Community phylogenetics and species invasion:

deconstructing Darwin's naturalization conundrum

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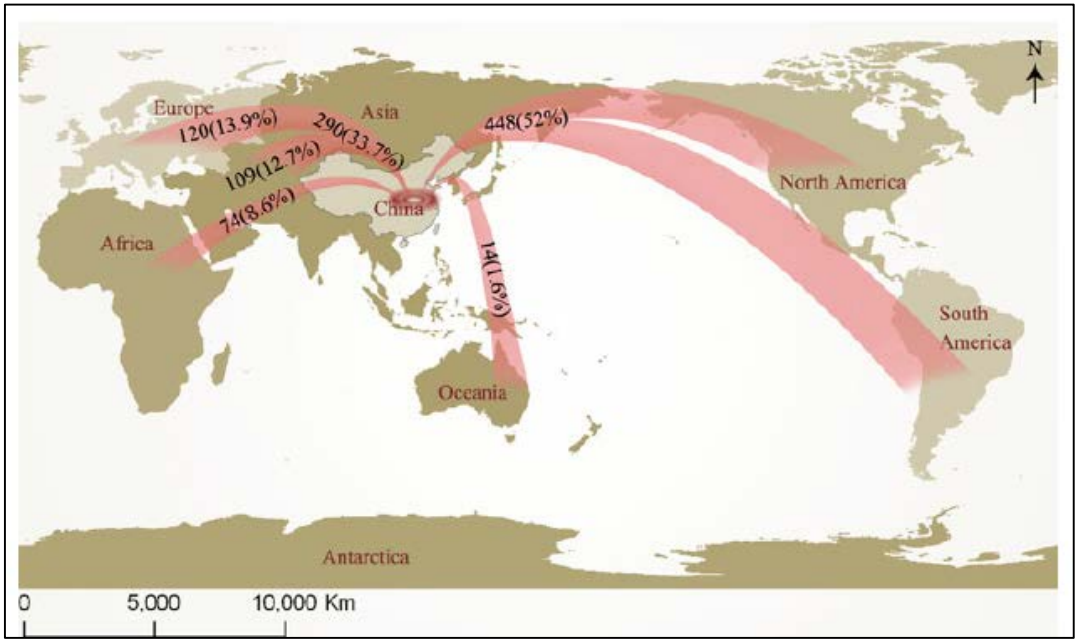
One big question in invasion ecology:

Why some, but not all, introduced species successfully establish in their recipient ecosystems, and even fewer of these species become problematic?



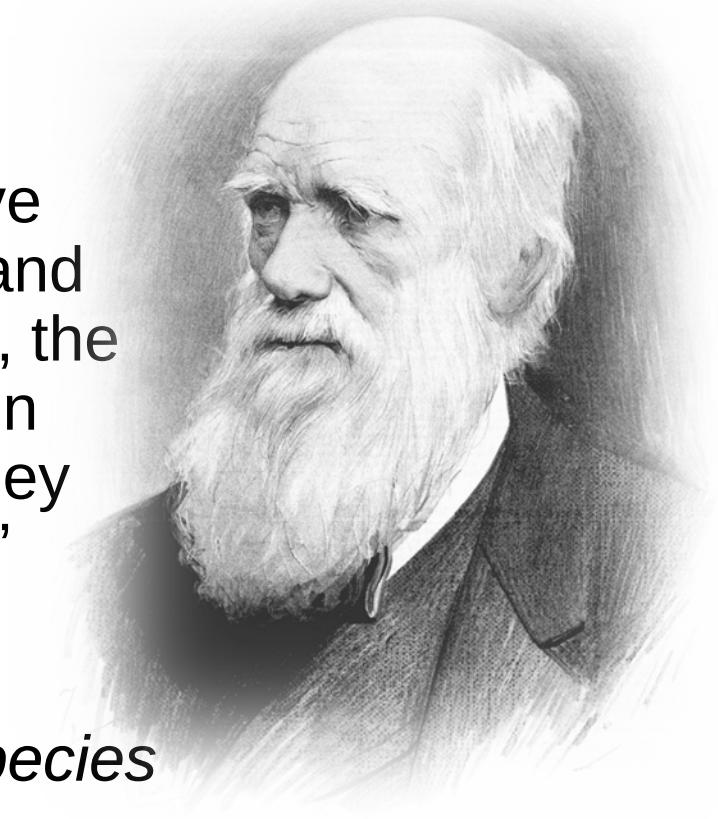
Jiang *et al.* 2011. *Biodivers Conserv.*

Invasion is a fight between invaders and the resident species in the invaded community, and invasion succession depends on the ecological similarities between invaders and residents.

Invaders versus Residents

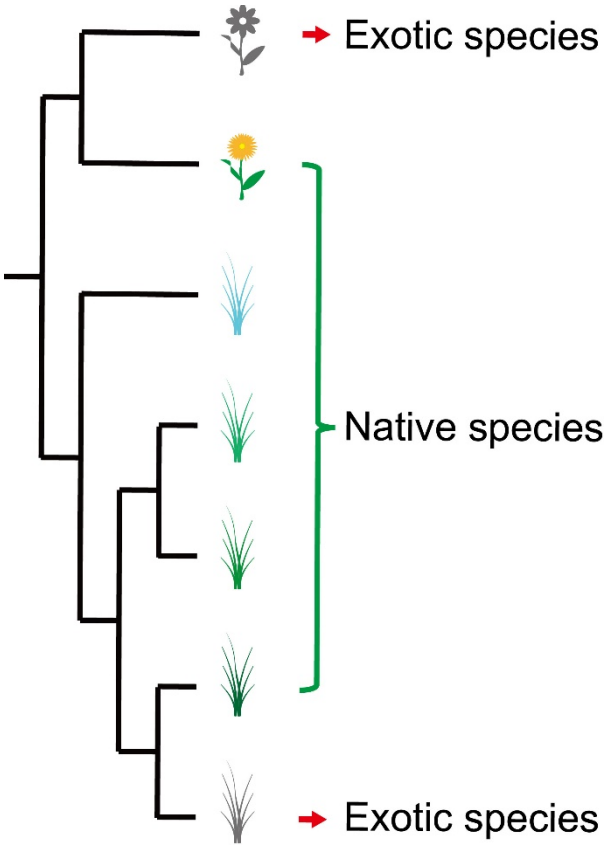
Darwin's naturalization hypothesis

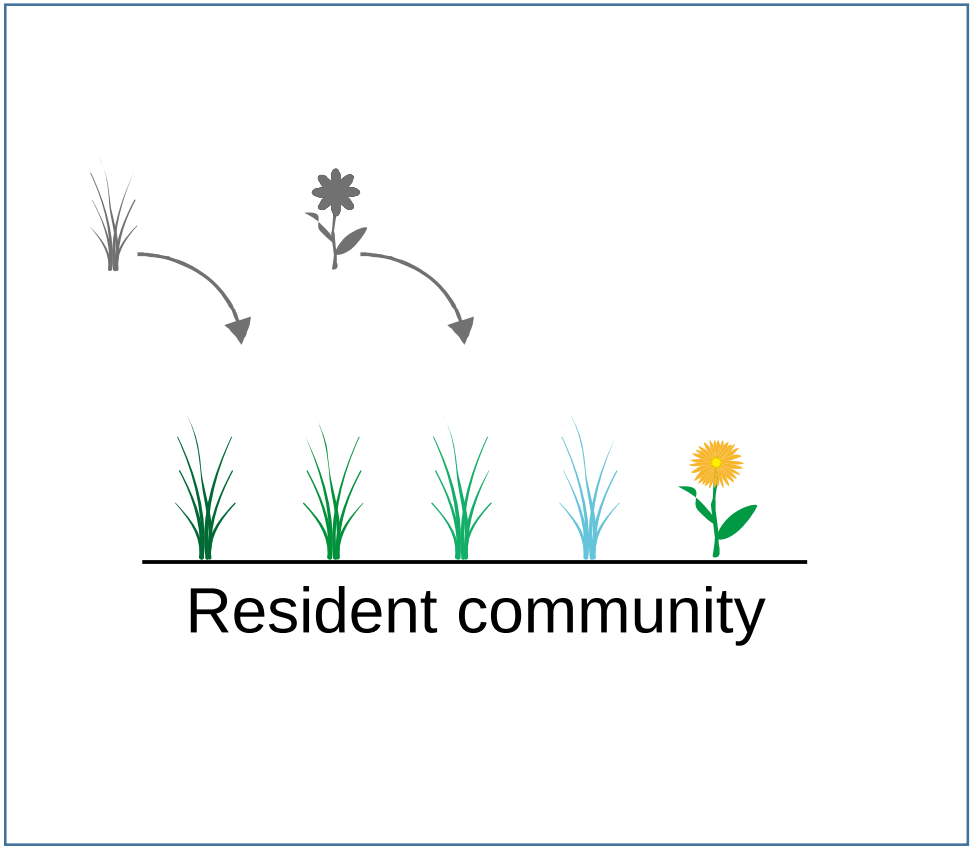
"As species of the same genus have usually … some similarity in habits and constitution, and always in structure, the struggle will be more severe between species of the same genus, when they come into contact with each other..."



