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Can model species be used to advance the field of invasion ecology?

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Abstract Hypotheses for explaining plant invasions have focused on a variety of factors that may influence invasion success, including propagule pressure, interactions of the introduced species with the biotic, abiotic, or disturbance properties of the new ecosystem, or the genetic characteristics of the invader itself. Evaluating the relative importance of these factors has been difficult because for most invaders key information about the introduced population or the introduction event is not available. We propose that natural experiments using model species is an important tool to test multiple invasion hypotheses at the same time, providing a complementary approach to meta-analysis and literature review. By focusing on a single candidate species, *Pinus contorta*, we explore several attributes that we propose constitute a good model, including: (a) intentional and relatively well documented introduction into a wide range of environments and countries across the world during the past century, where invasion success or failure has already occurred, (b) conspicuous growth form that simplifies assessment of growth rates, and comparisons across native and introduced ecosystems around the world, and, (c) documented and replicated variability of introduction intensity, genetic characteristics of the introduced populations, contrasting biotic communities present at sites of introduction, and abiotic conditions within and across introduced ecosystems. We propose that identifying model species with these characteristics will provide opportunities to disentangle the relative importance of different mechanisms hypothesized to influence invasion success, and thereby advance the field of invasion ecology.

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Introduction

Given the significant impacts of plant invasions, there
is great interest and substantial research aimed at
predicting when non-native species introductions will
result in invasions (Reinhart and Callaway 2006;
Richardson et al. 2011; Richardson and Rejmánek
2011; McGregor et al. 2012). Several approaches have
been taken to accomplish this goal, including identi-
fication of plant traits that are typical of invaders
(Rejmánek et al. 2005; van Kleunen et al. 2010), as
well as identification of geographical regions that are
susceptible to invasions (Lonsdale 1999; Sax 2001;
Rejmánek et al. 2005; Levine 2000). It has also been
shown that strong interactions between potential
invaders and recipient ecosystems can strongly influ-
ence invasion success or failure (Levine et al. 2004;
Moles et al. 2012). For instance, not all species that
become invasive are successful everywhere they are
introduced (Zenni and Nuñez 2013; Hierro et al. 2005;
Broennimann et al. 2007), and likewise, invasions
sometimes occur in atypical ecosystems or involve
atypical invaders (Moles et al. 2012). The frequency of
idiosyncratic invasion events suggests that our ability
to make generalizations can still be improved (Gu-
revitch et al. 2011), and that new tools are needed to
continue our forward progress (Jeschke et al. 2012;
Lockwood et al. 2005).

Most studies in invasion ecology are conducted at
local scales and focus on factors regulating invasion
success or the impacts of specific invaders (Moles
et al. 2012; Hierro et al. 2005; Vila et al. 2011; Pyšek
et al. 2012). Yet, numerous hypotheses have been
developed for addressing mechanisms that operate at
both small and large spatial and temporal scales to
help explain invasion success or failure (Hierro et al.
2005) (Table 1). These hypotheses include: propagule
pressure (Simberloff 2009), interaction of a given
introduced species with the abiotic (Hobbs and
Huenneke 1992; Broennimann et al. 2007) or biotic
environment (Elton 1958; Davis et al. 2000; Levine
2000; Callaway and Aschehoug 2000; Pringle et al.

2009) in the recipient ecosystem, and genetic diver-
gence following introduction (Blossey and Notzold
1995; Mayr 1970; Dlugosch and Parker 2008; Ell-
strand and Schierenbeck 2000; Maron et al. 2004).
While each of these factors likely influences invasion
success or failure to some degree, a number of
obstacles have made simultaneous testing of their
relative influence on invasions success difficult (sum-
marized in Table 1).

Invasion ecologists are increasingly recognizing
that investigative approaches are needed to simulta-
neously evaluate the multiple mechanisms proposed to
drive invasions (Gurevitch et al. 2011; Richardson
2006; Moles et al. 2012; Sanders et al. 2007; Kueffer
et al. 2013). One frequently used approach is meta-
analysis, whereby effect sizes are evaluated from
published studies where specific invasion hypotheses
have been tested (e.g. Chun et al. 2010; Colautti et al.
2004; Levine and D'Antonio 1999; Liu and Stiling
2006; Moles et al. 2012). While extremely useful in
evaluating the prevalence of various invasion mech-
anisms, meta-analyses have several limitations. First,
conclusions can be influenced by publishing biases,
where significant effects are more likely to be
published than studies finding no effects, easily tested
hypotheses are published more often than less easily
tested hypotheses (Gurevitch and Hedges 1999; Jes-
chke et al. 2012), and specific hypotheses are evalu-
ated more often for some taxonomic groups than for
others. Additionally, meta-analyses have a limited
ability to compare the relative influence of multiple
invasion hypotheses at the same time (Chun et al.
2010). While meta-analysis will continue to be a
useful tool for invasion ecology, it's utility is
constrained by the availability and quality of pub-
lished studies that simultaneously test multiple inva-
sion hypotheses (Gurevitch and Hedges 1999).

