number of studies have explored aspects of agricultural preadaptation in invasion of temperate grasslands, although not always untangling the potential influences of traits and human perturbation on success, or how these factors contribute to fitness differences between invading and resident species (Hufbauer *et al.*, 2011). To that end, the NPIH leads to several testable and highly interactive predictions (Table 1). These predictions are largely centred on two factors: that invaders show limited evolved changes between their ancestral habitats and the invaded ranges, and that invaders possess traits associated with tolerating or avoiding the impacts of agriculture-based perturbation that are absent in 'naïve' native flora. This combination is thought to lead to dominance of the invaders in their new ranges even though, interestingly, these species can sometimes be co-dominant or infrequent in their native community, as will be discussed below.

### 1. Individuals of a species from home and away ranges should perform similarly

The NPIH is based on the idea that introduced European species are preadapted to grassland management. Therefore, they already have the traits needed to succeed in their introduced range before introduction. If the NPIH is the mechanism of invasion, then under similar environmental conditions between home and away ranges (e.g. grazed, cultivated, fertilized) there should be limited differences in performance of invader plant genotypes (Table 1; see also Firn *et al.*, 2011; Seabloom *et al.*, 2015). That is, they should have similar germination rates, growth rates, fecundity, resource uptake efficiency, seed bank potential and plasticity in response to pastoralism or cultivation. If genotypes from the invaded away range differ from native home genotypes in some or all of these traits, post-introduction evolution may have occurred via factors such as evolving increased competitive ability and the hybridization of once distant populations (e.g., Blossey & Notzold, 1995; Ellstrand & Schierenbeck, 2000).

In order to test this prediction of trait similarity and performance, Thebauld & Simberloff (2001), compared height differences among 321 herbaceous species native to Europe and introduced to



California. They found no overall significant differences in maximum height of plants growing in the two regions, contrary to what might be expected if invaders were consistently allocating more resources towards growth in away areas. Several studies have more explicitly tested this with common garden trials. Leifso *et al.* (2012) observed an absence of trait differences in *Dactylis glomerata*, a widespread temperate grass invader native to Europe. Individuals from Europe, North America and South America generally grew similarly in a common environment, whereas New Zealand plants were significantly smaller – the opposite to expectations of *in situ* trait development associated with mechanisms such as enemy release (e.g. Blair & Wolfe, 2004). A similar result was found for the annual grass *Bromus tectorum* from New Zealand populations (Kinter & Mack, 2004) – *B. tectorum* is considered a ‘neolithic’ species originating from eastern Europe and associated with heavily disturbed habitats (Colledge & Conolly, 2007). Other common garden studies have found equivocal results on home vs away performance differences. In a study that used multiple common gardens in both home and away ranges in order to rule out genotype-by-environment interactions, Maron *et al.* (2004) detected higher fecundity of introduced populations of *Hypericum perforatum*, but only in one of their common gardens (Washington State). Similarly, Williams *et al.* (2008) found that *Cynoglossum officinale* plants from the introduced range in North America were larger and had higher fecundity than native plants, but only in one common garden (Germany).

Even if genetic differences between home and away populations are sometimes detected by common garden trials, it can be difficult to determine whether these are a result of post-introduction adaptation or founder effects (Ordóñez *et al.*, 2010). For example, Kinter & Mack (2004) suggest that the limited performance of *B. tectorum* populations from New Zealand (where the plant is naturalized but not invasive) could result from random founder effects where the initially introduced plants happened to be significantly smaller, slower growing or less fecund than is typical for European home populations (e.g. Fenesi *et al.*, 2011). Common garden trials performed in concert with genetic analyses are ultimately needed to sort this out (e.g. Maron *et al.*, 2004). In some cases, preadaptation and rapid post-introduction adaptation can significantly interact to drive invasion (Jenkins & Keller, 2011; Guo *et al.*, 2014), highlighting that the various hypotheses on plant invasion in grasslands (e.g. NPIH, enemy-escape, novel weapons) are not necessarily mutually exclusive and likely interact (Harrison *et al.*, 2015). Overall, support for this prediction is mixed, with some evidence for similar performance in home and away ranges for some species, but not others (Firn *et al.*, 2011). Common garden trials that combine more than one source genotype in more than one environment are rare, with such studies needed to determine how widespread is preadaptation among invasive grassland plants from Europe.