----Darwin. 1859. *The Origin of Species*

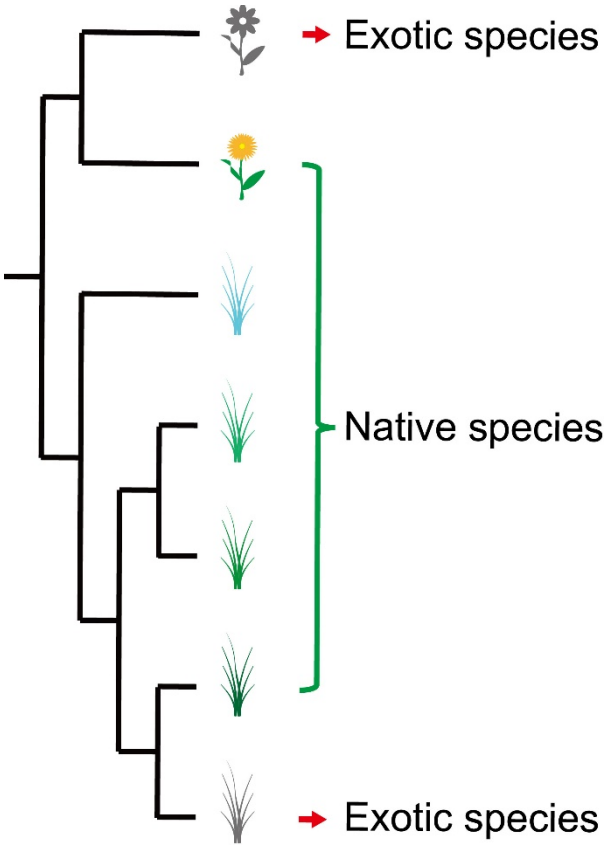
Darwin's naturalization hypothesis

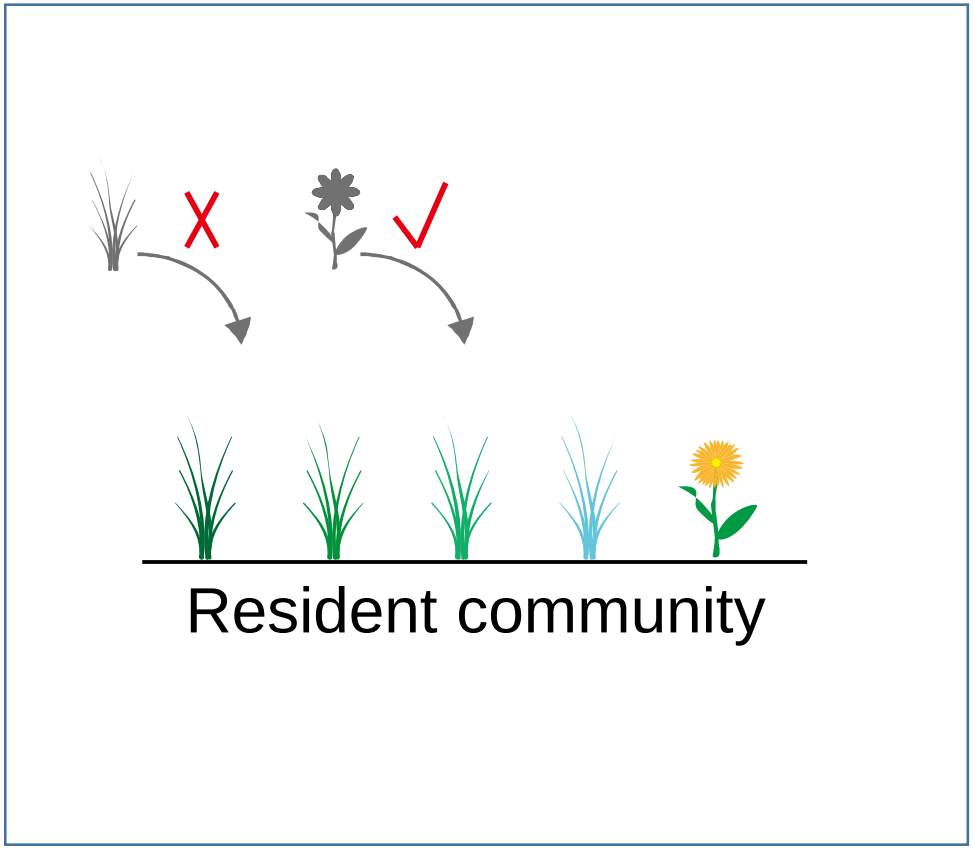




Daehler 2001. *Am. Nat.*

Darwin's naturalization hypothesis





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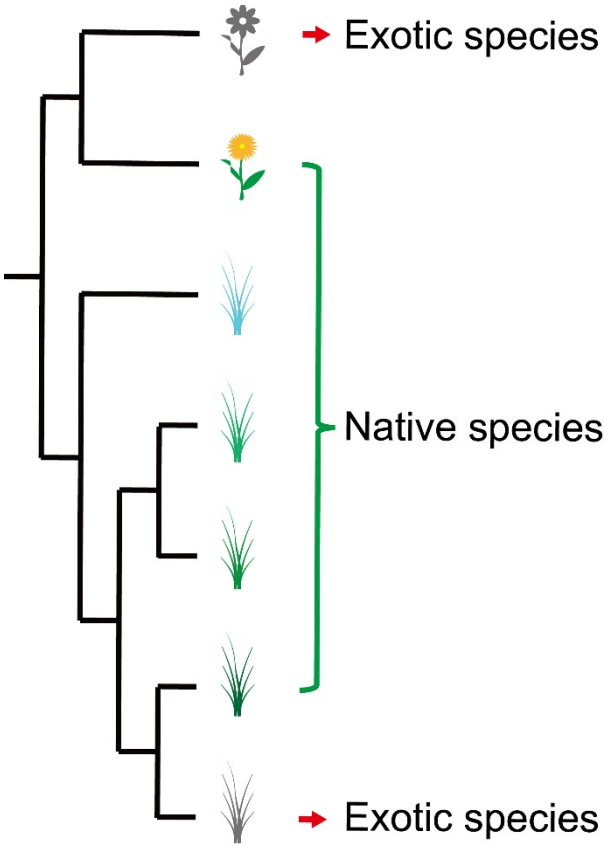
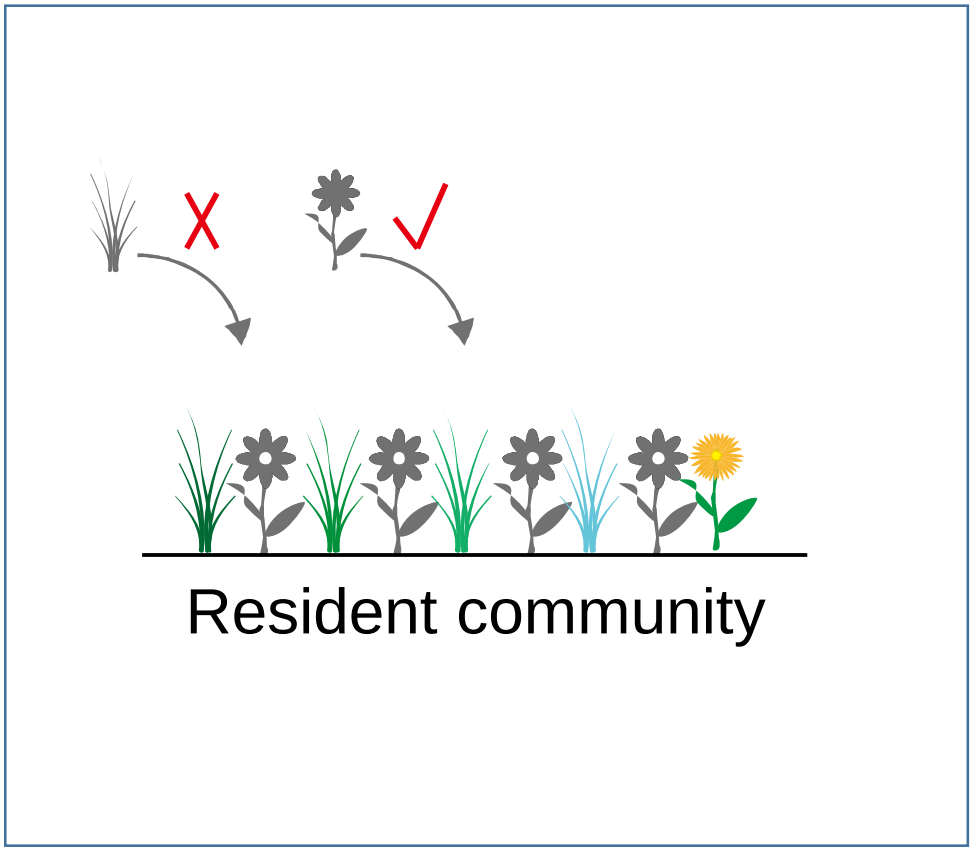
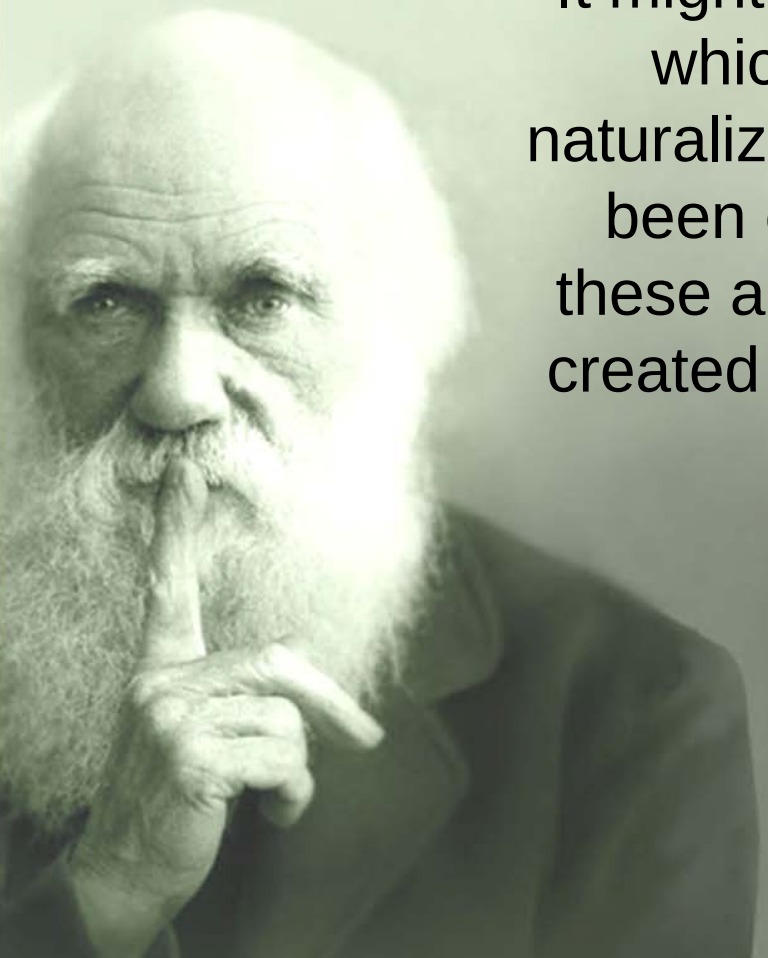


Competitive interactions



Daehler 2001. *Am. Nat.*

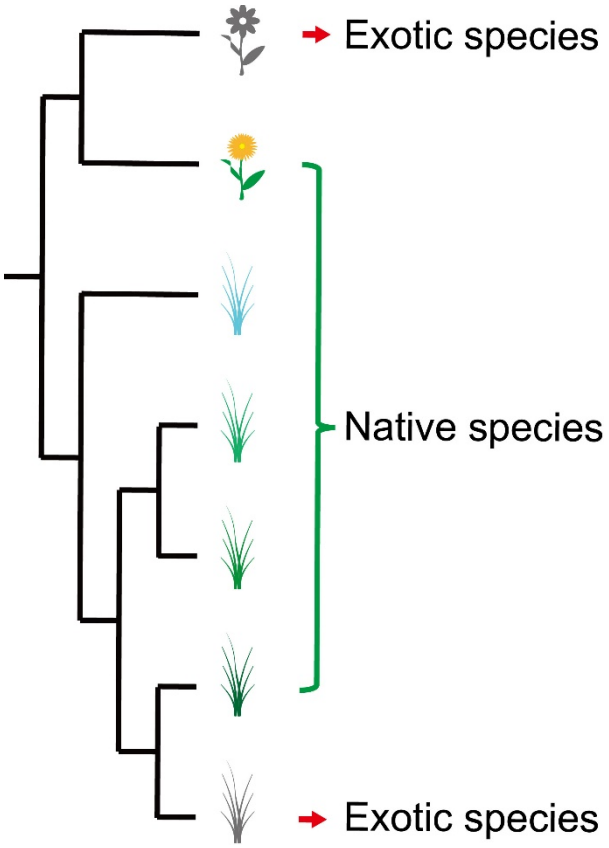
Pre-adaptation hypothesis

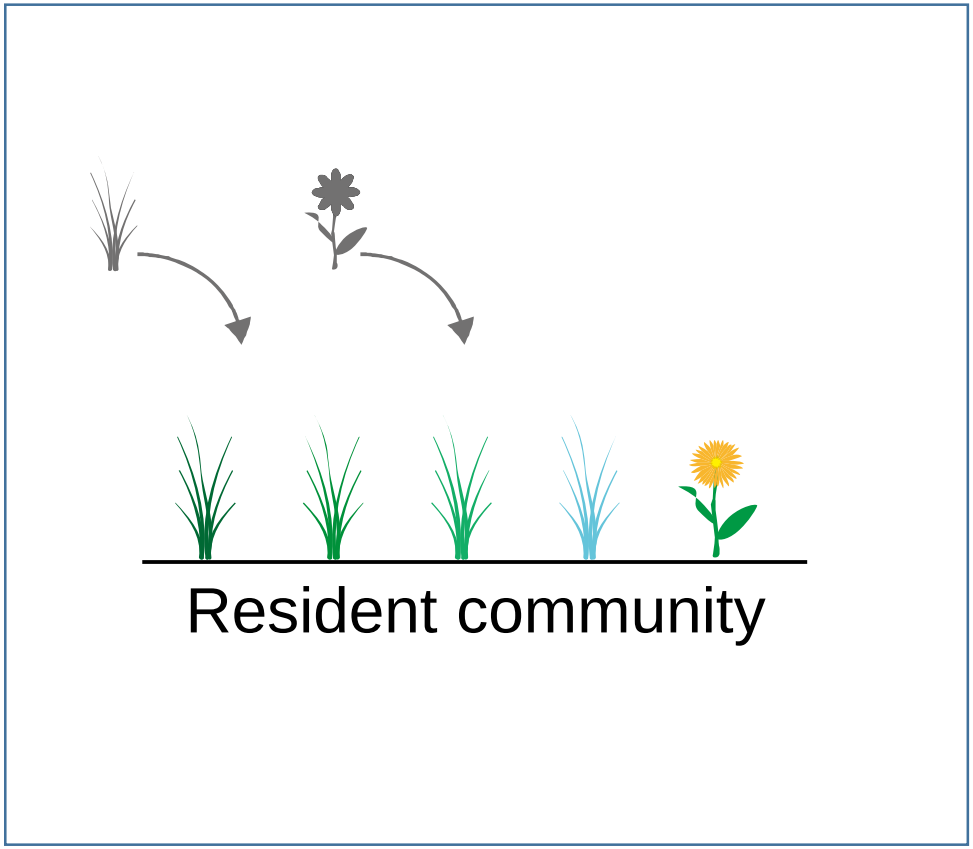


"It might have been expected that the plants which have succeeded in becoming naturalized in any land would generally have been closely allied to the indigenes; for these are commonly looked at as specially created and adapted for their own country."

