

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

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**AO1 Abstract** Hypotheses for explaining plant invasions  
10 have focused on a variety of factors that may influence  
11 invasion success, including propagule pressure, inter-  
12 actions of the introduced species with the biotic,  
13 abiotic, or disturbance properties of the new ecosys-  
14 tem, or the genetic characteristics of the invader itself.  
15 Evaluating the relative importance of these factors has  
16 been difficult because for most invaders key informa-  
17 tion about the introduced population or the introduc-  
18 tion event is not available. We propose that natural  
19 experiments using model species is an important tool  
20 to test multiple invasion hypotheses at the same time,  
21 providing a complementary approach to meta-analysis  
22 **AO2** and literature review. By focusing on a single candi-  
23 date species, *Pinus contorta*, we explore several  
24 attributes that we propose constitute a good model,  
25 including: (a) intentional and relatively well

documented introduction into a wide range of envi- 26  
ronments and countries across the world during the 27  
past century, where invasion success or failure has 28  
already occurred, (b) conspicuous growth form that 29  
simplifies assessment of growth rates, and compari- 30  
sons across native and introduced ecosystems around 31  
the world, and, (c) documented and replicated vari- 32  
ability of introduction intensity, genetic characteristics 33  
of the introduced populations, contrasting biotic 34  
communities present at sites of introduction, and 35  
abiotic conditions within and across introduced eco- 36  
systems. We propose that identifying model species 37  
with these characteristics will provide opportunities to 38  
disentangle the relative importance of different mech- 39  
anisms hypothesized to influence invasion success, 40  
and thereby advance the field of invasion ecology. 41

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 45 *contorta* · Tree invasions

## 48 Introduction

49 Given the significant impacts of plant invasions, there  
 50 is great interest and substantial research aimed at  
 51 predicting when non-native species introductions will  
 52 result in invasions (Reinhart and Callaway 2006;  
 53 Richardson et al. 2011; Richardson and Rejmánek  
 54 2011; McGregor et al. 2012). Several approaches have  
 55 been taken to accomplish this goal, including identi-  
 56 fication of plant traits that are typical of invaders  
 57 (Rejmánek et al. 2005; van Kleunen et al. 2010), as  
 58 well as identification of geographical regions that are  
 59 susceptible to invasions (Lonsdale 1999; Sax 2001;  
 60 Rejmánek et al. 2005; Levine 2000). It has also been  
 61 shown that strong interactions between potential  
 62 invaders and recipient ecosystems can strongly influ-  
 63 ence invasion success or failure (Levine et al. 2004;  
 64 Moles et al. 2012). For instance, not all species that  
 65 become invasive are successful everywhere they are  
 66 introduced (Zenni and Nuñez 2013; Hierro et al. 2005;  
 67 Broennimann et al. 2007), and likewise, invasions  
 68 sometimes occur in atypical ecosystems or involve  
 69 atypical invaders (Moles et al. 2012). The frequency of  
 70 idiosyncratic invasion events suggests that our ability  
 71 to make generalizations can still be improved (Gu-  
 72 revitch et al. 2011), and that new tools are needed to  
 73 continue our forward progress (Jeschke et al. 2012;  
 74 Lockwood et al. 2005).

75 Most studies in invasion ecology are conducted at  
 76 local scales and focus on factors regulating invasion  
 77 success or the impacts of specific invaders (Moles  
 78 et al. 2012; Hierro et al. 2005; Vila et al. 2011; Pyšek  
 79 et al. 2012). Yet, numerous hypotheses have been  
 80 developed for addressing mechanisms that operate at  
 81 both small and large spatial and temporal scales to  
 82 help explain invasion success or failure (Hierro et al.  
 83 2005) (Table 1). These hypotheses include: propagule  
 84 pressure (Simberloff 2009), interaction of a given  
 85 introduced species with the abiotic (Hobbs and  
 86 Huenneke 1992; Broennimann et al. 2007) or biotic  
 87 environment (Elton 1958; Davis et al. 2000; Levine  
 88 2000; Callaway and Aschehoug 2000; Pringle et al.