These limitations suggest that the field of invasion
ecology may greatly benefit from analytical approaches
where a wide range of mechanisms proposed to
influence invasion success or failure can be simulta-
neously evaluated (Richardson et al. 2000a; Moles et al.
2012). We propose that the identification of model
invasive species is an underutilized tool that may help
overcome methodological obstacles for simultaneously
testing the relative influence of multiple invasion
hypotheses (Richardson and Rejmánek 2004). We
propose one species in particular, *Pinus contorta*
Douglas *ex* Loudon (1838), as a potential candidate

Table 1 A list of prominent invasion hypotheses used to explain the variable success of species across different ecosystems

Hypothesis	References	Description	Obstacle	P. contorta attribute
Introduction intensity				
Propagule pressure	Williamson (1996), Lonsdale (1999), Simberloff (2009)	The diversity and abundance of invaders in a region is controlled by the diversity and abundance of non-native species introduced	Extremely difficult to measure propagule arrival, and thus evaluation requires proxy measurements such as social, economic, or land-use metrics	Introduction intensity and propagule production is easily quantified
Abiotic interactions				
Disturbance	Hobbs and Huenneke (1992), Moles et al. (2012), Hierro et al. (2006)	Differences in the intensity, frequency, or type of disturbance across ecosystems controls invader success or failure	Changes in disturbance regimes likely co-vary with other anthropogenic factors, such as nutrient enrichment and propagule pressure	Plantations have been intentionally introduced into a wide range of environments with variable disturbance regimes
Climate matching	Broennimann et al. (2007)	Native range climate distribution can be used to predict introduced range distribution	Difficult to know whether an introduced species has fully expanded into its potential range size, complicating native and introduced range comparisons	Plantations have been established in a wide range of climate and edaphic conditions within and across regions, allowing for invasion success and abiotic environment relationship to be easily evaluated
Biotic interactions				
Enemy release	Elton (1958), Keane and Crawley (2002)	Reduced pressure from herbivores or pathogens in introduced ranges enhances vigor	For many of the hypotheses in this category, species are predicted to perform differently in their native range and introduced range, thus requiring native versus home-range comparisons for successful evaluation, which is logistically difficult. Even when native and introduced range comparisons are done, it is difficult to hold all other factors (i.e. propagule pressure, abiotic, and genetic differences) constant during the comparisons, making it difficult to reveal the relative importance of the hypotheses	Plantations have been established in a wide range of biotic community types within and across ecosystems. The fact that introduction intensity, abiotic properties, and genetic characteristics are usually documented for individual introduction events, allows for the possibility to hold these factors constant through either experimental design or using statistical approaches
Co-invasion	Nunez et al. (2009), Pringle et al. (2009), Dickie et al. (2010)	Invasions limited if key positive interactions cannot be established in introduced ranges		

Table 1 continued

Hypothesis	References	Description	Obstacle	P. contorta attribute
Empty niche	Elton (1958), MacArthur (1970)	Invaders more successful if they utilize resources unused by the native community		
Diversity-invasibility	Elton (1958), MacArthur (1970), Levine (2000), Stohlgren et al. (1999, 2003)	Higher native species diversity results in niche saturation, whereby fewer resources are available for newly arriving species		
Fluctuating resources	Davis et al. (2000)	The balance between native community resource capture and resource inputs creates spatial and temporal variability of competition intensity between native and introduced species		
Novel weapons	Callaway and Aschehoug (2000)	Native communities are susceptible to allelopathic interactions of non-native species because they have not co-evolved		
Intraspecific-genetic				
Founder effects	Mayr (1970), Dlugosch and Parker (2008)	Introduced population started by anomalous individuals, causing the average phenotype to differ between a species native and introduced ranges	Evaluation of these genetic hypotheses is often done through direct comparison of native and home range populations in common garden environments, where biotic and abiotic factors are held constant. However, a major impediment to successfully making these comparisons is the high degree of uncertainty that exists in accurately pairing source populations with invasive populations for most invaders, given the high degree of genetic diversity that can be found in some species native ranges	Many countries where *P. contorta* has been introduced have established provenance field trials to determine which native range populations perform best across a range of sites within each introduced region. These trials provide the opportunity to evaluate the role of genetics, and genetic by environment interactions in controlling invasion. They also allow the possibility to hold genetic variability constant while evaluating other hypotheses
Enhanced hybridization	Ellstrand and Schierenbeck (2000), Moles et al. (2012)	Greater genetic mixing in the introduced range relative to the native range results in enhanced vigor		

Table 1 continued

Hypothesis	References	Description	Obstacle	*P. contorta* attribute
Evolution of increased competitive ability (EICA)	Blossey and Notzold (1995)	In the absence of enemies in introduced ranges, a negative selection for defense traits, and positive selection of growth and reproductive traits leads to a inherently more invasive individuals		

The hypotheses are grouped into four categories, those that focus on introduction intensity, interaction with abiotic factors, interactions with the resident biotic community, or variability in the genotypic characteristics of the introduced species itself. For each hypothesis we list key references and describe its basic tenet. We also list major obstacles for testing individual hypotheses or categories, and a key attribute of *P. contorta* that helps each obstacle to be overcome

model species, and identify a set of its attributes that should be considered when selecting additional model plant invaders (Richardson and Rejmánek 2004; Langdon et al. 2010; Higgins and Richardson 1998).