Darwin. 1859. *The Origin of Species*

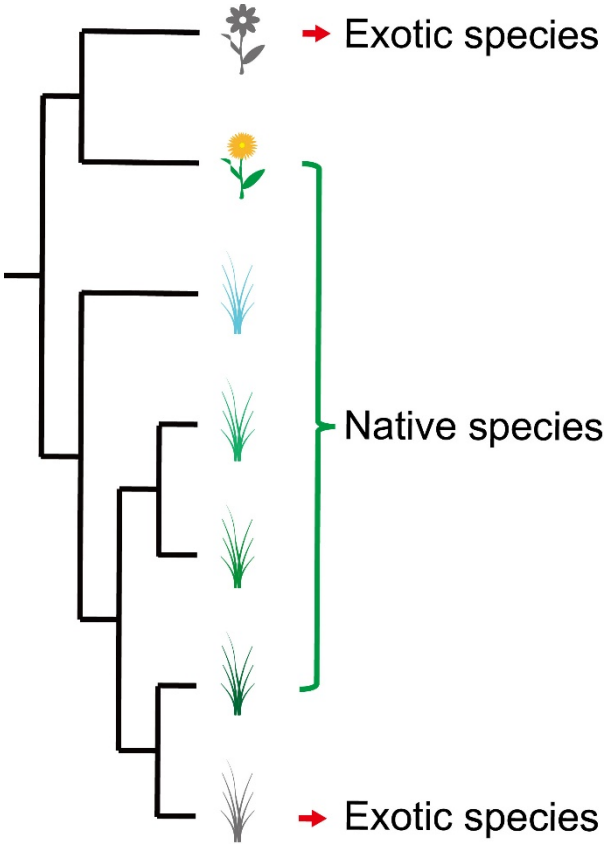
Pre-adaptation hypothesis

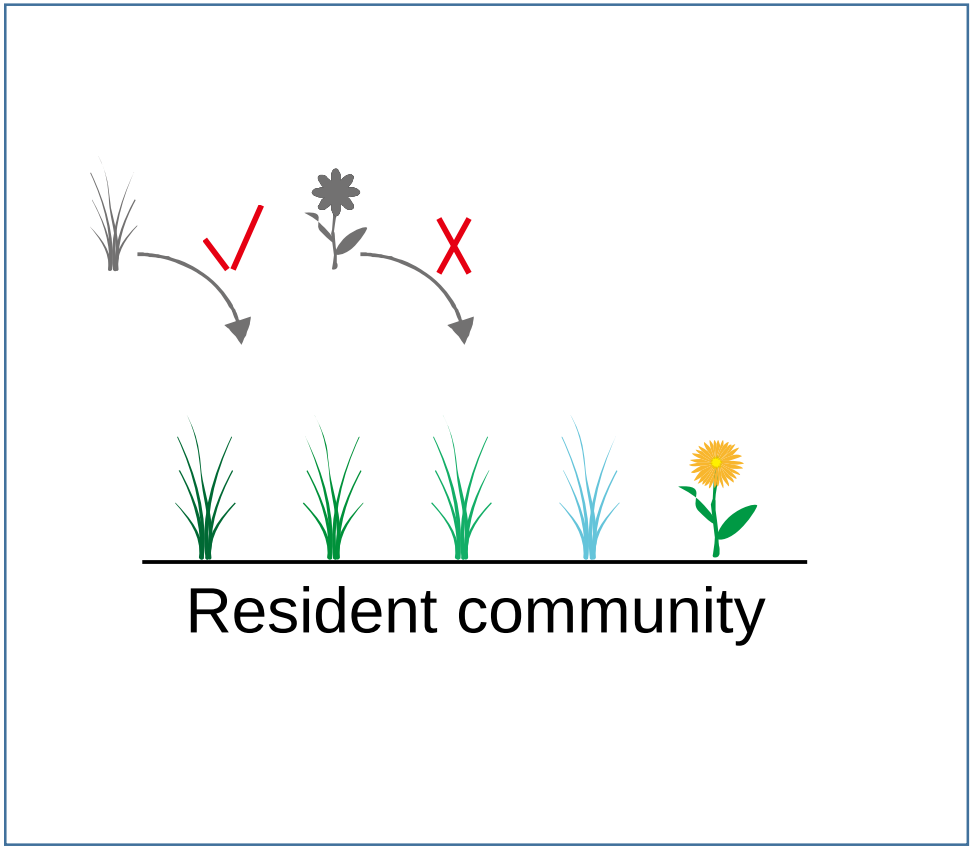




Ricciardi & Mottiar 2006. *Biol. Inv.*

Pre-adaptation hypothesis





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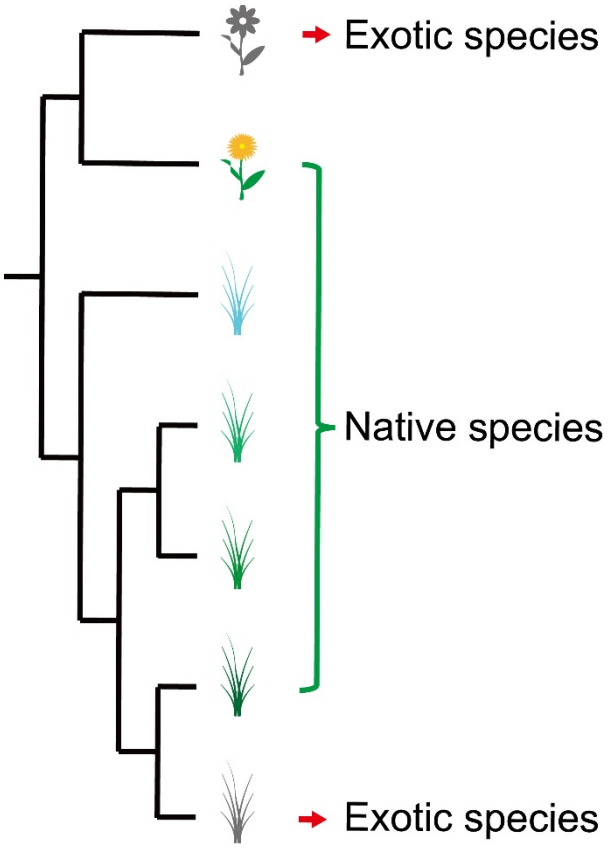
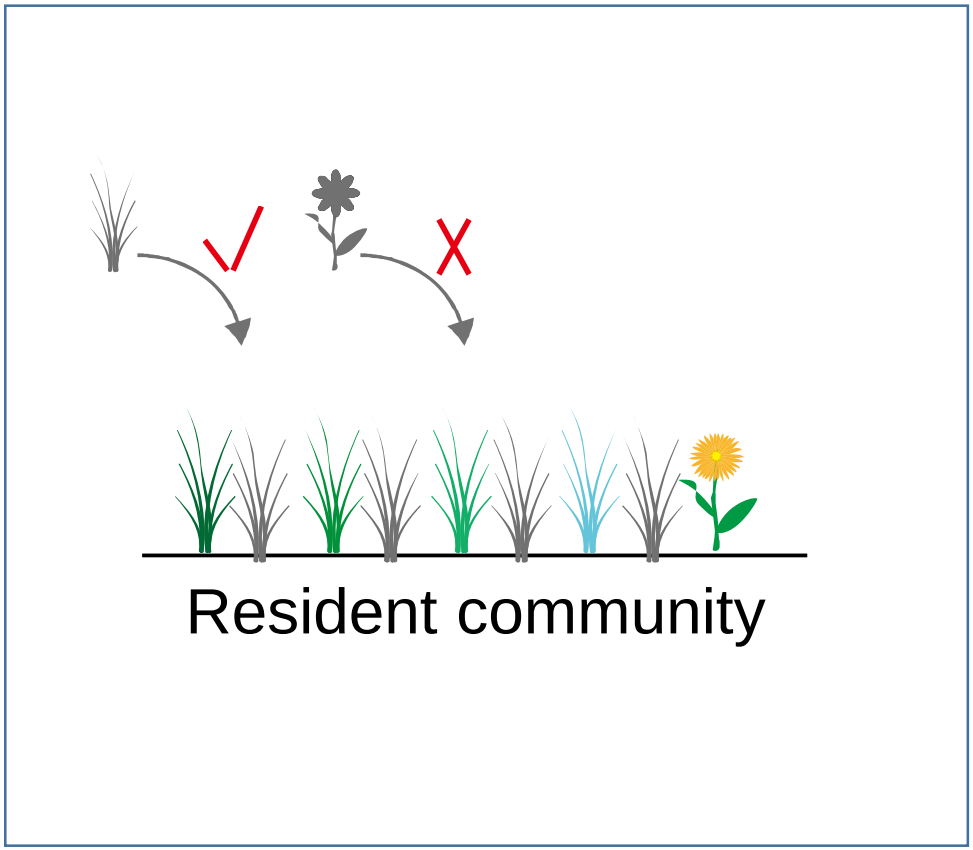
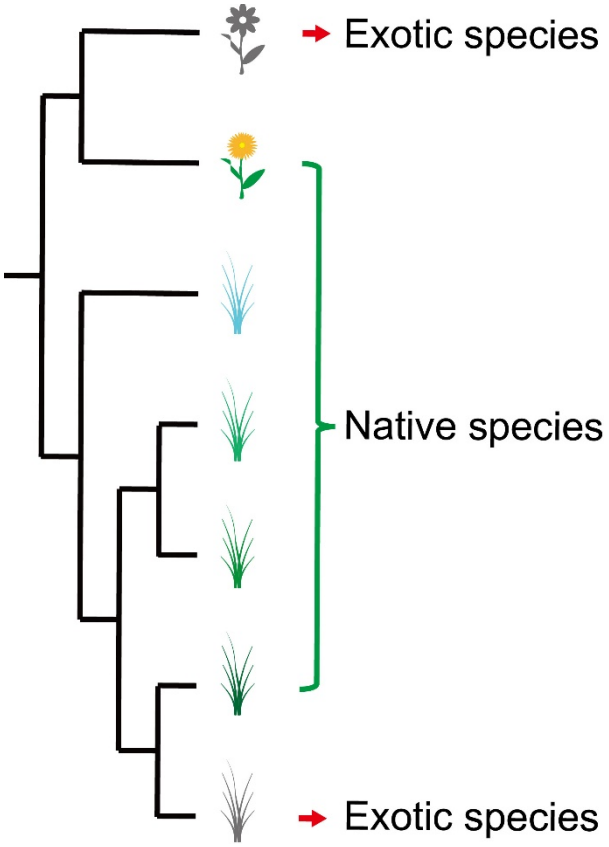


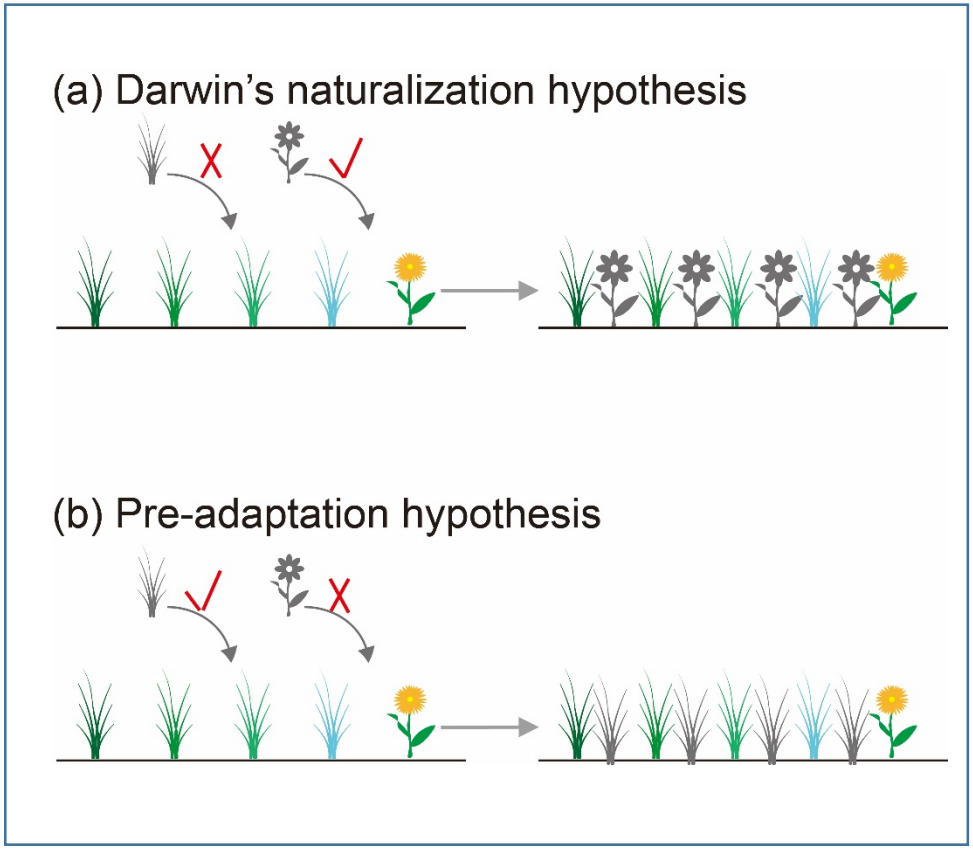
Environmental filtering



Ricciardi & Mottiar 2006. *Biol. Inv.*

Darwin's naturalization conundrum





Diez *et al*. 2008. *Ecol. Lett.*

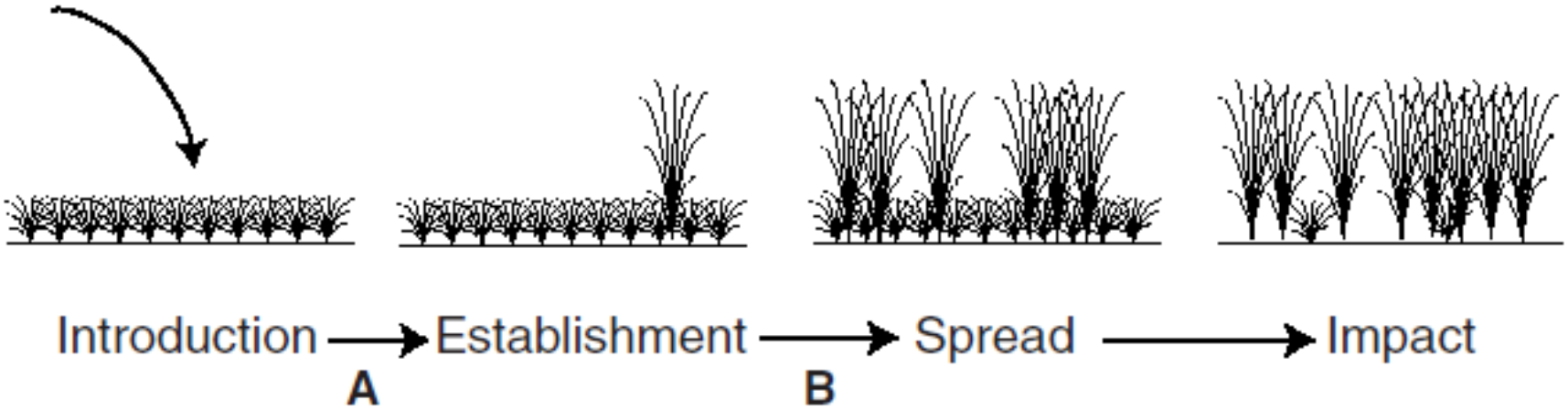
Recent studies produced mixed results…

Table 1. The effect of phylogenetic relatedness on the probability of establishment by nonnative species

Study	Taxon	Location	Effect of relatives
Mack et al., 1996 (32)	Plants	United States	–
Rejmanek, 1996 (33)	Plants	California	–
Daehler, 2001 (38)	Plants	Hawaii	+
Duncan and Williams, 2002 (39)	Plants	New Zealand	+
Diez et al., 2008 (40)			
Lambdon and Hulme, 2006 (47)	Plants	Mediterranean islands	0
Ricciardi and Mottiar, 2006 (48)	Fish	Global	0
Diez et al., 2009 (41)	Plants	Australia, New Zealand	+
Jiang et al., 2010 (34)	Bacteria	Experimental	–
Tan et al., 2012 (37)			
Davies et al., 2011 (35)	Plants	California (Serpentine)	–
Tingley et al., 2011 (42)	Amphibians	Global	+
van Wilgen and Richardson, 2011 (36)	Reptiles	California, Florida	–
Violle et al., 2011 (30)	Protists	Experimental	–
Ferreira et al., 2012 (43)	Reptiles	Global	+
Peay et al., 2012 (31)	Nectar yeast	Experimental	–
Maitner et al., 2012 (44)	Birds	Florida, Hawaii, New Zealand	+