## 2. European invaders should reach higher abundances in their introduced ranges compared to their native ranges, in the presence of pastoral management

Although the *per capita* responses of individual plants to similar environmental conditions should not widely differ (Prediction 1;

Table 1), the community-level implications of these traits, as expressed through the outcome of species interactions, are predicted to be substantially different in home vs away grasslands. Specifically, the preadapted traits are predicted to create competitive advantages against native flora that do not occur in ancestral home ranges where most species should be similarly adapted to pastoralism. Testing this prediction requires field observations and experiments in both native and introduced ranges.

Firn *et al.* (2011) tested for differences in the relative abundance of 26 European grassland species in grasslands of Europe (‘home’) and grasslands of North America, New Zealand, and Australia (‘away’), with most classified as invasive ‘weeds’ in away areas. Interestingly, the results did not conform to the prediction of the NPIH: abundance patterns were largely similar between home and away areas. The authors noted, however, that many of the away grasslands contained diverse collections of European grassland species, all introduced in similar fashion, such that these species were often interacting with the same species both home and away. Other studies have observed outcomes that do conform to the NPIH prediction. A more recent study confirmed the findings of Firn *et al.*, 2011 that plant species local abundance at native sites measured both as cover and occurrence can predict plant species abundance at introduced sites, and attributed these results to intrinsic species attributes (Pearson *et al.*, 2017), but with the caveat that the four species considered to be invasive were more abundant at introduced sites. Beckmann *et al.* (2014) found consistently higher plant densities in populations of invaders in the invaded range in New Zealand than in their native European range. Moroney & Rundel (2013) found *Centaurea melitensis* populations to be consistently more dense and more dominant in introduced communities than in their native range, and pointed out that the ability to detect these differences could vary with spatial scale. A meta-analysis including 27 of the world’s worst invasive plant species including European species found little evidence for a difference in cover at home and away sites, but did find evidence of increased fecundity and increased height at away sites (Parker *et al.*, 2013).

Although there are many well-known examples of species that are dominant in their introduced range, but co-dominant or even rare at home (e.g. Grigulis *et al.*, 2001; Kinter & Mack, 2004; Hierro *et al.*, 2006), there are still surprisingly few quantitative tests of this pattern (Hierro *et al.*, 2005). One exception is Fenesi *et al.* (2011), who used garden trials in central Europe to quantify trait differences among three species of annual brome grasses, of which two were considered ‘archaeophytes’ and include one of the most successful invasive grasses on the planet (*B. tectorum*). Although Fenesi *et al.* were able to detect the trait differences in these European populations responsible for invasion (e.g. plasticity and rapid responsiveness to nutrient inputs), they noted that each species was relatively low in abundance at home sites. Indeed, this seems to be a common observation in European grasslands (contrary to the Firn *et al.*, 2011, finding), where species that are pernicious invaders elsewhere readily coexist with large numbers of species at home (Eriksson, 2013). Possible explanations include the idea that all member species of these European grasslands possess traits for tolerating or avoiding the limiting impacts of perturbation and interspecific competition (e.g. Callaway & Aschehoug, 2000).

There seems to be more support for this prediction than for Prediction 1. However, few of these studies controlled for invader genotype, and therefore they do not rule out post-introduction adaptation. More studies that experimentally test the abundance of invaders in home vs away community contexts while controlling for genotype are needed to determine how often and for which species this prediction holds true.

### 3. European invaders should respond more positively than native species to pastoral management

If native grassland species outside Europe are in fact poorly adapted to European-style grassland management, then European invaders should respond more positively than natives to such disturbances. Seabloom *et al.* (2015) tested this prediction by examining the perturbation responses (nutrients, herbivore exclusion) of 193 non-native vs 1305 native grassland species in 64 temperate grasslands on five continents. They found that nutrient additions in particular significantly increased non-native cover compared to native cover, and reduced native richness whereas non-native richness was unchanged; although not all of the grassland invaders included in this study were from Europe. Given that grassland species generally tend to be nutrient-limited to varying degrees globally (Fay *et al.*, 2015), it seems unlikely that native plants would be unresponsive to nutrient additions. Instead, it is more likely that the non-native species responded more rapidly, in turn suppressing native flora. This can happen if competition shifts to other limiting resources such as moisture, light or other nutrients (phosphorus, potassium) (Harpole *et al.*, 2016, 2017). This possibility seems to be supported by a comparison of nutrient responses of 14 congeneric invasive and noninvasive European grassland species (Schlaepfer *et al.*, 2010); the invasive species responded to enrichment by producing more biomass and flowers.