The characteristics of an ideal model plant invader

Model species are intensively studied organisms used for the purpose of understanding poorly understood processes, with the ultimate goal of expanding the knowledge of those processes to other organisms. While no single species can be used to reveal the complexity of all other organisms, model species have been instrumental to further numerous fields in biology, including genetics and evolution (e.g. *Drosophila*, *Arabidopsis*, or *Populus*), development (e.g. *C. elegans*) and medicine (e.g. *E. coli*), because they have allowed for unambiguous testing of certain types of hypotheses for the first time (Taylor 2002). In each case, intensive research focus on the model organism has contributed to generalized knowledge that has facilitated research on other organisms in the particular field of science.

Model taxonomic and functional groups have already been proposed and successfully used in invasion ecology (Richardson et al. 2004; Richardson and Rejmánek 2004; Richardson 2006; Simberloff et al. 2002; Kueffer et al. 2013). For instance, several specific tree genera have been used to evaluate which plant characteristics can predict invasiveness, including *Pinus* (McGregor et al. 2012; Rejmánek and Richardson 1996) and *Acacia* (Richardson et al. 2011). We propose here that the careful selection of individual model species is the next logical step to address multiple invasion hypotheses simultaneously, and thereby further our understanding of the complex range of factors that control plant invasions. For several reasons, trees are an excellent functional group to look for potential model species. First, introductions of many tree species have widely occurred throughout the globe for production forestry purposes, creating the possibility to simultaneously address multiple invasion hypotheses that operate at widely different spatial and temporal scales (Richardson and Rejmánek 2011). Second, non-native invasive tree species are thought to have some of the largest community- and ecosystem-level impacts (Richardson 2006; Richardson and Rejmánek 2011), which is likely to generate

Table 2 A table describing *P. contorta* introduction and spread into three Southern hemisphere (New Zealand, Argentina, and Chile), and four European countries (Sweden, Finland, United Kingdom, and Ireland)

	USA, Canada[a]	New Zealand	Argentina	Chile	Sweden	Finland	UK	Ireland
Described Alien Status[b]	Native	Invasive[c,d,e]	Invasive[f] Naturalized[d]	Invasive[g,h]	Invasive[d,e]	No[i] naturalization[g]	Naturalized[j] Invasive[c,d]	Potentially Invasive[k] Invasive[d]
Invasive[l]		Yes[c,d,e]	Yes[f,n]	Yes[g,h]	Unknown	No[i]	Yes	Yes[e]
Temperature (°C) Max. monthly mean	27 to 38[m]	23	21.7	18.4	21.0	21.4	19.9	
Min. monthly mean	−57 to 7[m]	3.8	−2.2	−1.6	−14.0	−13.2	0.3	
Annual precipitation	250 to 500[m]	876	597	909	569	606	660	
Earliest Introduction (year)		1802	1960	1970s	1920s	1920s	1851	1918
Aerial extent (ha)	26,000,000[a]	Unknown	6,000 ha[n]	6,545	565,000	10,000	106,000	63,120 ha
Purpose of planting		Commercial & Erosion	Commercial	Commercial & Erosion	Commercial	Commercial	Commercial	Commercial
Published spread distance (km)		8[o]	3[f]	3[g]	0.3[d]	–	Unknown	Unknown
Invaded area (ha)		473,200[o]	Unknown	500[p]	–	–	–	–
Invaded or naturalized habitats		Grasslands and open/disturbed areas	Patagonian steppe and disturbed areas	Patagonian steppe, grasslands, and open/ disturbed area	Disturbed areas	–	Disturbed areas	Adjacent to plantations; dry and wet bogs
Active management and control		Yes	Yes	No	No	No	No	No

Introductions have also occurred in Russia, Norway, South Africa and Australia, but are not included in the table because of limited published information on introductions in these countries

[a] Lotan and Critchfield 1990, [b] as described in published literature, [c] Ledgard 2001, [d] Haysom and Murphy 2003, [e] Richardson and Rejmánek 2004, [f] Sarasola et al. 2008, [g] Pena et al. 2008, [h] Langdon et al. 2010, [i] Lähde et al. 1984, [j] McGregor et al. 2012, [k] National Biodiversity Data Centre 2010, [l] Spreading at a rate greater than 100 m in less than 50 years (Richardson et al. 2000a, b), [m] data considering the four varieties in their native ranges, [n] Personal communication with Mauro Sarasola, [o] Personal communication with Nick Ledgard, [p] Unpublished data, Aníbal Pauchard

substantial research and management funding support across multiple regions. While focusing on a single candidate species, *P. contorta*, we explore a variety of attributes that we propose constitute an ideal model.

Pinus contorta as a candidate model study system

Pinus contorta is native to Northwestern North American, including the United States and Canada. Within this region, it grows under a wide variety of climatic conditions (Lotan and Critchfield 1990; Ledgard 2001), including coastal and continental environments, from coastal to subalpine zones, from approximately 40–65°N latitude. In many portions of its native range it is predictably subjected to stand replacing wildfire, where it is adapted to quickly re-establish itself as the dominant tree species. Several traits that allow it to achieve exceptionally high densities after wildfire or other disturbance types in its native range include its prolific production of small seeds, a variety of seed dormancy mechanisms, and rapid seedling growth rates and young age of reproductive maturity (Grotkopp et al. 2002; Lotan and Critchfield 1990; Despain 2001).