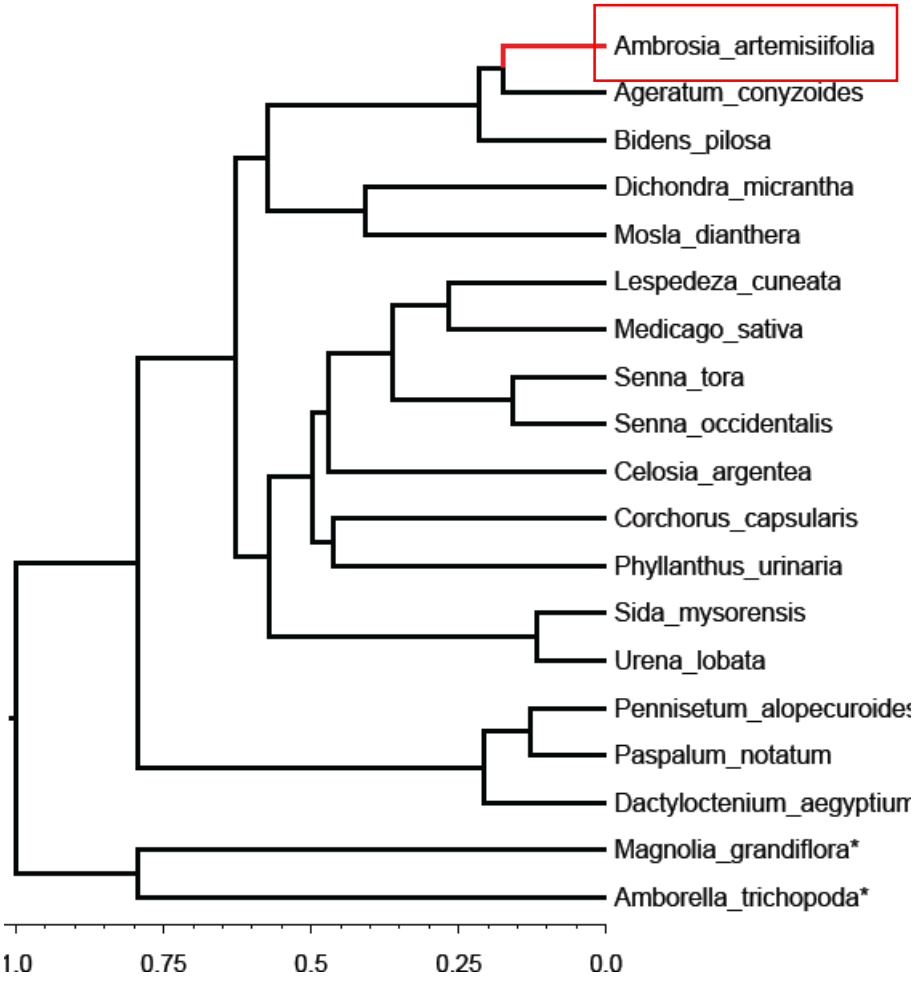
Jones *et al.* 2011. *PNAS*

The validity of Darwin's hypothesis is invasion stage dependent.

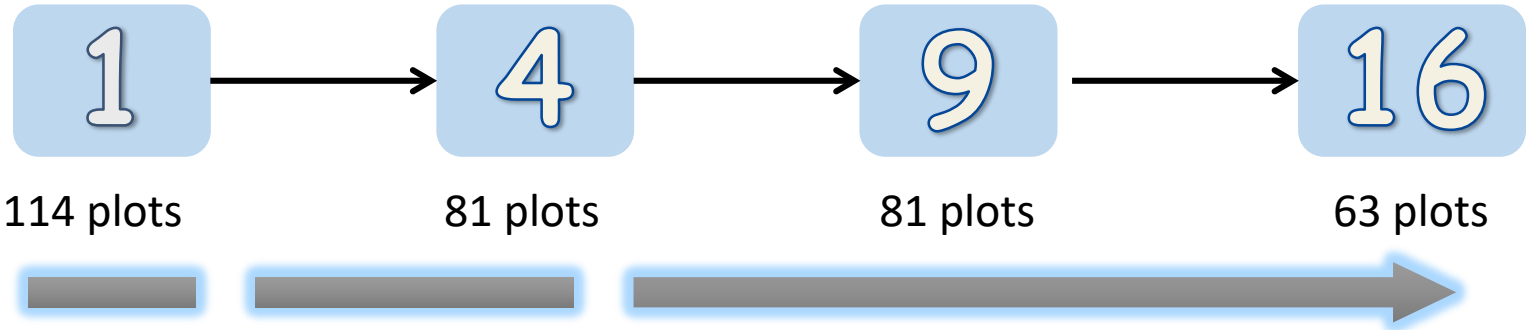


Levine et al. 2004. *Ecol. Lett.*

Species pool



Experimental design



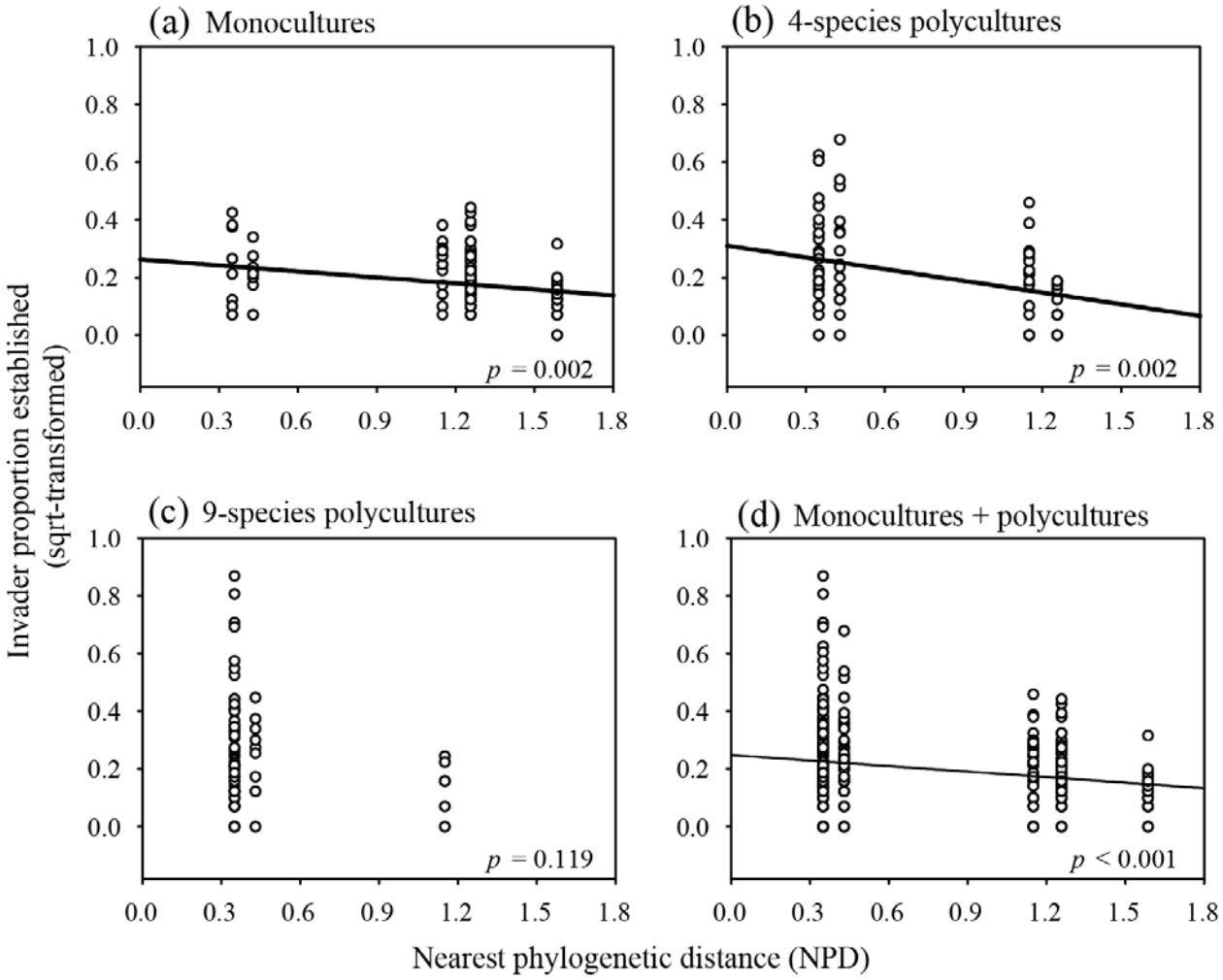






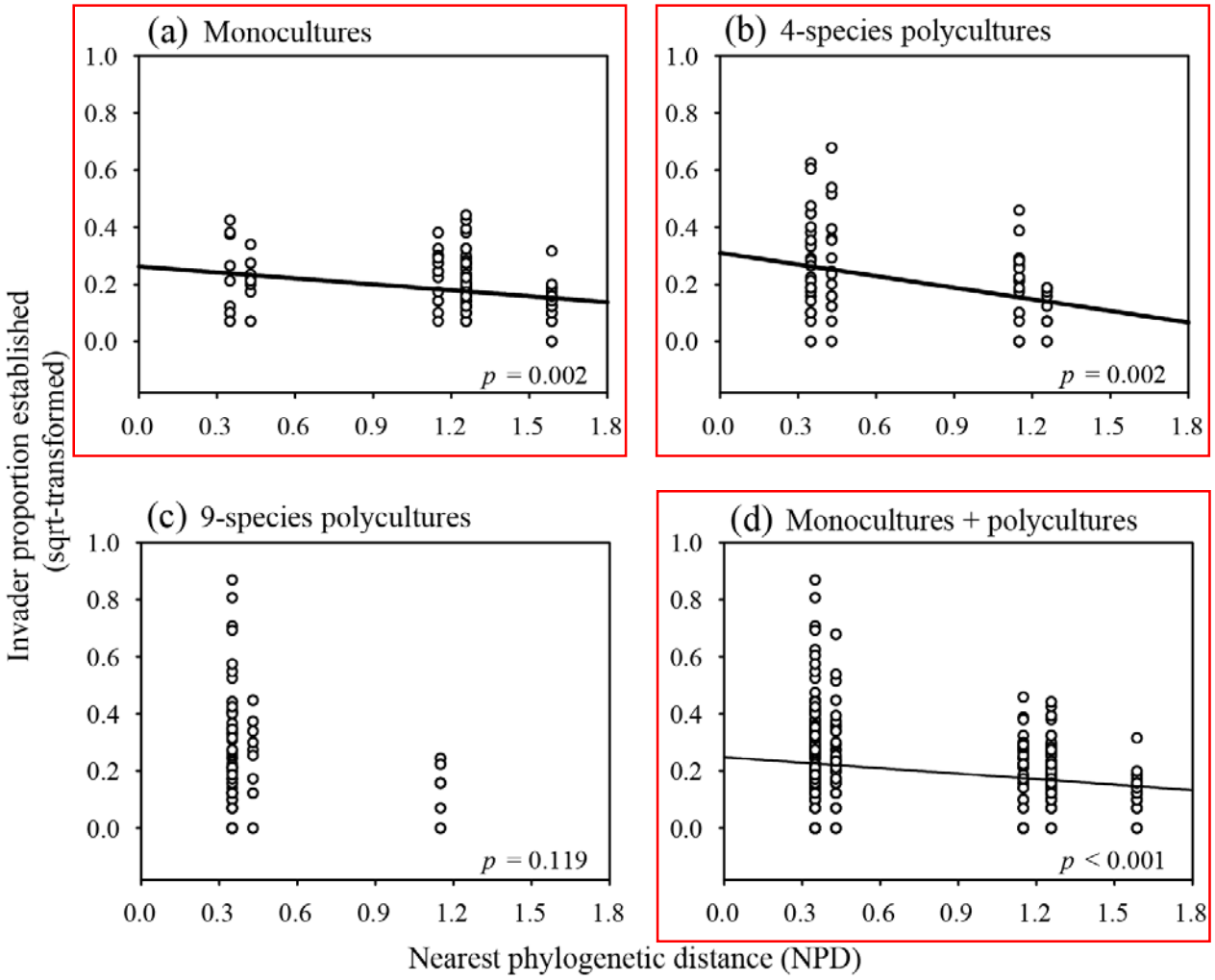


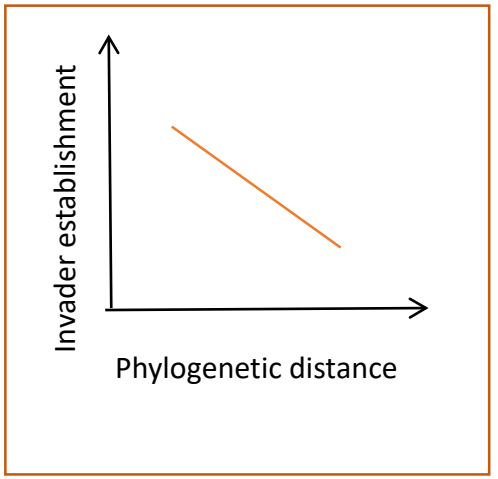
Phylogenetic relatedness on **Invader Density**