There are few comparative tests of the competitive ability of invaders against neighbouring species in home ranges vs away ranges. Ni *et al.* (2010) showed that the presence of invasive Russian knapweed (*Acroptilon repens*) suppressed the biomass of North American competitors more than European competitors. However, seed sources were all from introduced populations, so post-introduction evolution of competitive ability could not be ruled out. In addition, disturbance was not manipulated. A further study with Russian knapweed found that native species in the introduced range actually benefited from simulated disturbance (clipping plus soil turnover), whereas Russian knapweed had a greater positive response to disturbance in its native range (Callaway *et al.*, 2011a). However, the authors suggest that the minimal response of the invader to disturbance in the introduced range was due to the fact that it was already highly dominant there. In a study of the grassland invader *Centaurea solstitialis*, Hierro *et al.* (2006) compared the response to disturbance (clipping, fire and soil turnover) both in the native range in Turkey, and in introduced populations in Argentina and California. In the introduced range *C. solstitialis* showed a greater response in abundance to disturbance, which Hierro *et al.* suggest could be a result of escape from soil pathogens. However, they note that this difference also could be due to the lesser ability of the native community in the introduced range to handle

disturbance, particularly novel disturbances associated with European agricultural practices (e.g. D'Antonio *et al.*, 1999). In a recent study that builds on this previous research on *C. solstitialis* in Turkey, Argentina and the USA, Hierro *et al.* (2017) found that the speed of recovery of plant communities following disturbance was negatively correlated with the success of the focal invader. This is a possible explanation for why species native to the home range of a focal non-native species can compete with that species more successfully than species in the introduced range (e.g. Callaway *et al.*, 2011b).

Further studies of the responses to disturbance and competitive abilities of grassland invaders and the associated native species in the introduced and native ranges of the invader are needed in order to understand whether the greater dominance/density of non-native species in the introduced range is due to the inability of the native species to effectively compete under pastoral management regimes, as predicted by the NPIH.

### 4. European invaders require pastoral grassland management regime to invade

The NPIH hinges on a species displaying an adaptation to pastoral management coupled with the introduction of this management regime to new regions (Mack & Thompson, 1982). Therefore, the introduced European plant species should not easily establish and spread without a change in management (e.g. changes in grazer identity, or grazing intensity, frequency, or seasonality). Testing this prediction requires manipulative field experiments and/or observational studies across grasslands with different grazing/disturbance histories.

In a meta-analysis of 63 studies examining responses of over 100 non-native species, Parker *et al.* (2006) found that many grassland invaders are prevented from establishing, unless the identity of the grazers switches from native ungulates to domestic livestock. In support of the NPIH, this implies that a change to European-style ungulate grazers is necessary in order for European species to have competitive advantages over native species. Although this study only focuses on grazer identity, a conversion to domestic grazing likely also represents a significant change in the intensity of biomass removal – native ungulates tend to be migratory and seasonal grazers, whereas domestic species tend to be spatially constrained by fencing with more localized and intense impacts (e.g. McNaughton, 1986). Similarly, Corbin & D'Antonio (2004) found that European grasses did not invade native perennial grasslands of coastal California unless there was soil disturbance, even when propagule pressure was high.

The differing evolutionary histories of grasslands outside Europe could make them more or less susceptible to invasion via the NPIH process. For example, some studies have postulated that the grasslands of the Great Plains of North America are less invaded by European grassland species because they were subject to grazing by large herds of bison for much of the Holocene, and therefore the switch to domesticated livestock did not represent a significant change in grazing regimes (Oriens, 1986; Mack, 1989). By contrast, grazers were likely never abundant in California's central valley or the Intermountain West (Mack, 1989; MacDougall,

2008) or in Australia where the introduction of grazers has facilitated establishment of invasive grasses (Lunt *et al.*, 2007). Therefore, the process invoked by the NPIH likely does not apply to all temperate grasslands. We need more field experiments that manipulate disturbance, and test the ability of European grassland species to invade, while controlling for potential post-introduction adaptation.