Given its high growth rate and its commercial value, *P. contorta* has been widely introduced around the world during the past two centuries (Table 2). These introductions have occurred in many European countries (Ireland, the United Kingdom, Norway, Sweden, Finland, and Russia) where many native species of the *Pinaceae* are present, and has also been introduced to many Southern Hemisphere countries where no native species of the *Pinaceae* exist (Chile, Argentina, New Zealand, Australia, and South Africa). Across these regions, it has been described as a naturalized or invasive species in almost every country where it has been introduced for more than 25 years (Richardson and Higgins 1998; Haysom and Murphy 2003; Ledgard 2001; Despain 2001; Richardson 2006; Richardson et al. 1994; Langdon et al. 2010; Sarasola et al. 2006; Pena et al. 2008; National Biodiversity Data Centre. *Pinus contorta*. National Invasive Species Database 2010). However, invasiveness according to the definition of Richardson et al. (2000b; 100 m in less than 50 years) has only occurred in the southern hemisphere (e.g. New Zealand, Argentina, and Chile) (Langdon et al. 2010; Richardson and Rejmánek 2004; Ledgard 2001; Rejmánek and Richardson 2013),

whereas in European countries its naturalization and invasion have occurred at much slower rates (Lähde et al. 1984; Haysom and Murphy 2003). We propose that the following attributes make *P. contorta* an excellent candidate for a model species to test the relative importance of multiple mechanisms proposed to influence plant invasion:

(1) A model plant species should exhibit traits typically associated with invasiveness. Rejmánek and Richardson's (1996) analysis of key invasion traits showed that of 24 globally introduced *Pinus* species (consisting of 12 known invasive and non-invasive species), that *P. contorta*'s Z-score ranking (derived from mean juvenile period, seed mass, and mean interval between large seed crops) was the highest among the group of invasive pine species. These traits assure that *P. contorta* has a great potential to become an invader following introduction (Richardson 2006; Rejmánek and Richardson 1996), and more-so than other pines has fecundity traits similar to many non-woody invaders.

(2) A model plant species should also be introduced into a wide range of environments throughout the world, and show varying degrees of invasiveness across these environments. As described above, controlled and documented introductions of *P. contorta* have been carried out in many regions of the world simultaneously during the past century (Richardson and Rejmánek 2004), where invasion success greatly differs (Richardson and Rejmánek 2004; Langdon et al. 2010; Lähde et al. 1984) (Fig. 1; Table 2).

(3) A model plant species should also have detectable impacts on ecosystems it invades, so that the various components of invasion impact (i.e., distribution, abundance and ecological effects, sensu Parker et al. 1999) can be revealed. *Pinus contorta* is a non-trivial invader, meaning it has substantial impacts in some of the regions it invades. *Pinus contorta* has been shown to compete with endangered native species (e.g. *Araucaria araucana*) and reduce the diversity and abundance of native plants (Urrutia 2012; Nilsson et al. 2008). The species may also increase fuel loads, generating a more fire-prone environment (Simberloff et al. 2010; Despain 2001). In New Zealand and Chile, *P. contorta* was initially planted for erosion control in mountainous lands, but has subsequently had transformative effects in these landscapes (Wardle 1985). It commonly invades native tussock grasslands, thus transforming these
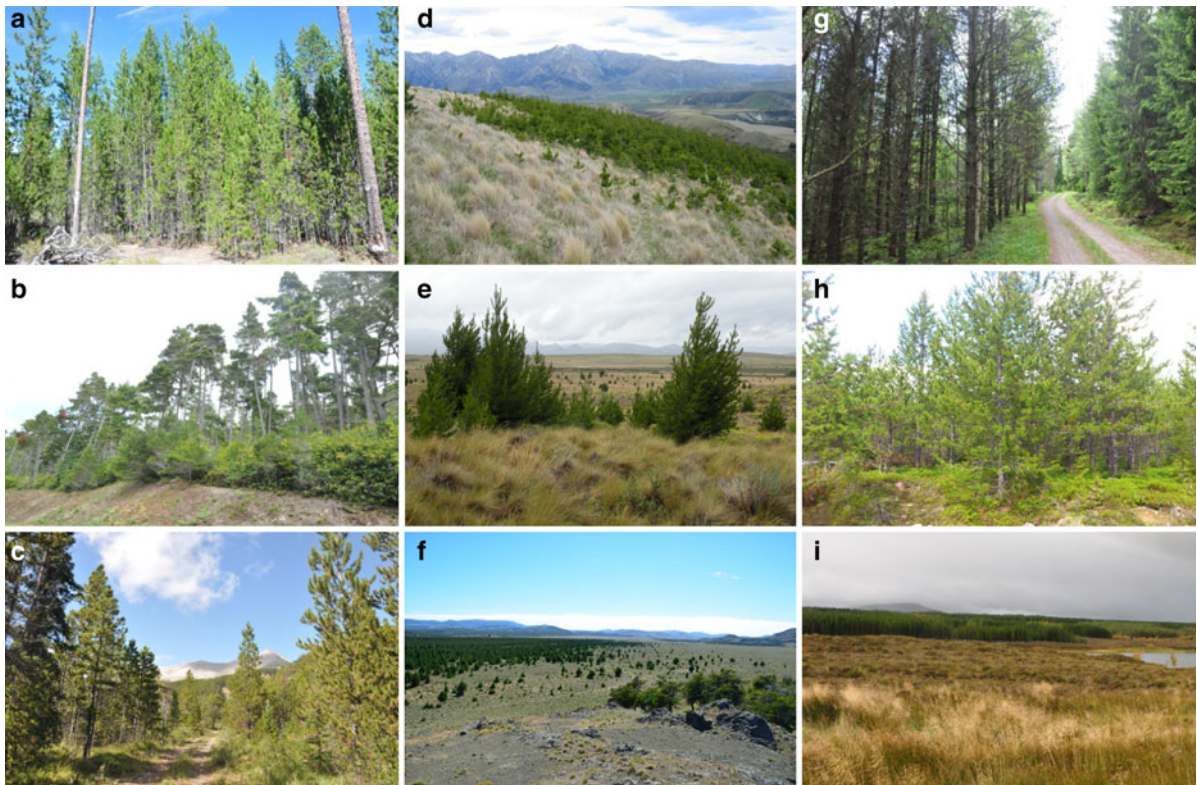
Fig. 1 *Pinus contorta* in its native (**a–c**) and introduced ranges in the Southern Hemisphere (**d–f**) and Europe (**g–i**). Native range photos depict three distinct *Pinus contorta* subspecies, including subspecies *murrayana* on the east slope of the Cascade Mountains, Oregon (**a**), subspecies *contorta* near Pacific coast, Oregon (**b**), and subspecies *latifolia* in northern British Columbia (**c**). Southern hemisphere photos show active