2009) in the recipient ecosystem, and genetic diver-  
 90 gence following introduction (Blossey and Notzold  
 91 1995; Mayr 1970; Dlugosch and Parker 2008; Ell-  
 92 strand and Schierenbeck 2000; Maron et al. 2004).  
 93 While each of these factors likely influences invasion  
 94 success or failure to some degree, a number of  
 95 obstacles have made simultaneous testing of their  
 96 relative influence on invasions success difficult (sum-  
 97 marized in Table 1).

98 Invasion ecologists are increasingly recognizing  
 99 that investigative approaches are needed to simulta-  
 100 neously evaluate the multiple mechanisms proposed to  
 101 drive invasions (Gurevitch et al. 2011; Richardson  
 102 2006; Moles et al. 2012; Sanders et al. 2007; Kueffer  
 103 et al. 2013). One frequently used approach is meta-  
 104 analysis, whereby effect sizes are evaluated from  
 105 published studies where specific invasion hypotheses  
 106 have been tested (e.g. Chun et al. 2010; Colautti et al.  
 107 2004; Levine and D'Antonio 1999; Liu and Stiling  
 108 2006; Moles et al. 2012). While extremely useful in  
 109 evaluating the prevalence of various invasion mech-  
 110 anisms, meta-analyses have several limitations. First,  
 111 conclusions can be influenced by publishing biases,  
 112 where significant effects are more likely to be  
 113 published than studies finding no effects, easily tested  
 114 hypotheses are published more often than less easily  
 115 tested hypotheses (Gurevitch and Hedges 1999; Jes-  
 116 chke et al. 2012), and specific hypotheses are evalu-  
 117 ated more often for some taxonomic groups than for  
 118 others. Additionally, meta-analyses have a limited  
 119 ability to compare the relative influence of multiple  
 120 invasion hypotheses at the same time (Chun et al.  
 121 2010). While meta-analysis will continue to be a  
 122 useful tool for invasion ecology, it's utility is  
 123 constrained by the availability and quality of pub-  
 124 lished studies that simultaneously test multiple inva-  
 125 sion hypotheses (Gurevitch and Hedges 1999).

126 These limitations suggest that the field of invasion  
 127 ecology may greatly benefit from analytical approaches  
 128 where a wide range of mechanisms proposed to  
 129 influence invasion success or failure can be simulta-  
 130 neously evaluated (Richardson et al. 2000a; Moles et al.  
 131 2012). We propose that the identification of model  
 132 invasive species is an underutilized tool that may help  
 133 overcome methodological obstacles for simultaneously  
 134 testing the relative influence of multiple invasion  
 135 hypotheses (Richardson and Rejmánek 2004). We  
 136 propose one species in particular, *Pinus contorta*  
 137 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	<i>P. contorta</i> attribute
<i>Introduction intensity</i>				
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
<i>Abiotic interactions</i>				
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	Broenimann 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
<i>Biotic interactions</i>				
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	<i>P. contorta</i> attribute
Empty niche	Elton (1958), MacArthur (1970)	Invasers 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		
<i>Intraspecific-genetic</i>				
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 <i>P. contorta</i> 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	<i>P. contorta</i> 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 <sup>a</sup>	New Zealand	Argentina	Chile	Sweden	Finland	UK	Ireland
Described Alien Status <sup>b</sup>	Native	Invasive <sup>c,d,e</sup>	Invasive <sup>f</sup> Naturalized <sup>d</sup>	Invasive <sup>g,h</sup>	Invasive <sup>d,e</sup>	No <sup>i</sup> naturalization <sup>g</sup>	Naturalized <sup>i</sup> Invasive <sup>c,d</sup>	Potentially Invasive <sup>k</sup>
Invasive <sup>l</sup> Temperature (°C)	Yes <sup>c,d,e</sup>	Yes <sup>c,d,e</sup>	Yes <sup>f,n</sup>	Yes <sup>g,h</sup>	Unknown	No <sup>i</sup>	Yes	Yes <sup>e</sup>
Max. monthly mean	27 to 38 <sup>m</sup>	23	21.7	18.4	21.0	21.4	19.9	
Min. monthly mean	-57 to 7 <sup>m</sup>	3.8	-2.2	-1.6	-14.0	-13.2	0.3	
Annual precipitation	250 to 500 <sup>m</sup>	876	597	909	569	606	660	
Earliest Introduction (year)	1802		1960	1970s	1920s	1920s	1851	1918
Aerial extent (ha)	26,000,000 <sup>a</sup>	Unknown	6,000 ha <sup>n</sup>	6,545	565,000	10,000	106,000	63,120 ha
Purpose of planting	Commercial & Erosion	Commercial & Erosion	Commercial	Commercial & Erosion	Commercial	Commercial	Commercial	Commercial
Published spread distance (km)	8 <sup>o</sup>		3 <sup>f</sup>	3 <sup>g</sup>	0.3 <sup>d</sup>	-	Unknown	Unknown
Invaded area (ha)	473,200 <sup>o</sup>		Unknown	500 <sup>p</sup>	-	-	-	-
Invaded or naturalized habitats	Grasslands and open/disturbed areas	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	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