##### 5. European invaders are better colonizers of managed grasslands than natives, even if natives are not seed limited

An alternative explanation for European grassland species dominating outside Europe is that severe disturbances at the initiation of European settlement in many parts of the world caused drastic reductions in native species cover (e.g. overgrazing, cultivation, fire). Following this, high propagule pressure of introduced European plant species, coupled with seed limitation of the (now very rare) natives, meant that native species could not recolonize even if they could persist with the new grassland management regime (Fig. 1, path 4). If this is the case, then European invaders succeeded more because of higher propagule pressure than by superior adaptation to grassland management, as predicted by the NPIH.

Testing this requires field experiments comparing the ability of natives and European plant species to colonize grasslands outside Europe given equal levels of seed availability but in consideration of germination success rates, and preferably in combination with different disturbance regimes. For example, Seabloom *et al.* (2003) manipulated disturbance, nutrient levels, and seed availability of native forbs in California grasslands. They found that mowing and burning did not affect native species richness or abundance, but that these native species were strongly seed-limited. A recent field and glasshouse invasion experiment tested the colonization ability of 10 herbaceous species (including European and native species) in a grassland in Canada, with different disturbances (simulated grazing, fertilization) and three densities of added seed (M. Rogers & A. MacDougall, unpublished). Nine of the 10 species were capable of invading (successful establishment from seed, after one growing season), yet the interacting influences of traits, environment, and seed rain on success were unique to each species. For some, invasion derived from interactions between nutrient levels and propagule pressure, for others disturbance alone was sufficient. This study illustrates how the mechanisms that explain successful invasion of non-native plant species can be species-specific, with preadapted trait differences playing varying roles in contributing to establishment success.

We found very few studies that tested the potential role of high propagule pressure in the invasion of grasslands outside Europe by European species, and we found none that controlled for the genotype of the introduced species (thus controlling for potential post-introduction adaptation). Invasion of grasslands by some European species may have required only high propagule pressure, or propagule pressure in addition to the preadaptation posited by the NPIH. However, without more tests of the role of propagule pressure, its role in invasion relative to preadaptation and post-introduction adaptation is unknown for most species and most regions.

##### 6. Temperate grasslands outside of Europe should be more invaded by European species than vice versa

Finally, the NPIH suggests that if European grassland species are adapted to the long history of European-style pastoral management, and grassland species elsewhere are not, then European grasslands should be less invaded than other temperate grasslands globally (see Visser *et al.*, 2016). Given the long history of the introduction of European weeds and grassland species globally in association with colonial-based European colonization (Crosby, 1986), it might seem obvious that European plants should dominate invasive floras. However, this actually differs by habitat. For example, Fridley (2008), examining forest understories rather than grasslands, showed that while 45% of the non-native plants of the Eastern US are from Europe, invaders of the forests of this region are dominated by woody species from Asia. Therefore, this prediction requires biogeographical studies that distinguish invaders by habitat affinity, as well as by origin. Kalusová *et al.* (2015) carried out just such an analysis using detailed plot-level data from the Czech Republic compared to North and South Carolina, and showed that grasslands in the latter are indeed more invaded than grasslands of the Czech Republic. Further studies that compare European grassland composition with temperate grasslands elsewhere at large scales are needed to determine whether this prediction holds in other regions.

## Conclusion

The potential interactions among preadapted traits, perturbation of native communities and high propagule pressure during invasion can make it hard to tease apart the relative importance of these factors. However, this uncertainty is consistent with the increasing recognition that invasions tend to be complex and multivariate phenomena, deriving from feedbacks among trait differences, environmental context and stochastic processes, including dispersal (Burke & Grime, 1996; Fridley *et al.*, 2007; Catford *et al.*, 2009; Seabloom *et al.*, 2015). Preadaptation undoubtedly plays a key role for some European grassland species invading some temperate grasslands – the question is which species, which grasslands, and to what degree?