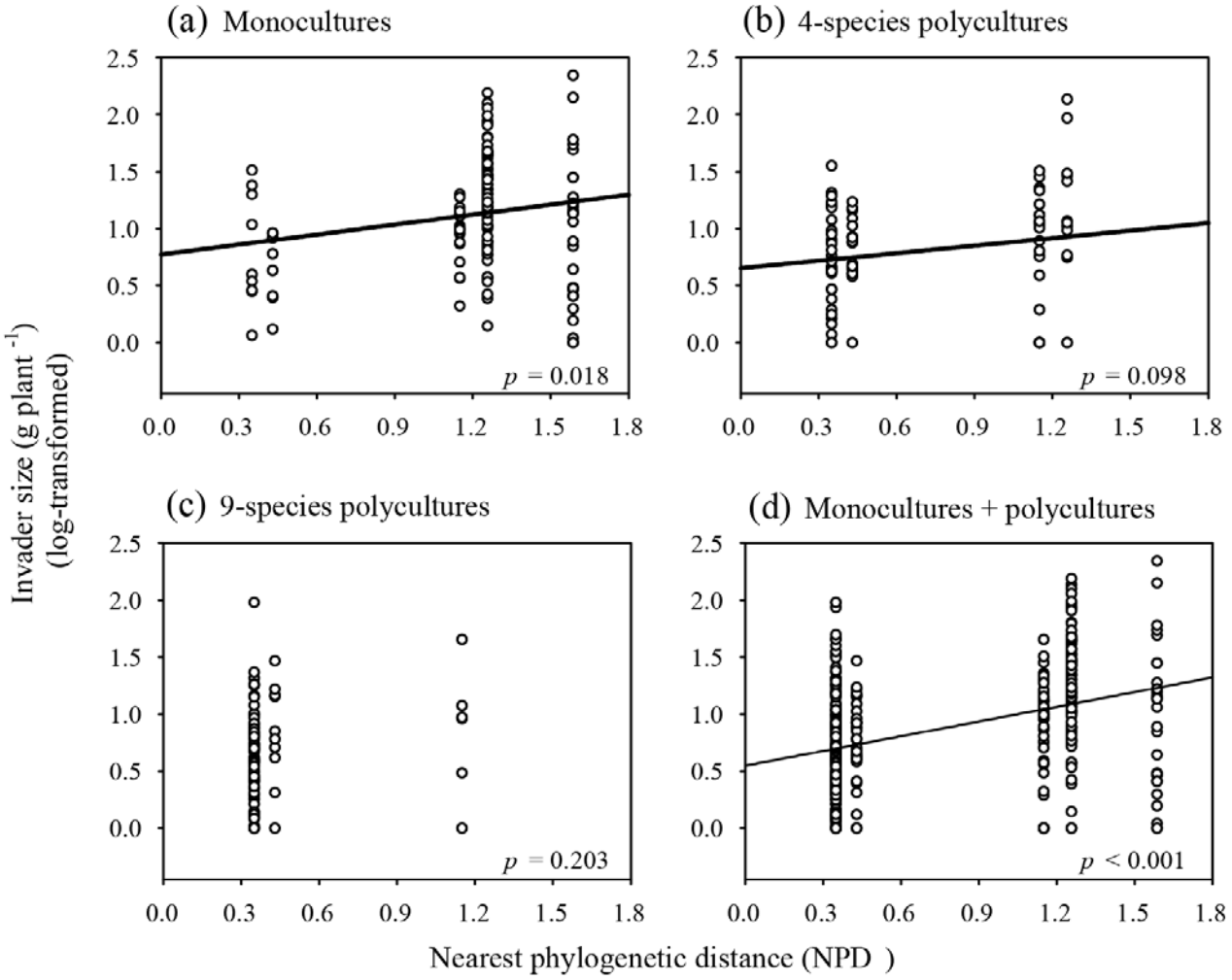
Phylogenetic relatedness on **Invader Density**

Pre-adaptation hypothesis



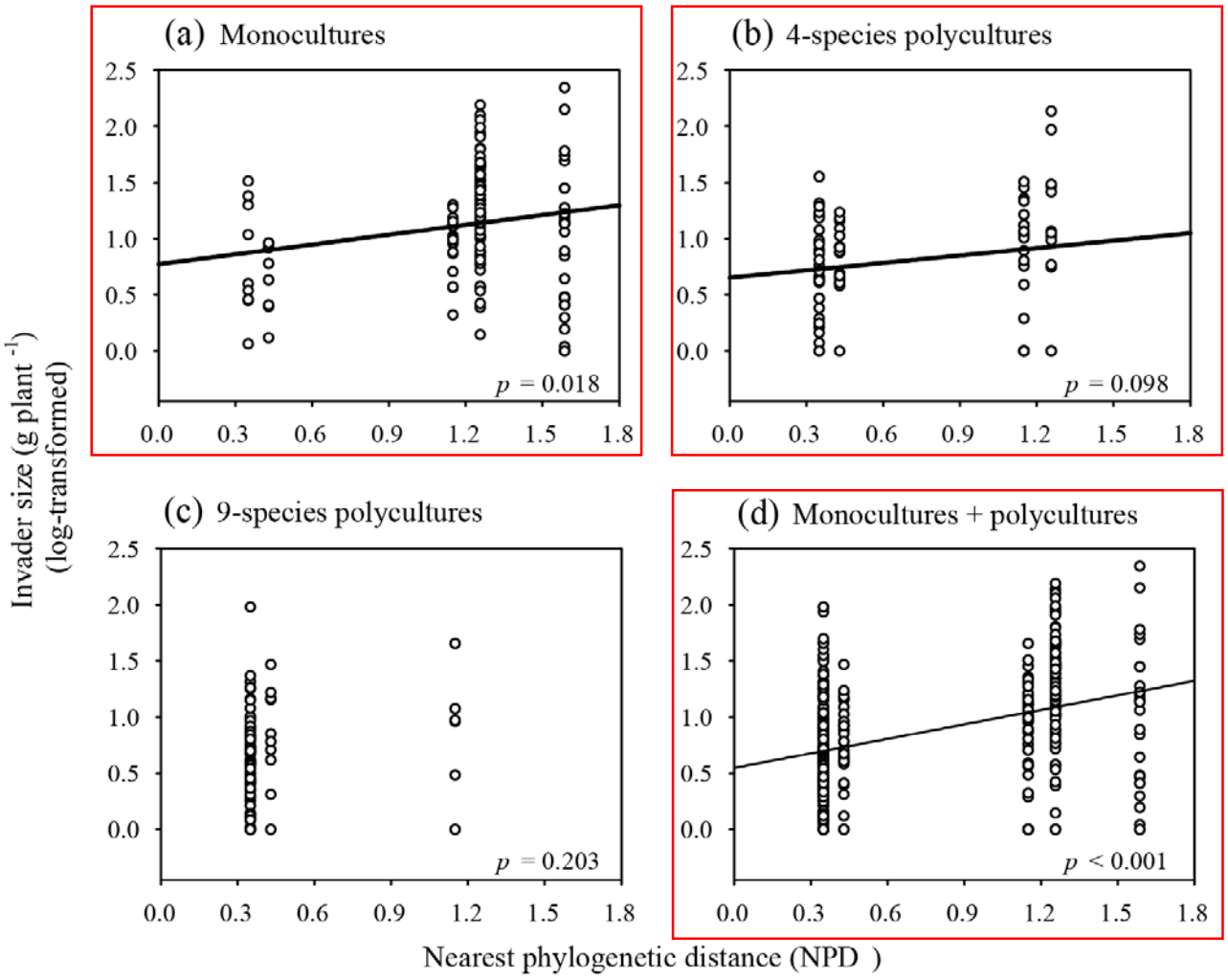


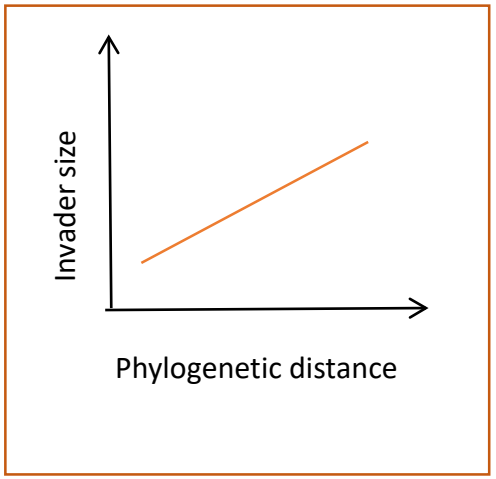
Phylogenetic relatedness on **Invader Individual Size**



Phylogenetic relatedness on **Invader Individual Size**

Darwin's naturalization hypothesis





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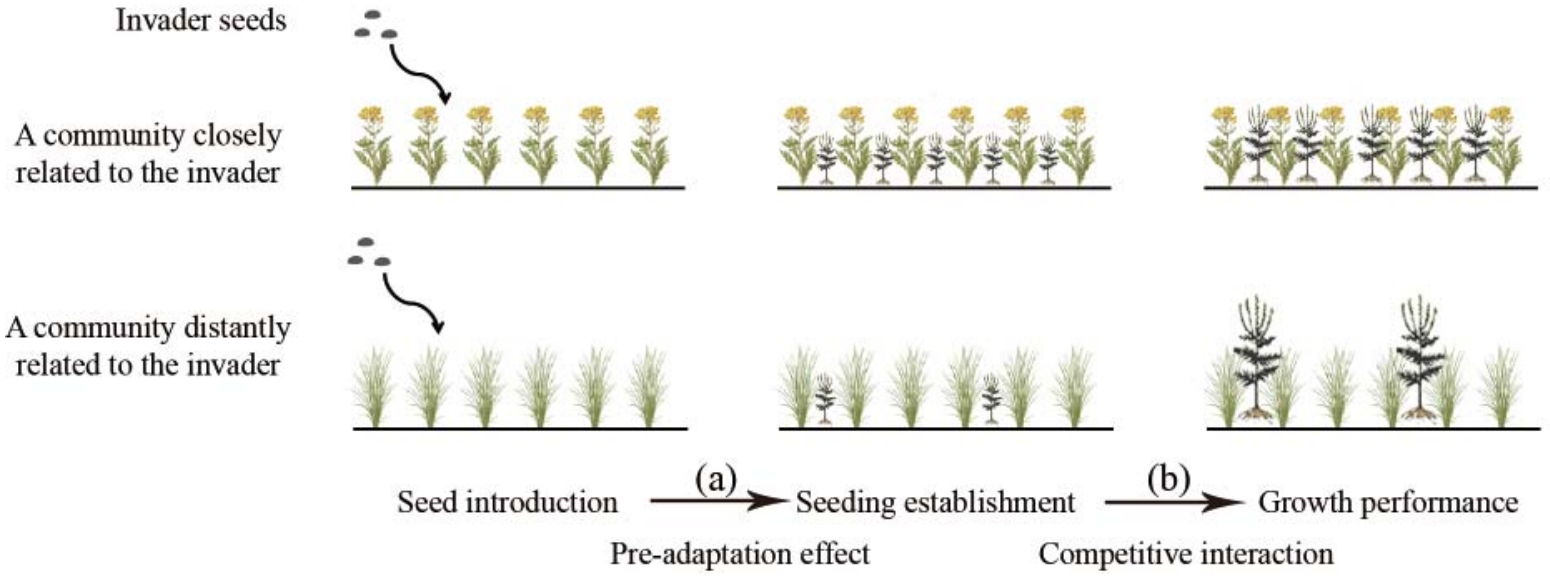
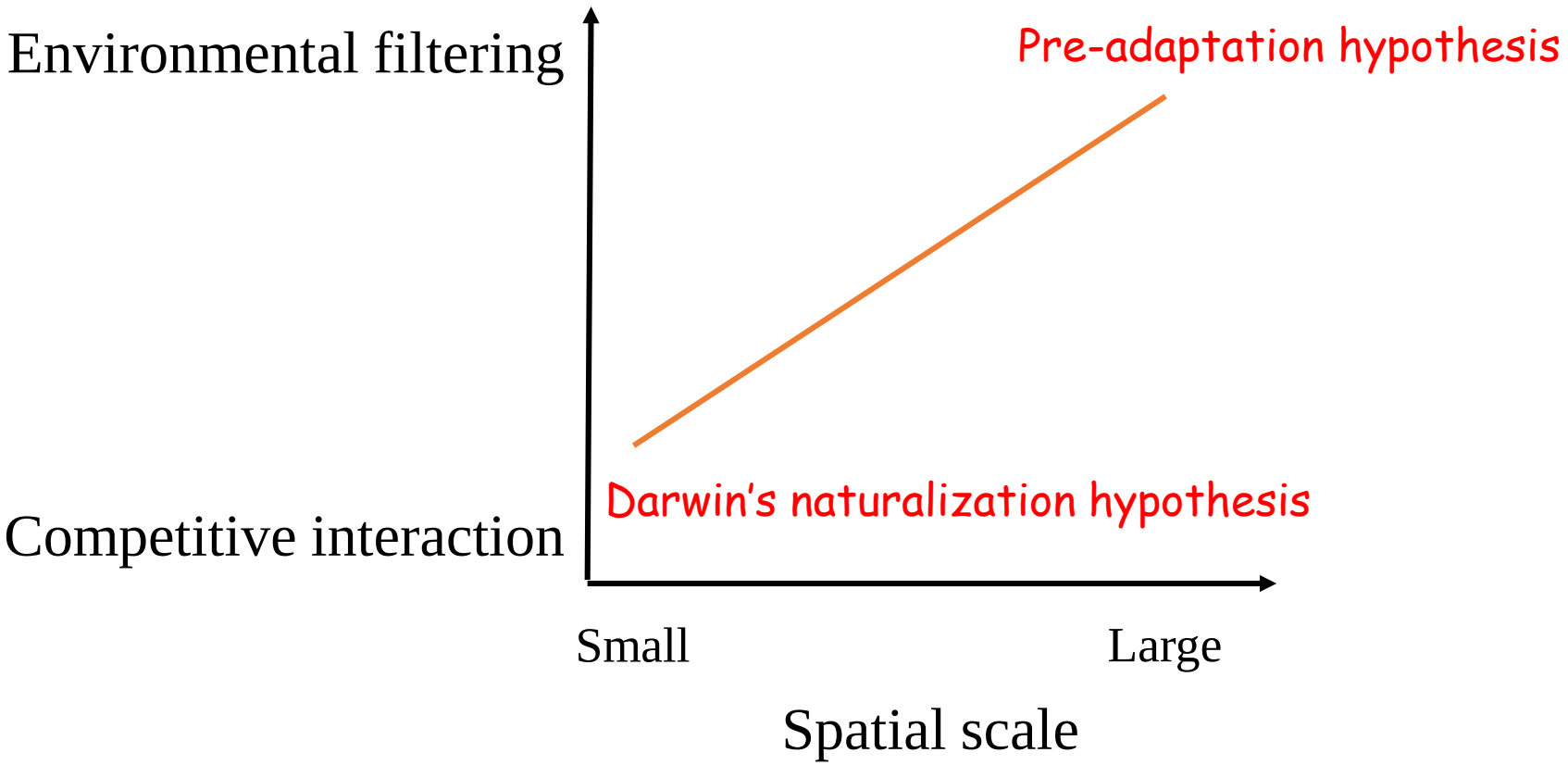


Li *et al.* 2015. *J. Appl. Ecol.*

The validity of Darwin's hypothesis is spatial scale dependent.