<sup>a</sup> Lotan and Critchfield 1990, <sup>b</sup> as described in published literature, <sup>c</sup> Ledgard 2001, <sup>d</sup> Haysom and Murphy 2003, <sup>e</sup>Richardson and Rejmánek 2004, <sup>f</sup> Sarasola et al. 2006, <sup>g</sup> Pena et al. 2008, <sup>h</sup> Langdon et al. 2010, <sup>i</sup> Lähde et al. 1984, <sup>j</sup> McGregor et al. 2012, <sup>k</sup> National Biodiversity Data Centre 2010, <sup>l</sup> Spreading at a rate greater than 100 m in less than 50 years (Richardson et al. 2000a, b), <sup>m</sup> data considering the four varieties in their native ranges, <sup>n</sup> Personal communication with Mauro Sarasola, <sup>o</sup> Personal communication with Nick Ledgard, <sup>p</sup> Unpublished data, Aníbal Pauchard

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

### 188 *Pinus contorta* as a candidate model study system

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

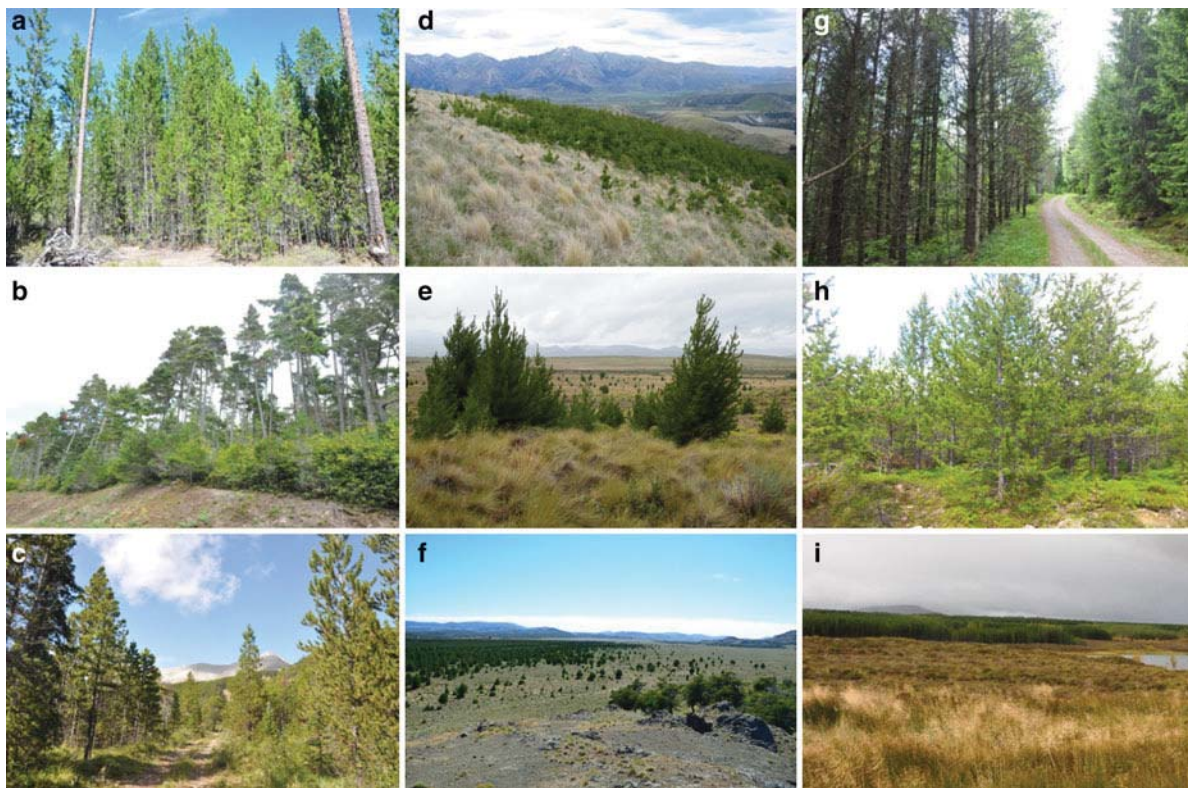
206 Given its high growth rate and its commercial  
207 value, *P. contorta* has been widely introduced around  
208 the world during the past two centuries (Table 2).  
209 These introductions have occurred in many European  
210 countries (Ireland, the United Kingdom, Norway,  
211 Sweden, Finland, and Russia) where many native  
212 species of the *Pinaceae* are present, and has also been  
213 introduced to many Southern Hemisphere countries  
214 where no native species of the *Pinaceae* exist (Chile,  
215 Argentina, New Zealand, Australia, and South Africa).  
216 Across these regions, it has been described as a  
217 naturalized or invasive species in almost every country  
218 where it has been introduced for more than 25 years  
219 (Richardson and Higgins 1998; Haysom and Murphy  
220 2003; Ledgard 2001; Despain 2001; Richardson 2006;  
221 Richardson et al. 1994; Langdon et al. 2010; Sarasola  
222 et al. 2006; Pena et al. 2008; National Biodiversity  
223 Data Centre. *Pinus contorta*. National Invasive Spe-  
224 cies Database 2010). However, invasiveness accord-  