P. contorta invasions in New Zealand (**d**), Argentina (**e**), and Chile (**f**). European photos show *Pinus contorta* plantations in southern Finland (**g**), Northern Sweden (**h**), and northwest Scotland (**i**). Photos **a–c**, **g**, **h**, and **i** were taken by M. Gundale; photo **d** was taken by D. Peltzer; Photo **e** was taken by M. Nunez; and photo **f** was taken by A. Pauchard

from grassland or open shrublands to forest systems (Dickie et al. 2010; Ledgard 2001), and diminishes soil C (Dickie et al. 2010). These examples demonstrate that in ecosystems where *P. contorta* does become a serious invader, it causes a rapid shift in vegetation structure and function, alters availability of soil nutrients (e.g. phosphorous), decreases water inputs into watershed catchments, and causes reductions in indigenous biodiversity (Davis and Lang 1991; Mark and Dickinson 2008).

(4) A model plant species should be easy to compare within and across a wide variety of introduced ranges. Because *P. contorta* has been introduced throughout temperate and boreal ecosystems throughout the world for the purpose of production forestry or erosion control, key background data is usually available about the introduction event, including the precise time and location where the

introduction event occurred (Elfving et al. 2001; Miller and Ecroyd 1987; Ledgard and Baker 1988). Initially, most introductions of this species were done by government agencies or forest companies which often created detailed records of plantation density and source populations (i.e. provenance). Because pine trees are large and very conspicuous, this basic knowledge of introduction allows for easy quantification of two important steps in the invasion process, growth rates of individual plants and spread rates from plantations, which can be easily compared across multiple sites within and across ecosystems (Richardson et al. 2004; Richardson 2006). An additional property of *P. contorta* that facilitates simple comparisons across sites is that it is usually established in discreet plantations, where planted area and tree density within that area are known or easily quantified (Visser et al. 2014), allowing propagule pressure to be

easily estimated. In addition, the seed morphology is very similar to other *Pinus* species from which detailed seed dispersal models have been developed (Caplat et al. 2012). These attributes greatly simplify studies evaluating the role of propagule pressure on local scale invasion patterns, as well as provide the opportunity to hold propagule pressure constant through statistical techniques or through study design while evaluating other invasion hypotheses.

(5) A model plant species should also allow accurate comparisons between a species' native and introduced ranges. In most portions of its native range, *P. contorta* grows in dense mono-cultures. Because it is also planted in mono-cultures in its introduced ranges and the invasions are usually very dense and mono-specific (Fig. 1), this allows for straightforward comparisons of its growth rates in native and introduced ranges, which is critical for testing several specific invasion hypotheses (Hierro et al. 2005) (Table 1).

(6) A model plant species should allow for evaluation of different stages of the invasion process (i.e. transport, introduction, establishment and spread) (Blackburn et al. 2011) to be compared across a range of sites with variable abiotic conditions both within and between each region of introduction. Within each country of introduction, discreet plantations of *P. contorta* have been established across sites with variable edaphic and climatic properties. In several countries, replicated field trials have been established for the purpose of assessing *P. contorta* performance against similar native forestry species or other introduced species across a range of edaphic properties (i.e. site fertility) or management practices. These studies can be used to explicitly evaluate the role of abiotic factors on growth and invasion success within and across regions.

(7) A model plant species should be introduced into a range of ecosystems with different levels of anthropogenic change, allowing for the effect of disturbance and environmental change to be evaluated. *P. contorta* has been introduced in temperate and boreal ecosystems with different histories of anthropogenic change, including disturbances such as grazing, logging, human-induced fires, and pollution (e.g. nitrogen or sulfur deposition). In many countries where introductions have occurred, detailed records of anthropogenic change factors exist (Phil-Karlsson et al. 2009;

Josefsson et al. 2010; Walker et al. 2004; Wilmshurst et al. 2008; Gundale et al. 2011a). Therefore, hypotheses about the role of human disturbances and other anthropogenic factors can be tested within and across regions.