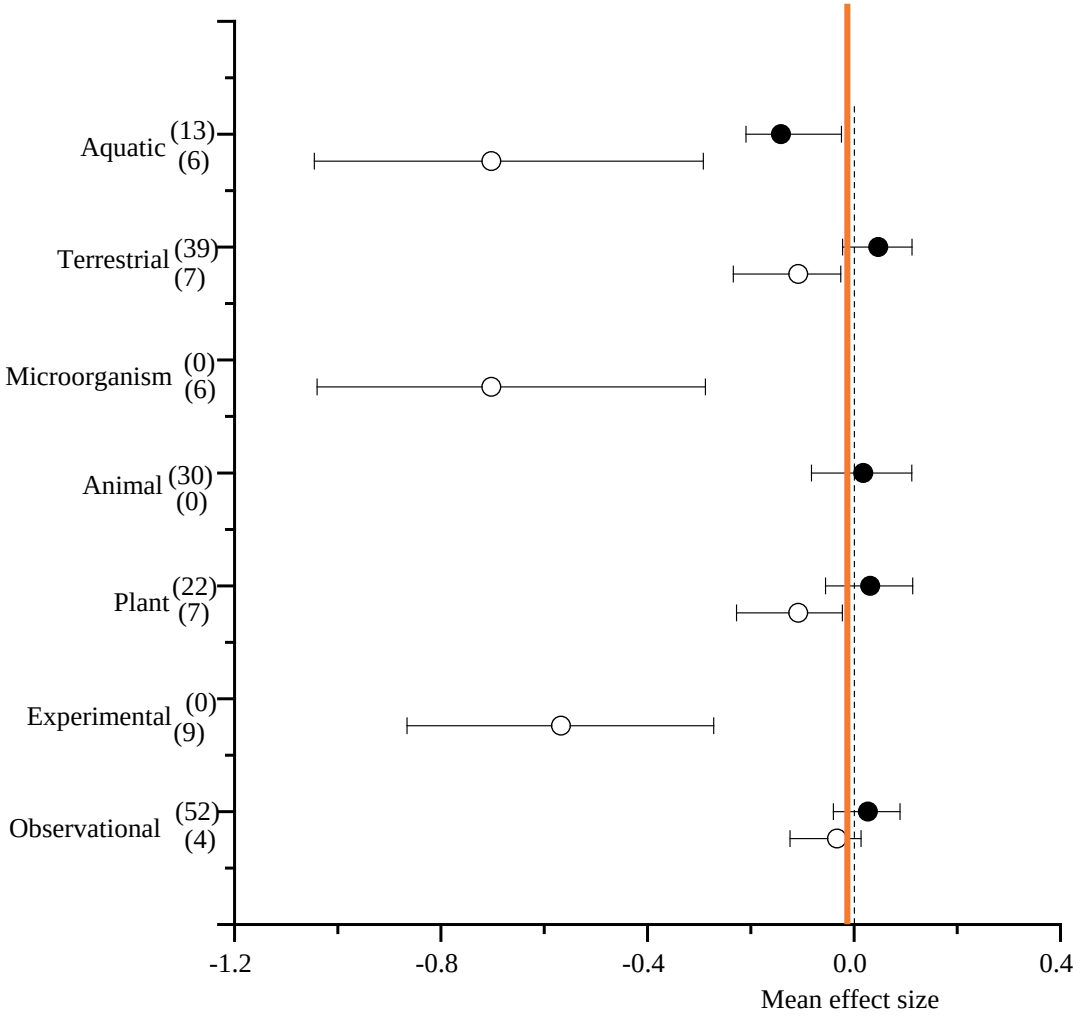


Proches *et al*. 2008. *Global Ecol. Biogeogr.*

A meta-analysis of 87 data entries

Darwin's naturalization hypothesis

Pre-adaptation hypothesis



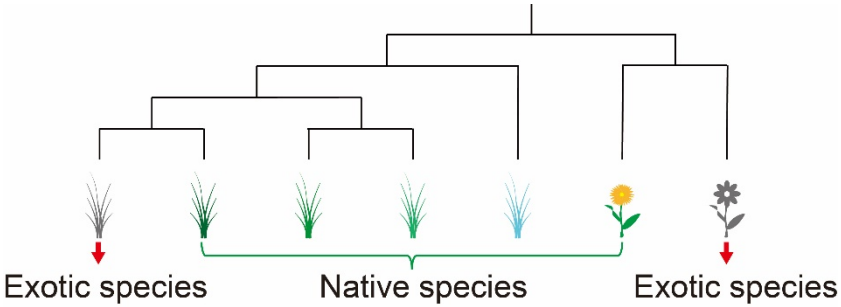
○ Local scale studies

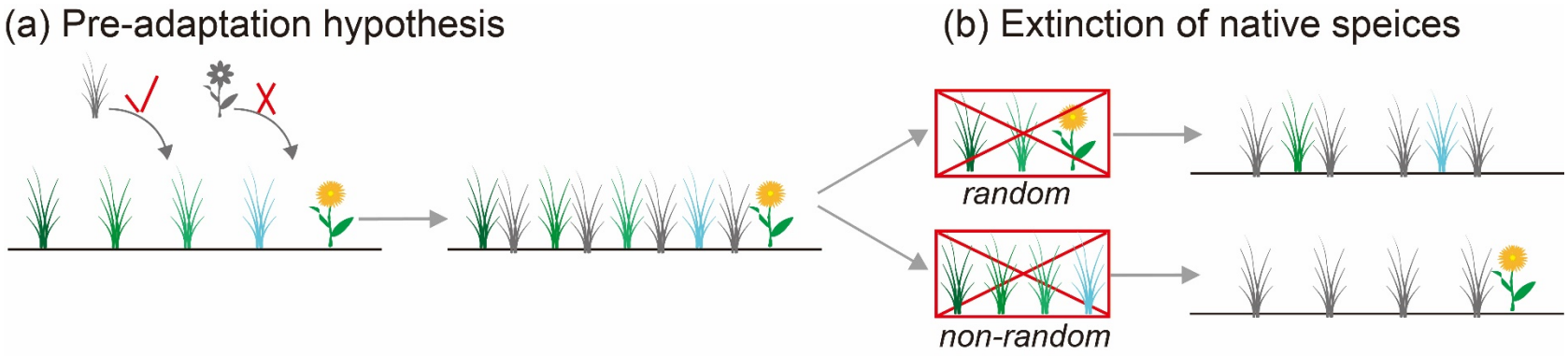
● Regional scale studies

Chao *et al*. 2016. *Proc. Biol. Sci.* (under review)

1. Darwin's naturalization conundrum is **stage** and **scale** dependent.
2. Most studies only comprised large-scale observations at a **single snapshot** in time, and therefore **obscure mechanisms**.
3. Native communities are not static, which could be shaped by invading species. The phylogenetic patterns **before** and **after** invasion could be different.
4. All studies ignore native species that have been **displaced** by the exotics during invasion.

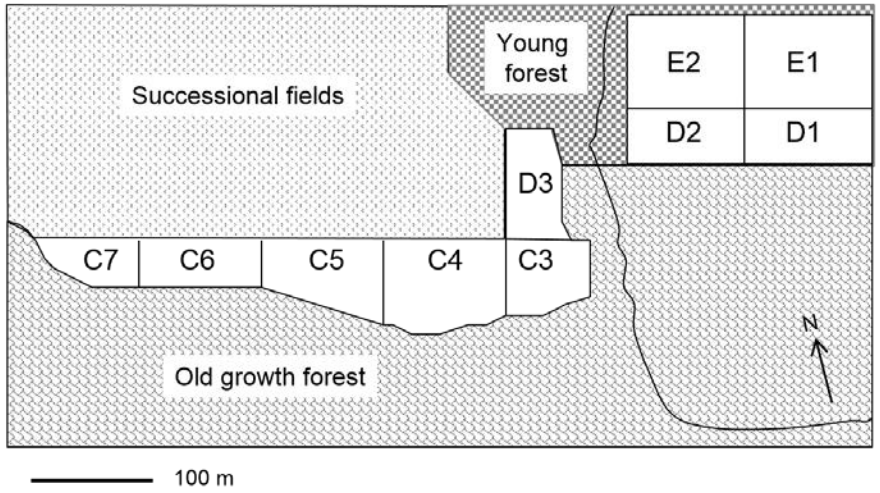
Non-random displacement of natives could reverse the pattern.

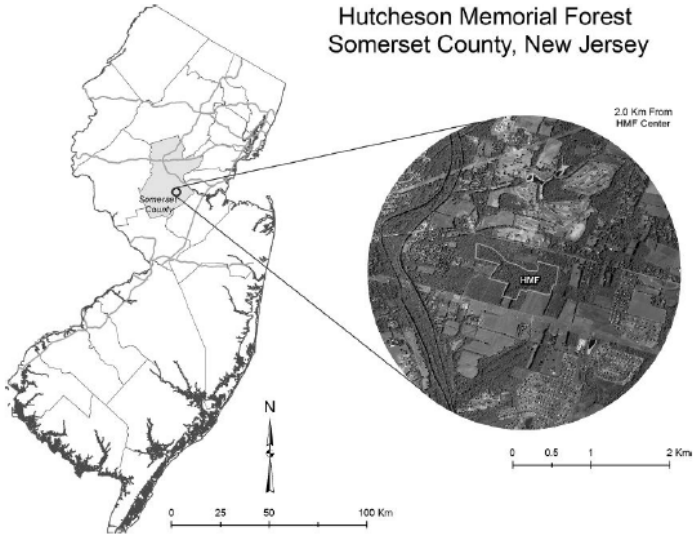




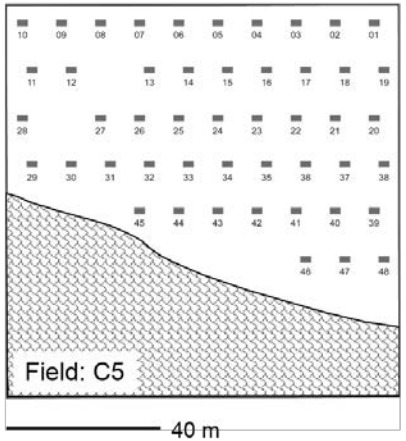
The Buell-Small Succession Study

(a)

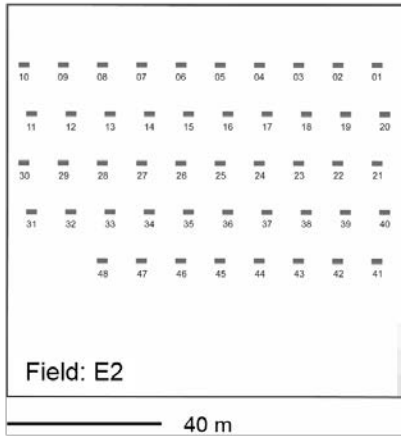




(b)



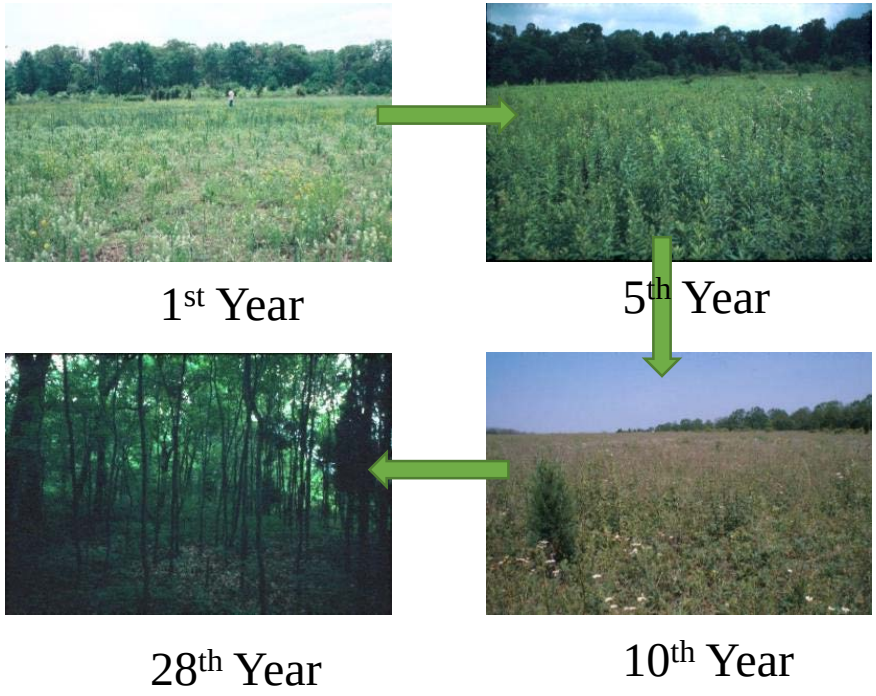
(c)



Murray Buell, Helen Buell and John Small

The Buell-Small Succession Study

1. Plots started in 1958.
2. Youngest plots 45 years old.
3. Sampled every second year.
4. 10 fields with 48 plots per field (480 plots).