225 ing to the definition of Richardson et al. (2000b; 100 m  
226 in less than 50 years) has only occurred in the southern  
227 hemisphere (e.g. New Zealand, Argentina, and Chile)  
228 (Langdon et al. 2010; Richardson and Rejmánek 2004;  
229 Ledgard 2001; Rejmánek and Richardson 2013),

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

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

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

261 (3) A model plant species should also have  
262 detectable impacts on ecosystems it invades, so that  
263 the various components of invasion impact (i.e.,  
264 distribution, abundance and ecological effects, sensu  
265 Parker et al. 1999) can be revealed. *Pinus contorta* is a  
266 non-trivial invader, meaning it has substantial impacts  
267 in some of the regions it invades. *Pinus contorta* has  
268 been shown to compete with endangered native  
269 species (e.g. *Araucaria araucana*) and reduce the  
270 diversity and abundance of native plants (Urrutia  
271 2012; Nilsson et al. 2008). The species may also  
272 increase fuel loads, generating a more fire-prone  
273 environment (Simberloff et al. 2010; Despain 2001).  
274 In New Zealand and Chile, *P. contorta* was initially  
275 planted for erosion control in mountainous lands, but  
276 has subsequently had transformative effects in these  
277 landscapes (Wardle 1985). It commonly invades  
278 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

279 from grassland or open shrublands to forest systems  
 280 (Dickie et al. 2010; Ledgard 2001), and diminishes  
 281 soil C (Dickie et al. 2010). These examples demon-  
 282 strate that in ecosystems where *P. contorta* does  
 283 become a serious invader, it causes a rapid shift in  
 284 vegetation structure and function, alters availability of  
 285 soil nutrients (e.g. phosphorous), decreases water  
 286 inputs into watershed catchments, and causes reduc-  
 287 tions in indigenous biodiversity (Davis and Lang  
 288 1991; Mark and Dickinson 2008).