(8) A model plant species should also be introduced into highly variable biotic communities in order to evaluate the role that biotic interactions may play in controlling invasion. As described earlier, *P. contorta* has been introduced into European ecosystems dominated by *P. sylvestris*, *P. abies*, or grasses, and southern hemisphere herbaceous or *Nothofagus* dominated ecosystems that contain no native species of the *Pinaceae* (Elfving et al. 2001; Langdon et al. 2010). These contrasting regions serve as an opportunity to evaluate the influence that phylogenetic similarity of the introduced species with the native species pool may have in determining the strength, direction, and consequences of key biotic interactions and invasion governing mechanisms in introduced ranges.

(9) A model plant species should allow for precise pairing of native and introduced populations, so that genetic differences can be explicitly evaluated or held constant. Many intentional tree introductions are done with careful consideration of the genetic characteristics of the source population. Many plants have large native range distributions and exhibit substantial genetic variability across those ranges (Parchman et al. 2011). At course spatial scales, genetic differences within the native range populations allow species to be locally adapted to broad scale differences in climate and latitude. Like most intentional tree introductions, introduction of *P. contorta* into each recipient region was done through the selection of appropriate native range populations that were matched for the abiotic properties of the introduced range. Additionally, multiple provenances from a particular native range location were often introduced to each recipient country in common plantations to evaluate which provenances perform best in the introduced region (Fries et al. 1998; Elfving et al. 2001; Lähde et al. 1984; Ledgard 2001). Using these provenance trials in combination with genetic analysis would allow for straightforward comparisons across introduced regions to evaluate how genetic differences among introduced populations influence patterns of invasions (Zenni and Simberloff 2013).

The use of *Pinus contorta* for hypothesis testing

The extent to which invasion patterns are controlled by introduction intensity, abiotic or biotic factors in the receiving environment, or genetic variability of the invader, or the interaction of these factors, is a key question in invasion ecology which has direct implications for managing introduced species (Gurevitch et al. 2011; Moles et al. 2008; Theoharides and Dukes 2007). While the relative contribution of these factors are difficult to evaluate for most invaders, the nine attributes described above highlight the utility of forestry species in general, and *P. contorta* specifically, to serve as models to investigate plant invasion hypotheses. Here we provide three examples of how this study system could be used to broaden our knowledge of multiple mechanisms proposed to influence invasion success.

Antagonistic biotic interactions

Several hypotheses seeking to better understand species invasion patterns propose that differences in the presence or strength of biotic interactions can be an influential factor on invasion success or failure (Elton 1958; Davis et al. 2000; Levine and D'Antonio 1999) (Table 1). One of the most frequently cited explanations for successful invasions is the Enemy Release Hypothesis (ERH) (Elton 1958; Keane and Crawley 2002), which proposes that all plants are negatively affected to some degree by specialist herbivores or pathogens in their native ranges, and that escape from these negative interactions allows non-native species to achieve higher individual growth and reproductive rates and subsequently higher population and metapopulation growth rates relative to what they achieve in their native ranges, and relative to native species in their introduced range (Keane and Crawley 2002; Mitchell and Power 2003). Other invasion hypotheses have focused on the role of plant–plant competition as a regulator of invasion success (for thorough review see MacDougall et al. 2009). Three such hypotheses, The Empty Niche Hypothesis (Elton 1958), the Diversity-Invasibility Hypothesis (Kennedy et al. 2002; Levine et al. 2004), and the Fluctuating Resources Hypothesis (Davis et al. 2000) each predict that competition intensity between a potential invader and native species is a key determinant of invader success.

While these hypotheses feature prominently in the invasion ecology literature, Hierro et al. (2005) noted that their successful evaluation requires explicit comparisons of the strength of these interactions in both a species native ("home") and introduced ("away") ranges. As home versus native range comparisons are now being done with increasing frequency (e.g. Callaway et al. 2011; Hinz et al. 2012; McIntosh et al. 2012), in many cases native and introduced populations are arbitrarily paired, allowing for the possibility that other key differences co-vary across the comparison. For instance, because several invasion hypotheses focus on the role that genetic divergence may have on invasion success or failure (Table 1), haphazard pairing of native and introduced populations may result in unintentional underlying comparisons of different genotypes. The global extent of *P. contorta* introductions we have described provides a key advantage for testing the relative importance of biotic interactions because key factors that underlie several of the other invasion hypotheses can be accounted for (e.g. genetics and introduction intensity).

Overcoming these major obstacles opens up a wide range of broad questions regarding the context in which antagonistic interactions may control invasion success or failure. For instance: Are species more likely to encounter negative biotic interactions when introduced into ecosystems where very similar native species exist, and what are the consequences of those interactions for invasion success? *Pinus sylvestris* is a closely related tree species (i.e. two needle pines) in Northern European Ecosystems that occupies a similar climate, soil, and regeneration niche, whereas in southern hemisphere locations no such similar species exist. The close functional and phylogenetic similarity of *P. contorta* with *P. sylvestris* may result in a greater resource use overlap, and therefore may result in more intense competition relative to Southern Hemisphere regions where no taxonomically similar species exist (Brodribb and Feild 2008; Strauss et al. 2006). Additionally, *P. contorta* has a wide array of enemies in its native range, including a variety of foliar and root pathogens and parasites (Krebill 1973), and mammalian and insect herbivores (Lindsey 1973). One particular insect enemy, the mountain pine beetle (*Dendroctonus ponderosae*), is currently causing extremely high levels of mortality in a large portion of its native range (Edburg et al. 2012). Many of the