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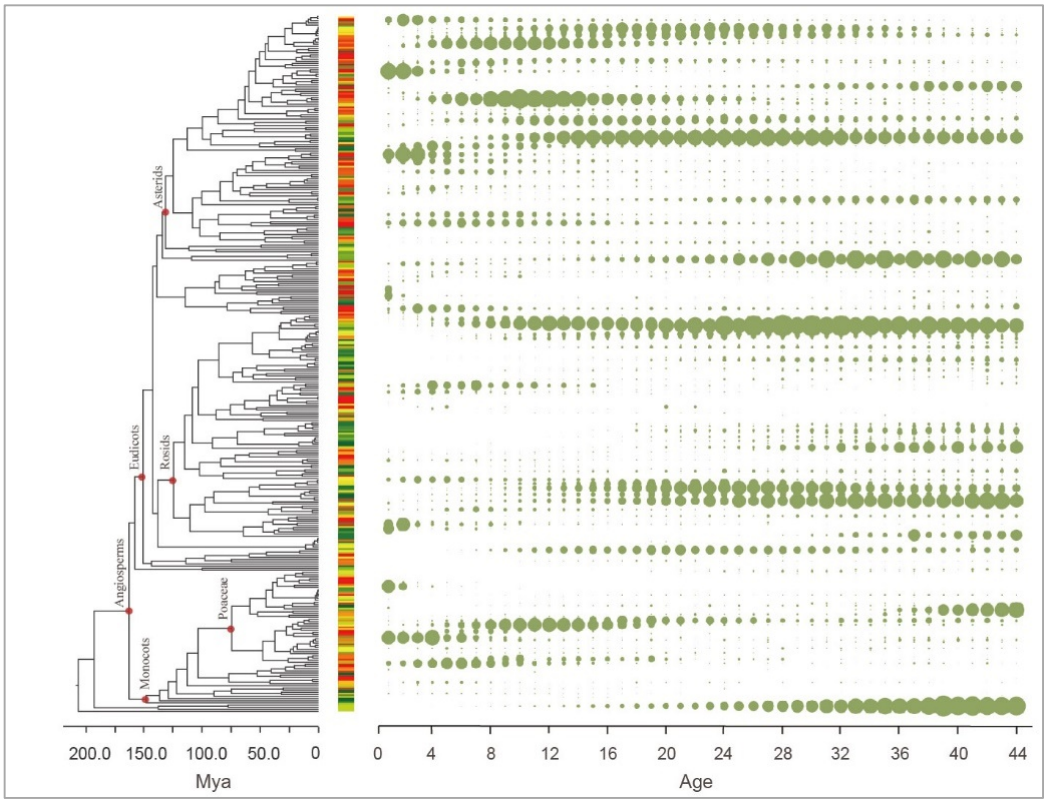

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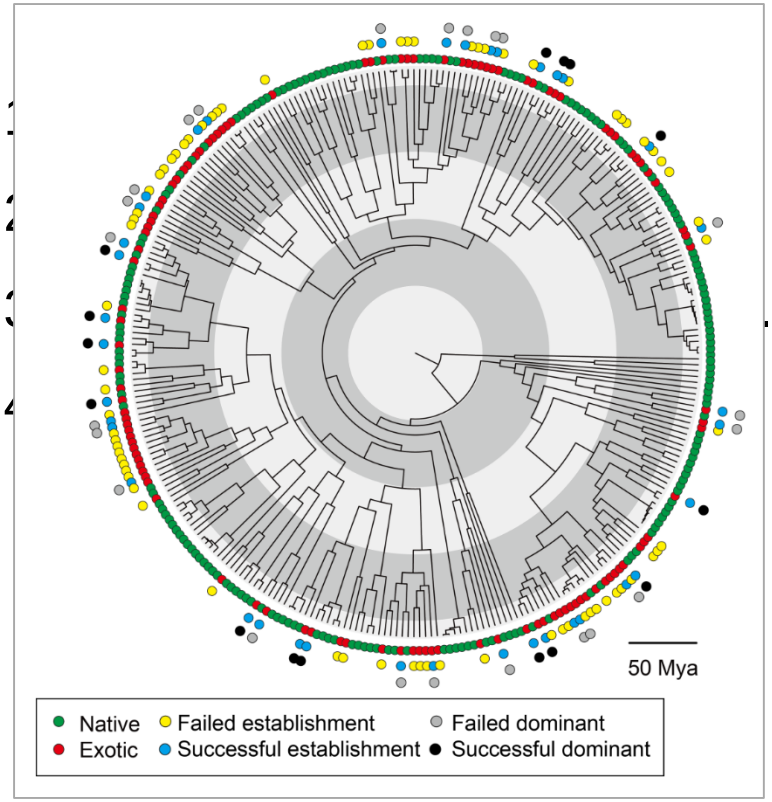
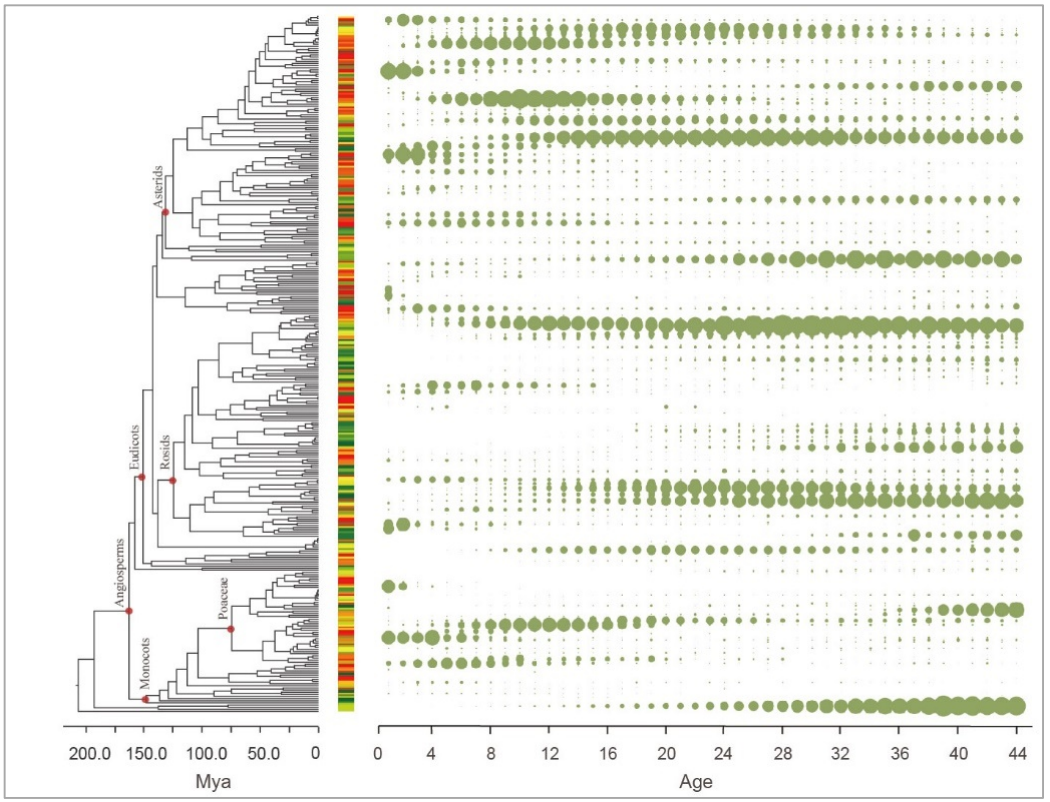
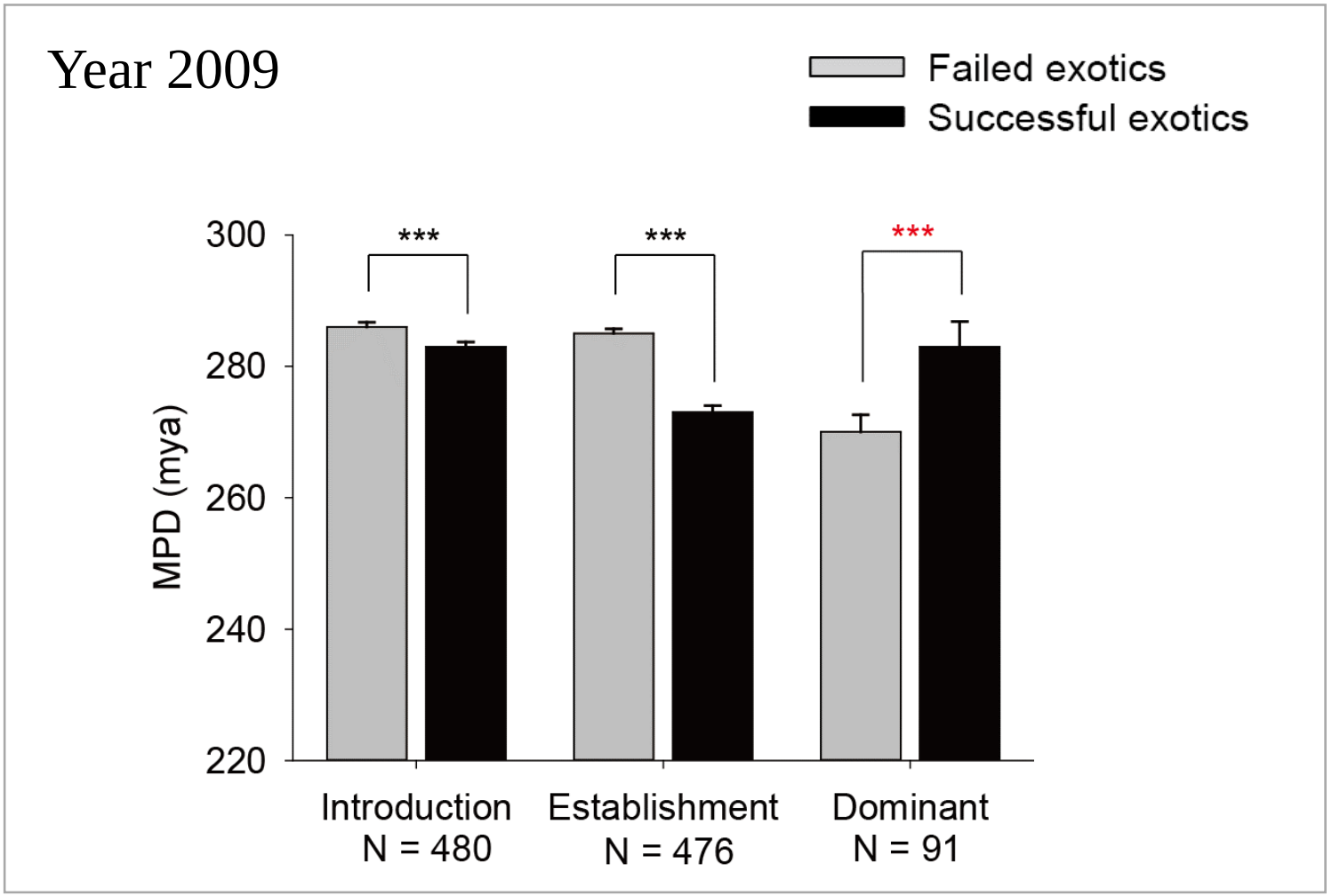




Static samples show complex patterns

The exotic species more closely related to native species were still more likely to enter and establish, but less likely to dominate.