289 (4) A model plant species should be easy to  
 290 compare within and across a wide variety of intro-  
 291 duced ranges. Because *P. contorta* has been intro-  
 292 duced throughout temperate and boreal ecosystems  
 293 throughout the world for the purpose of production  
 294 forestry or erosion control, key background data is  
 295 usually available about the introduction event, includ-  
 296 ing the precise time and location where the

introduction event occurred (Elfving et al. 2001; 297  
 Miller and Ecroyd 1987; Ledgard and Baker 1988). 298  
 Initially, most introductions of this species were done 299  
 by government agencies or forest companies which 300  
 often created detailed records of plantation density and 301  
 source populations (i.e. provenance). Because pine 302  
 trees are large and very conspicuous, this basic 303  
 knowledge of introduction allows for easy quantifica- 304  
 tion of two important steps in the invasion process, 305  
 growth rates of individual plants and spread rates from 306  
 plantations, which can be easily compared across 307  
 multiple sites within and across ecosystems (Richard- 308  
 son et al. 2004; Richardson 2006). An additional 309  
 property of *P. contorta* that facilitates simple com- 310  
 parisons across sites is that it is usually established in 311  
 discreet plantations, where planted area and tree 312  
 density within that area are known or easily quantified 313  
 (Visser et al. 2014), allowing propagule pressure to be 314



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

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

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

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

son et al. 2010; Walker et al. 2004; Wilmshurst et al. 361  
 2008; Gundale et al. 2011a). Therefore, hypotheses 362  
 about the role of human disturbances and other anthro- 363  
 pogenic factors can be tested within and across regions. 364

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

380 (9) A model plant species should allow for precise  
 381 pairing of native and introduced populations, so that  
 382 genetic differences can be explicitly evaluated or held  
 383 constant. Many intentional tree introductions are done  
 384 with careful consideration of the genetic characteris-  
 385 tics of the source population. Many plants have large  
 386 native range distributions and exhibit substantial  
 387 genetic variability across those ranges (Parchman  
 388 et al. 2011). At course spatial scales, genetic differ-  
 389 ences within the native range populations allow  
 390 species to be locally adapted to broad scale differences  
 391 in climate and latitude. Like most intentional tree  
 392 introductions, introduction of *P. contorta* into each  
 393 recipient region was done through the selection of  
 394 appropriate native range populations that were  
 395 matched for the abiotic properties of the introduced  
 396 range. Additionally, multiple provenances from a  
 397 particular native range location were often introduced  
 398 to each recipient country in common plantations to  
 399 evaluate which provenances perform best in the  
 400 introduced region (Fries et al. 1998; Elfving et al.  
 401 2001; Lähde et al. 1984; Ledgard 2001). Using these  
 402 provenance trials in combination with genetic analysis  
 403 would allow for straightforward comparisons across  
 404 introduced regions to evaluate how genetic differences  
 405 among introduced populations influence patterns of  
 406 invasions (Zenni and Simberloff 2013).

407 **The use of *Pinus contorta* for hypothesis testing**

408 The extent to which invasion patterns are controlled by  
 409 introduction intensity, abiotic or biotic factors in the  
 410 receiving environment, or genetic variability of the  
 411 invader, or the interaction of these factors, is a key  
 412 question in invasion ecology which has direct impli-  
 413 cations for managing introduced species (Gurevitch  
 414 et al. 2011; Moles et al. 2008; Theoharides and Dukes  
 415 2007). While the relative contribution of these factors  
 416 are difficult to evaluate for most invaders, the nine  
 417 attributes described above highlight the utility of  
 418 forestry species in general, and *P. contorta* specifi-  
 419 cally, to serve as models to investigate plant invasion  
 420 hypotheses. Here we provide three examples of how  
 421 this study system could be used to broaden our  
 422 knowledge of multiple mechanisms proposed to  
 423 influence invasion success.