same or closely related enemy species have co-evolved with *P. sylvestris* in Europe (e.g. Moose, *Alces alces*, or bark beetles, *Dendroctronus*; Bejer 1981), and therefore have the potential to negatively impact *P. contorta* following introduction in those regions (Lindelow and Bjorkman 2001). *Pinus contorta* may also have a greater likelihood of encountering novel enemies in European forests that can utilize either tree species as a host (Lindelow and Bjorkman 2001). For instance, the European fungal pathogen *Gremmeniella abietina* has been shown in some locations to strongly impact *P. contorta* growth in Sweden, albeit to a lesser degree than its impact on *P. sylvestris* (Bernhold et al. 2009). These interactions with novel enemies may be less common in southern hemisphere locations, due to much more distant co-evolutionary histories of the pathogens and herbivores in those regions. Because the global network of *P. contorta* introductions we have described covers a variety of countries in both northern European and Southern Hemisphere environments, this general question about the phylogenetic relatedness of native vegetation as a determinant of antagonistic interactions with introduced species can be robustly evaluated.

Mycorrhizal co-invasion

A logical corollary to antagonistic interaction hypotheses is that the absence of key mutualists in introduced ranges may constrain invasions (Dickie et al. 2010; Nunez et al. 2009; Pringle et al. 2009). Currently a very active area of research is focused on the interaction of introduced plant species with soil biota (Klironomos 2002), including both soil pathogens (Diez et al. 2010; Reinhart and Callaway 2006) and soil mutualists (Richardson et al. 2000a; Nunez et al. 2009; Pringle et al. 2009; Schwartz et al. 2006). Parallel research in several different countries has examined the role of ectomycorrhizal fungi in the establishment of *P. contorta*, including in its native range (Ashkannejhad and Horton 2006; Byrd et al. 2000; Cullings et al. 2000) and as an invasive species in Argentina (Nunez et al. 2009) and New Zealand (Dickie et al. 2010). *Pinus contorta* mutualisms with ectomycorrhizal fungi are of particular interest, as a lack of mycorrhizal inoculum was initially a barrier to establishing plantations (Marx 1991). In some countries a lack of mycorrhizal fungi remains a limiting

factor for spatial spread. In Argentina, for example, Nunez et al. (2009) showed that *P. contorta* does not grow well in soils distant from plantations, unless they are first inoculated with soil microbes associated with the plantation (Fig. 2a), whereas, this is no longer a barrier in other countries, where *P. contorta* now spreads widely (Ledgard 2001; Pringle et al. 2009). Understanding how *P. contorta* has overcome the initial limitation is important not just in the context of *Pinus*, but also in predicting future invasiveness of other mutualist-dependent species (Díez 2005; Pringle et al. 2009).
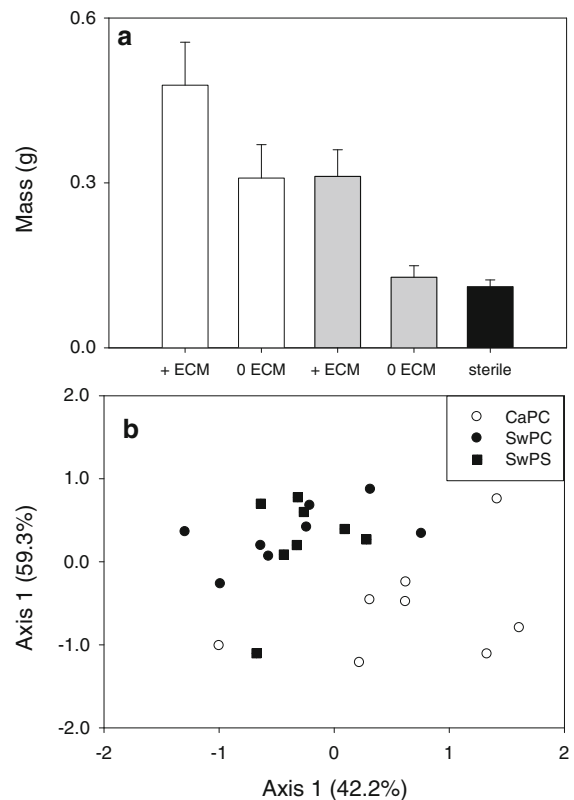
Fig. 2 Depiction of the relationship between soil microbial communities and *Pinus contorta* introduced into Argentina (**a**), and Sweden (**b**). Data from subpanel a is derived from Nunez et al. (2009), where a greenhouse experiment showed the growth of *P. contorta* in soil collected from near (*grey bars*) and far (*white bars*) from a *P. contorta* plantation, either with or without ectomycorrhizal (ECM) inoculation added from plantation soil. All soils were compared to a sterilized control soil (*black bar*). *Subpanel* **b** is derived from McIntosh et al. (2012), and depicts axis 1 and 2 of an NMS ordination of microbial phospholipid fatty acid (PLFA) data measured from Canadian *P. contorta* soil (CaPC), introduced Swedish *P. contorta* soil (SwPC), and soil associated with the native Swedish tree, *P. sylvestris* (SwPS)

M. J. Gundale et al.

As with questions focused on antagonistic interactions, a highly relevant broad scale question that can be asked regarding mycorrhizal associations is whether the phylogenetic similarity of native vegetation determines whether suitable mycorrhizal species are present or not, and therefore constitute an invasion barrier? Using a very course technique to evaluate soil microbial communities (phospholipid fatty acid technique, PLFA), McIntosh et al. (2012) showed that microbial communities did not differ between introduced *P. contorta* and native *P. sylvestris* plantations, whereas both these stand types differed significantly from soil in the native range of *P. contorta* (Fig. 2b). Further, Kardell et al. (1987) evaluated fungal sporocarps in Swedish *P. contorta* and *P. sylvestris* stands, and found that the community composition of known ectomycorrhizal species were present in both stand types. While further analyses are required to specifically evaluate ectomycorrhizal associations in European forests, these studies suggest that the phylogenetic relatedness of the vegetation of the recipient community likely determine whether these key mutualisms can be successfully established, and thereby may influence initial growth and invasion patterns among contrasting regions.