The difference in resident levels of diversity between home and away is one of several compelling factors connected with invaders deriving from these European grasslands. Species persistence in European grasslands appears to be closely connected with human land use and species composition in these grasslands appears to be remarkably stable over time – Pärtel *et al.* (2007) found that patterns of grassland diversity in Estonia correlated with population densities of humans 800–1000 yr earlier. Eriksson *et al.* (2006) demonstrated these species-rich grasslands to be unsaturated with species, with no evidence for diversity-regulated resistance to the establishment of new species. This finding is consistent with observations that some of these European grassland species can invade from seed without requiring spatially extensive canopy perturbation (e.g. Harnden *et al.*, 2011). Yet despite this demonstrated capacity to absorb more species, these systems in Europe are largely uninvaded in recent times (Eriksson, pers. observ.). It is



interesting as well that the extent of species-rich, extensively managed grasslands continues to decline in Europe, reflecting changes in management intensity and illustrating the importance of human influences on the life history of these species – approximately 70% of all red-listed Swedish plants, for example, reside in these grassland habitats (Eriksson, 2013).

We found mixed support for the six predictions that flow logically from the NPIH. Although all of these predictions should hold if the NPIH is the mechanism behind invasions of grasslands outside Europe by European species, not all of them are necessary to support the NPIH in individual cases. For example, the NPIH may apply to a few particular invader species, but not be widespread enough to lead to a greater degree of invasion of grasslands outside Europe (prediction 6). The most crucial predictions are those ruling out post-introduction adaptation, establishing the necessity of European-style pastoral management for invasion, and ruling out overwhelming propagule pressure (or seed limitation of native plants) as the cause of invasion success (predictions 1, 3, 4 and 5). Testing these predictions is necessary to determine whether the combination of preadaptation by European species and introduced pastoral management was sufficient to lead to invasion, or whether other factors contributed or were the main cause.

Although many of the studies that we examined generally support the possibility of preadaptation by European grassland species, it is difficult to conclude that these mechanisms are solely responsible for their global spread (e.g. Fridley, 2008). Many of these species have been residents of grasslands outside Europe for centuries, and local adaptations have undoubtedly occurred that can obscure trait differences between home and away populations. It also is necessary to demonstrate that adaptive evolution has occurred, and that these adaptations have positive implications for plant fitness, both in Europe and in away ranges in comparison to native resident species (Hufbauer *et al.*, 2011). There may be other mechanisms beyond pastoralism that drive coexistence among European grassland species, and which contribute to their invasion success elsewhere. These mechanisms can include novel weapons such as toxic root exudates (Callaway & Ridenour, 2004) and the possibility of reduced pathogen loads compared to native species (MacDougall *et al.*, 2011). Another contributing factor may be the repeated, widespread and high-density propagule pressure that often accompanied the arrival of these grassland species, as has been observed for other invaders (e.g., Veltman *et al.*, 1996; Visser *et al.*, 2016). Finally, the co-occurrence of intense and repeated perturbation with colonial-based European settlement may simultaneously favour preadapted traits or make them largely unnecessary for invasion because biotic resistance has largely been destroyed – the difference may depend on the local history of settlement including the timing of species introductions, the role of species interactions in invasion especially during establishment and spread (plant-plant and plant-herbivore), and subsequent grassland management (Mack, 1989; Stromberg & Griffin, 1996; Hamilton, 1997; Corbin & D'Antonio, 2004; MacDougall & Turkington, 2005; MacDougall *et al.*, 2014). Preadaptation is thus a potentially powerful mechanism for invasion but its relative influence remains more speculative than confirmed.

In closing, the NPIH is an intuitively appealing hypothesis for the invasion success of European species in temperate grasslands outside Europe. The NPIH describes how adaptation to millennia of human land use could be a driving factor in the global spread of species deriving from European grasslands. Indeed, these grasslands have been recognized as an epicentre for invasion globally, possibly contributing more invasive herbaceous plants than any other terrestrial system (Hejda *et al.*, 2015). That being said, we have described some of the uncertainty over whether advantageous traits evolve before or after introduction, and how they may operate in conjunction with perturbation and propagule pressure. This uncertainty is consistent with some of the more fundamental questions surrounding plant invasions (Sax *et al.*, 2005), including whether non-native plant species are driving change through species interactions, merely passengers along for the environmental ride by occupying habitat created by disturbance, or a combination of the two (MacDougall & Turkington, 2005). Testing the predictions of the NPIH can help unravel the mechanisms that explain successful grassland invasion of European species in other parts of the world, and more generally provide insight into the ecological and evolutionary processes that are shaping plant diversity in contemporary human-influenced landscapes. This understanding could ultimately lead to a better ability to predict the abiotic and biotic conditions that lead to successful invasion, and therefore better quarantine procedures and conservation efforts for native habitats yet to be radically disturbed by anthropogenic pressure.

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