424 **Antagonistic biotic interactions**

425 Several hypotheses seeking to better understand  
 426 species invasion patterns propose that differences in  
 427 the presence or strength of biotic interactions can be an  
 428 influential factor on invasion success or failure (Elton  
 429 1958; Davis et al. 2000; Levine and D'Antonio 1999)  
 430 (Table 1). One of the most frequently cited explana-  
 431 tions for successful invasions is the Enemy Release  
 432 Hypothesis (ERH) (Elton 1958; Keane and Crawley  
 433 2002), which proposes that all plants are negatively  
 434 affected to some degree by specialist herbivores or  
 435 pathogens in their native ranges, and that escape from  
 436 these negative interactions allows non-native species  
 437 to achieve higher individual growth and reproductive  
 438 rates and subsequently higher population and meta-  
 439 population growth rates relative to what they achieve  
 440 in their native ranges, and relative to native species in  
 441 their introduced range (Keane and Crawley 2002;  
 442 Mitchell and Power 2003). Other invasion hypotheses  
 443 have focused on the role of plant–plant competition as  
 444 a regulator of invasion success (for thorough review  
 445 see MacDougall et al. 2009). Three such hypotheses,  
 446 The Empty Niche Hypothesis (Elton 1958), the  
 447 Diversity-Invasibility Hypothesis (Kennedy et al.  
 448 2002; Levine et al. 2004), and the Fluctuating  
 449 Resources Hypothesis (Davis et al. 2000) each predict  
 450 that competition intensity between a potential invader  
 451 and native species is a key determinant of invader  
 452 success.

While these hypotheses feature prominently in the  
 invasion ecology literature, Hierro et al. (2005) noted  
 that their successful evaluation requires explicit com-  
 parisons 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 popula-  
 tions may result in unintentional underlying compar-  
 isons 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).

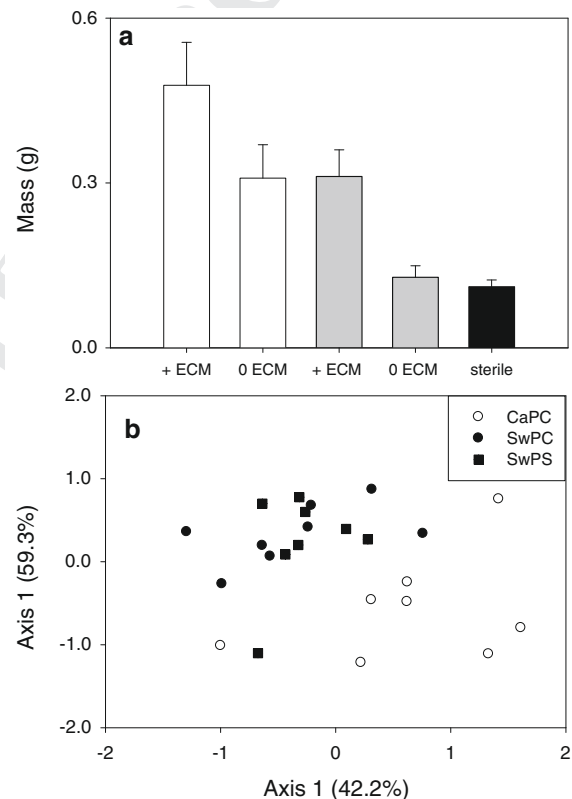
Overcoming these major obstacles opens up a wide  
 range of broad questions regarding the context in  
 which antagonistic interactions may control invasion  
 success or failure. For instance: Are species more  
 likely to encounter negative biotic interactions when  
 introduced into ecosystems where 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  
 (Brodrribb 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 mamma-  
 lian 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