Biotic-environment-genotype interactions

These questions focused on either positive or antagonistic biotic interactions invoke a range of larger scale questions that can be addressed using model species, such as the *P. contorta* system we have described. As described earlier, because *P. contorta* is introduced for forestry purposes, field trials have been established in many different countries to identify which genetic provenances perform most optimally under different environmental conditions within each country, providing an opportunity to investigate the importance of interactions between genes, the biotic community, and abiotic environment. As an example, one specific hypothesis, the Evolution of Increased Competitive Ability (EICA) (Blossey and Notzold 1995), proposes that when an introduced species has escaped enemies from its native range, that there will be a positive selection for growth traits and a de-selection of defense traits, thereby increasing vigor of the introduced population relative to native range populations. The global setting of *P. contorta* could be used to ask questions relevant to this hypothesis, such

as: how does the magnitude of herbivore or pathogen damage vary across tree provenances? Likewise, the *P. contorta* introduction network could address genetic aspects of co-invasion, such as: Do all introduced provenances equally rely on ectomycorrhizas for successful growth, or can some provenances more readily associate with cosmopolitan ectomycorrhizas, leading to divergence of native and introduced populations?

Likewise, the global system of *P. contorta* introductions could be used to address how environmental, biotic, and genetic factors interact to control growth and invasion success. For instance, a variety of ecological theories predict that competition intensity as well as damage by pathogens and herbivores should increase with increasing resource availability (Grime 1973, Stamp 2003), or that positive biotic interactions should be strongest under resource poor conditions (Callaway et al. 2002; Gundale et al. 2011b). Therefore, the global *P. contorta* network could be used to address questions such as: Do introduced species encounter greater enemy damage in resource rich sites, and is this relationship dependent on the phylogenetic similarity of the native vegetation? Does the dependency of *P. contorta* on ectomycorrhizas vary across sites with differing fertility, and if so, can this explain local scale invasion patterns? We argue that the use of model study species, such as *P. contorta*, in the field of invasion ecology will greatly facilitate empirical evaluation of broader questions that seek to understand the relative role of different invasion hypotheses, and their interactions, and therefore help establish context for when and where certain factors are important and when they are not (Jeschke et al. 2012; Gurevitch et al. 2011).

Limitations of *P. contorta* as a model

Despite the 9 characteristics we propose that make *P. contorta* a good model species for the study of plant invasion ecology, we should also note some of its characteristics that are less than ideal for this purpose. These limitations may help other model invaders with complementary attributes to be identified:

1. While *P. contorta* has been introduced into a wide range of temperate and boreal habitats, its distribution is not as widespread as many other invaders

(Stohlgren et al. 2011). Many invasive grasses or herbs are more widespread (Stohlgren et al. 2011), and thus may serve as better invasion models, provided that detailed introduction histories could also be established.

2. Many problematic invaders are herbs or grasses with very short generation times. The longer generation time of *P. contorta* relative to these types of plant invaders, as well as its large size, creates practical issues for conducting artificial experiments, especially at the population and meta-population scales. Short-lived invaders are likely to be evaluated more frequently in greenhouse studies, and thus are likely to be more accessible as focal species to certain types of researchers (e.g. graduate students).

3. The relatively long generation time of *P. contorta* also diminishes the speed at which genetic divergence may occur among invading populations, thereby potentially making it difficult to evaluate some aspects of the EICA hypothesis; however, as noted above, this same characteristic may be useful for testing some invasion hypotheses, where it is desirable to hold genetic differences constant.

Beyond *Pinus contorta*

No single species can be used to answer all questions in the field of invasion ecology. Invasive plant species exhibit a wide range of morphologies, physiologies, and life history strategies that make it difficult to draw general conclusions from investigation of a single species. However, for most invasive species, it is difficult or impossible to disentangle the influence of propagule pressure, abiotic interactions, biotic interactions, and intraspecific genetic differences, simply because there is no documented history of the introduction, and growth and invasion patterns are not easily measured or compared across regions. Selection of model species following the criteria we have described would greatly improve our ability to test multiple invasion hypotheses simultaneously, and therefore improves our understanding of the relative importance of multiple mechanisms controlling invasion success across multiple scales. Given that not all invasive species are the same, we hope that the *P. contorta* global experiment we have described here will inspire the establishment of other similar global study systems with a complementary set of attributes that overcome some of the limitation we describe for *P. contorta*. The use of multiple model invaders, in parallel with meta-analysis and literature reviews, will help progress the field of invasion ecology further down the pathway towards the general principles needed to prevent and manage plant invasions globally.

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