502 same or closely related enemy species have co-  
 503 evolved with *P. sylvestris* in Europe (e.g. Moose,  
 504 *Alces alces*, or bark beetles, *Dendroctonus*; Bejer  
 505 1981), and therefore have the potential to negatively  
 506 impact *P. contorta* following introduction in those  
 507 regions (Lindelow and Bjorkman 2001). *Pinus contorta*  
 508 may also have a greater likelihood of encountering  
 509 novel enemies in European forests that can  
 510 utilize either tree species as a host (Lindelow and  
 511 Bjorkman 2001). For instance, the European fungal  
 512 pathogen *Gremmeniella abietina* has been shown in  
 513 some locations to strongly impact *P. contorta* growth  
 514 in Sweden, albeit to a lesser degree than its impact on  
 515 *P. sylvestris* (Bernhold et al. 2009). These interactions  
 516 with novel enemies may be less common in southern  
 517 hemisphere locations, due to much more distant co-  
 518 evolutionary histories of the pathogens and herbivores  
 519 in those regions. Because the global network of *P.*  
 520 *contorta* introductions we have described covers a  
 521 variety of countries in both northern European and  
 522 Southern Hemisphere environments, this general  
 523 question about the phylogenetic relatedness of native  
 524 vegetation as a determinant of antagonistic interac-  
 525 tions with introduced species can be robustly  
 526 evaluated.

### 527 Mycorrhizal co-invasion

528 A logical corollary to antagonistic interaction hypoth-  
 529 eses is that the absence of key mutualists in introduced  
 530 ranges may constrain invasions (Dickie et al. 2010;  
 531 Nunez et al. 2009; Pringle et al. 2009). Currently a  
 532 very active area of research is focused on the  
 533 interaction of introduced plant species with soil biota  
 534 (Klironomos 2002), including both soil pathogens  
 535 (Diez et al. 2010; Reinhart and Callaway 2006) and  
 536 soil mutualists (Richardson et al. 2000a; Nunez et al.  
 537 2009; Pringle et al. 2009; Schwartz et al. 2006).  
 538 Parallel research in several different countries has  
 539 examined the role of ectomycorrhizal fungi in the  
 540 establishment of *P. contorta*, including in its native  
 541 range (Ashkannejhad and Horton 2006; Byrd et al.  
 542 2000; Cullings et al. 2000) and as an invasive species  
 543 in Argentina (Nunez et al. 2009) and New Zealand  
 544 (Dickie et al. 2010). *Pinus contorta* mutualisms with  
 545 ectomycorrhizal fungi are of particular interest, as a  
 546 lack of mycorrhizal inoculum was initially a barrier to  
 547 establishing plantations (Marx 1991). In some coun-  
 548 tries a lack of mycorrhizal fungi remains a limiting

549 factor for spatial spread. In Argentina, for example,  
 550 Nunez et al. (2009) showed that *P. contorta* does not  
 551 grow well in soils distant from plantations, unless they  
 552 are first inoculated with soil microbes associated with  
 553 the plantation (Fig. 2a), whereas, this is no longer a  
 554 barrier in other countries, where *P. contorta* now  
 555 spreads widely (Ledgard 2001; Pringle et al. 2009).  
 556 Understanding how *P. contorta* has overcome the  
 557 initial limitation is important not just in the context of  
 558 *Pinus*, but also in predicting future invasiveness of  
 559 other mutualist-dependent species (Diez 2005; Pringle  
 560 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)

561 As with questions focused on antagonistic interac-  
 562 tions, a highly relevant broad scale question that can  
 563 be asked regarding mycorrhizal associations is  
 564 whether the phylogenetic similarity of native vegeta-  
 565 tion determines whether suitable mycorrhizal species  
 566 are present or not, and therefore constitute an invasion  
 567 barrier? Using a very coarse technique to evaluate soil  
 568 microbial communities (phospholipid fatty acid tech-  
 569 nique, PLFA), McIntosh et al. (2012) showed that  
 570 microbial communities did not differ between intro-  
 571 duced *P. contorta* and native *P. sylvestris* plantations,  
 572 whereas both these stand types differed significantly  
 573 from soil in the native range of *P. contorta* (Fig. 2b).  
 574 Further, Kardell et al. (1987) evaluated fungal sporo-  
 575 carps in Swedish *P. contorta* and *P. sylvestris* stands,  
 576 and found that the community composition of known  
 577 ectomycorrhizal species were present in both stand  
 578 types. While further analyses are required to specifi-  
 579 cally evaluate ectomycorrhizal associations in Euro-  
 580 pean forests, these studies suggest that the  
 581 phylogenetic relatedness of the vegetation of the  
 582 recipient community likely determine whether these  
 583 key mutualisms can be successfully established, and  
 584 thereby may influence initial growth and invasion  
 585 patterns among contrasting regions.

#### 586 Biotic-environment-genotype interactions

587 These questions focused on either positive or antag-  
 588 onistic biotic interactions invoke a range of larger  
 589 scale questions that can be addressed using model  
 590 species, such as the *P. contorta* system we have  
 591 described. As described earlier, because *P. contorta* is  
 592 introduced for forestry purposes, field trials have been  
 593 established in many different countries to identify  
 594 which genetic provenances perform most optimally  
 595 under different environmental conditions within each  
 596 country, providing an opportunity to investigate the  
 597 importance of interactions between genes, the biotic  
 598 community, and abiotic environment. As an example,  
 599 one specific hypothesis, the Evolution of Increased  
 600 Competitive Ability (EICA) (Blossey and Notzold  
 601 1995), proposes that when an introduced species has  
 602 escaped enemies from its native range, that there will  
 603 be a positive selection for growth traits and a de-  
 604 selection of defense traits, thereby increasing vigor of  
 605 the introduced population relative to native range  
 606 populations. The global setting of *P. contorta* could be  
 607 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 ectomycor-  
 rhizas for successful growth, or can some provenances  
 more readily associate with cosmopolitan ectomycor-  
 rhizas, leading to divergence of native and introduced  
 populations?

Likewise, the global system of *P. contorta* intro-  
 ductions 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). There-  
 fore, 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 depen-  
 dency 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 under-  
 stand 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).

#### 643 Limitations of *P. contorta* as a model

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

- 650 1. While *P. contorta* has been introduced into a wide  
 651 range of temperate and boreal habitats, its distri-  
 652 bution is not as widespread as many other invaders



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

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

669 3. The relatively long generation time of *P. contorta*  
 670 also diminishes the speed at which genetic  
 671 divergence may occur among invading popula-  
 672 tions, thereby potentially making it difficult to  
 673 evaluate some aspects of the EICA hypothesis;  
 674 however, as noted above, this same characteristic  
 675 may be useful for testing some invasion hypoth-  
 676 eses, where it is desirable to hold genetic differ-  
 677 ences constant.

678

### 679 Beyond *Pinus contorta*

680 No single species can be used to answer all questions  
 681 in the field of invasion ecology. Invasive plant species  
 682 exhibit a wide range of morphologies, physiologies,  
 683 and life history strategies that make it difficult to draw  
 684 general conclusions from investigation of a single  
 685 species. However, for most invasive species, it is  
 686 difficult or impossible to disentangle the influence of  
 687 propagule pressure, abiotic interactions, biotic inter-  
 688 actions, and intraspecific genetic differences, simply  
 689 because there is no documented history of the  
 690 introduction, and growth and invasion patterns are  
 691 not easily measured or compared across regions.  
 692 Selection of model species following the criteria we  
 693 have described would greatly improve our ability to  
 694 test multiple invasion hypotheses simultaneously, and  
 695 therefore improves our understanding of the relative  
 696 importance of multiple mechanisms controlling inva-  
 697 sion success across multiple scales. Given that not all  
 698 invasive species are the same, we hope that the  
 699 *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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