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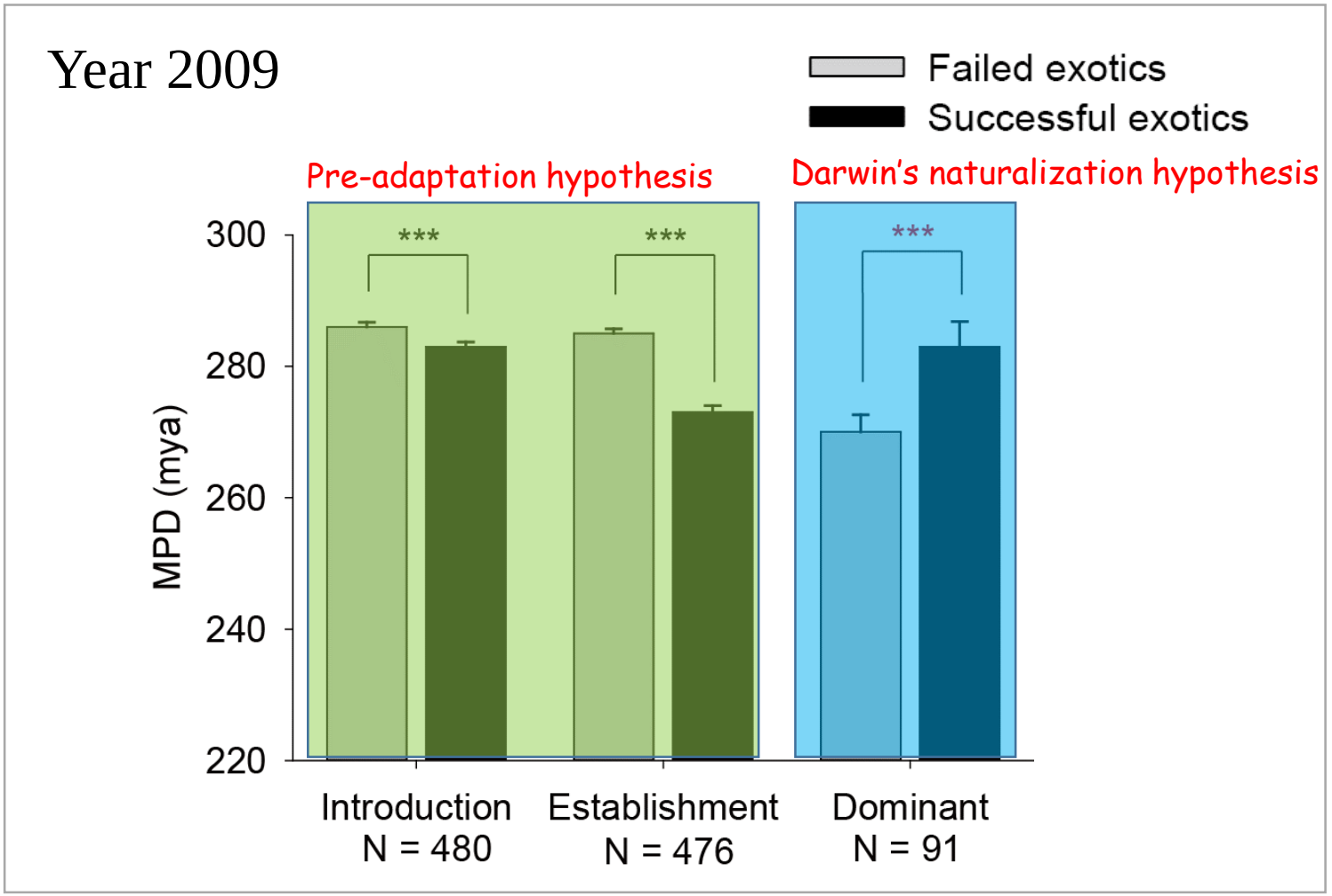
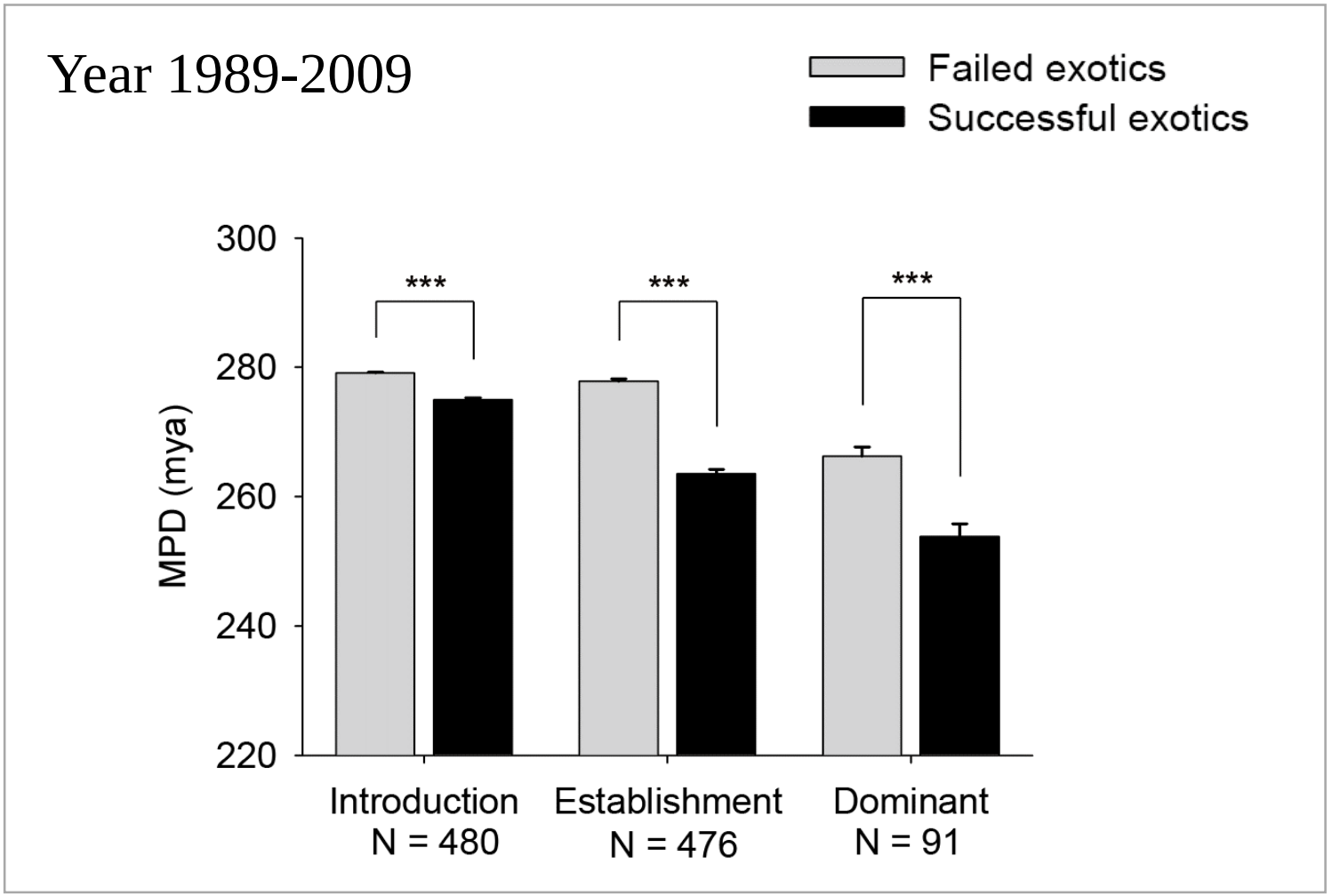


Historical samples show consistent patterns

Successful exotics were more closely related to natives than unsuccessful ones. This pattern becomes stronger at later stage.



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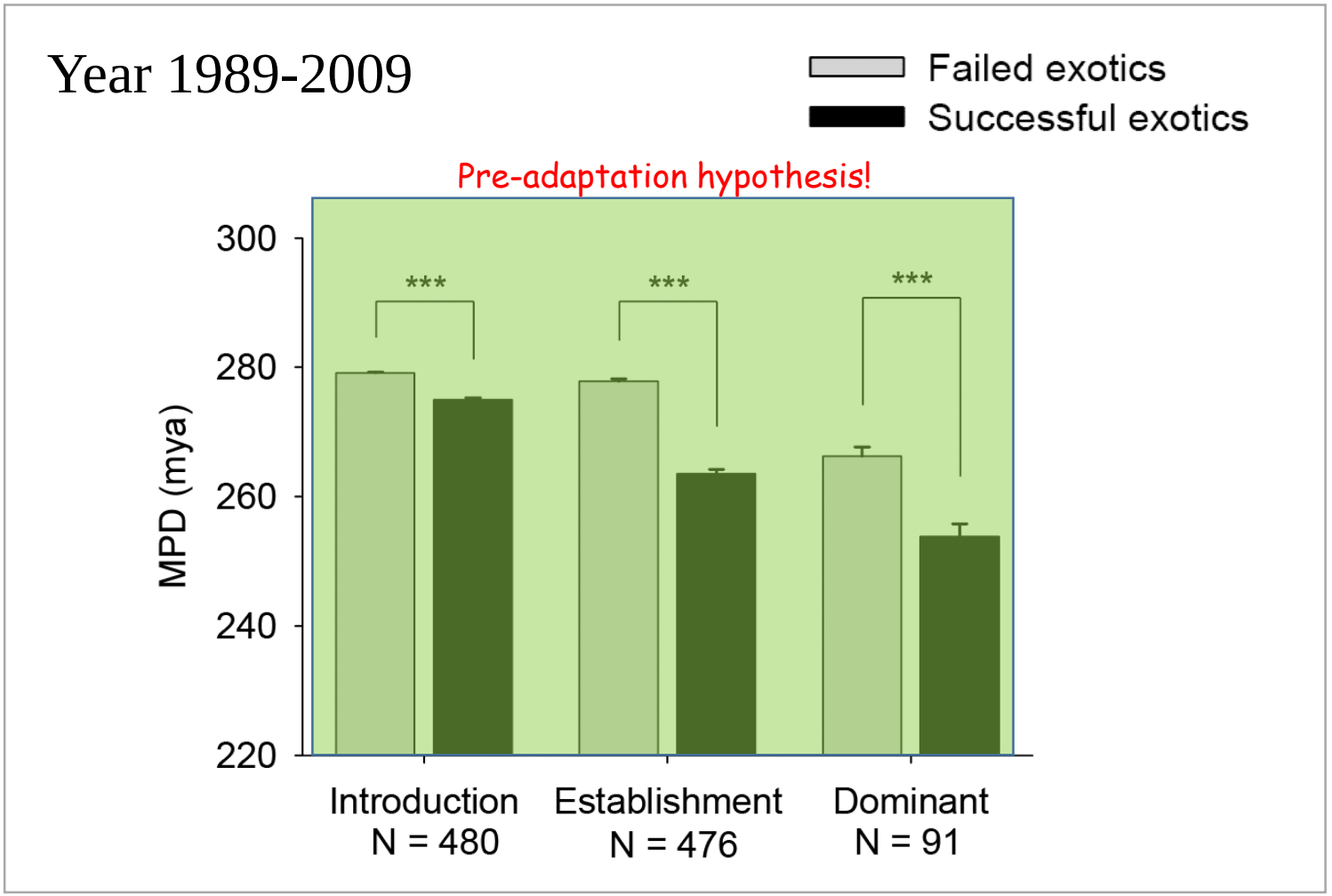


Static vs. dynamic patterns?

1. Single-year observation underestimate the negative effects of exotic–native phylogenetic distances on invasion success.
2. Native species displacement should be incorporated into Darwin's phylogenetic framework.

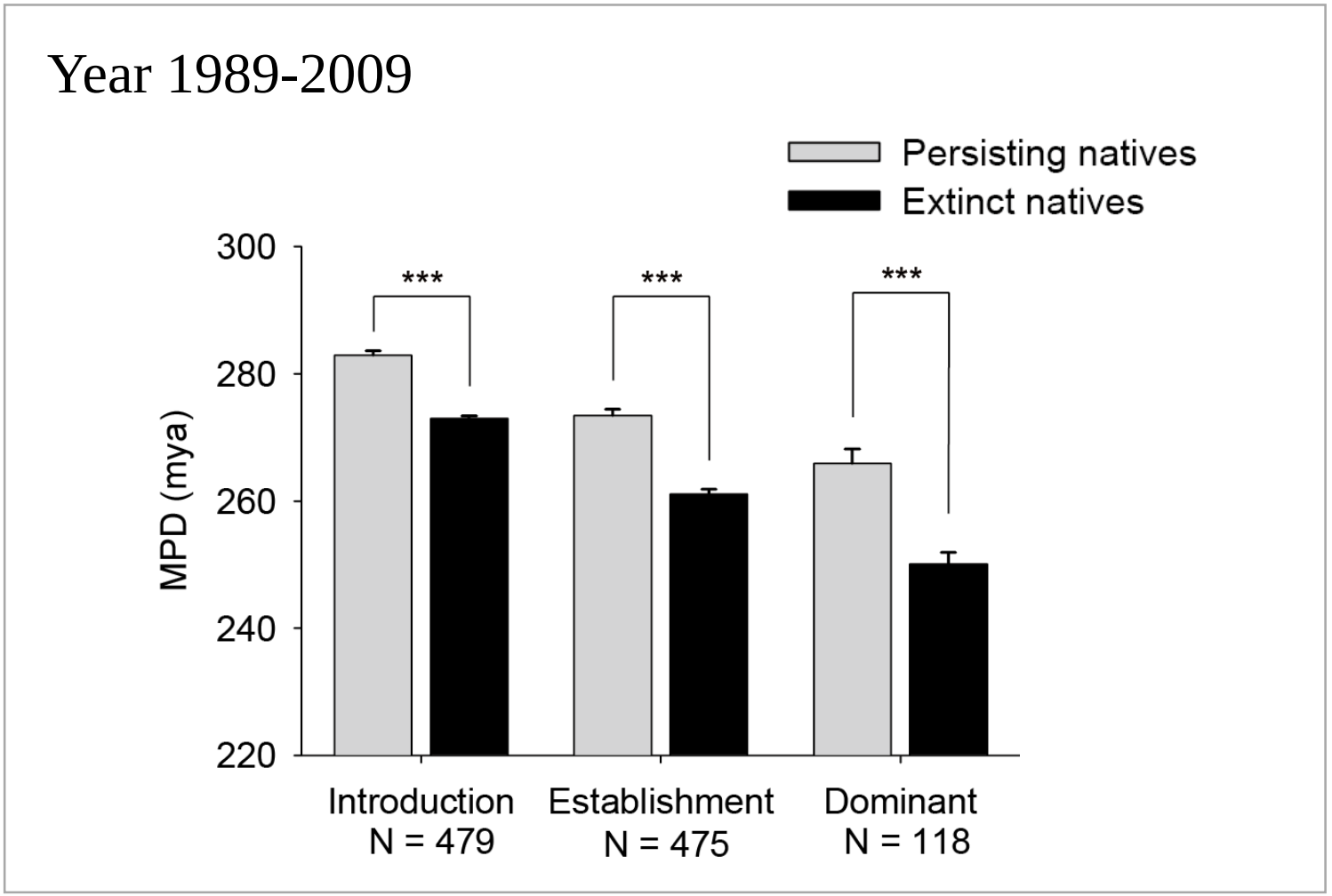
Invaders versus Residents

Static vs. dynamic patterns?

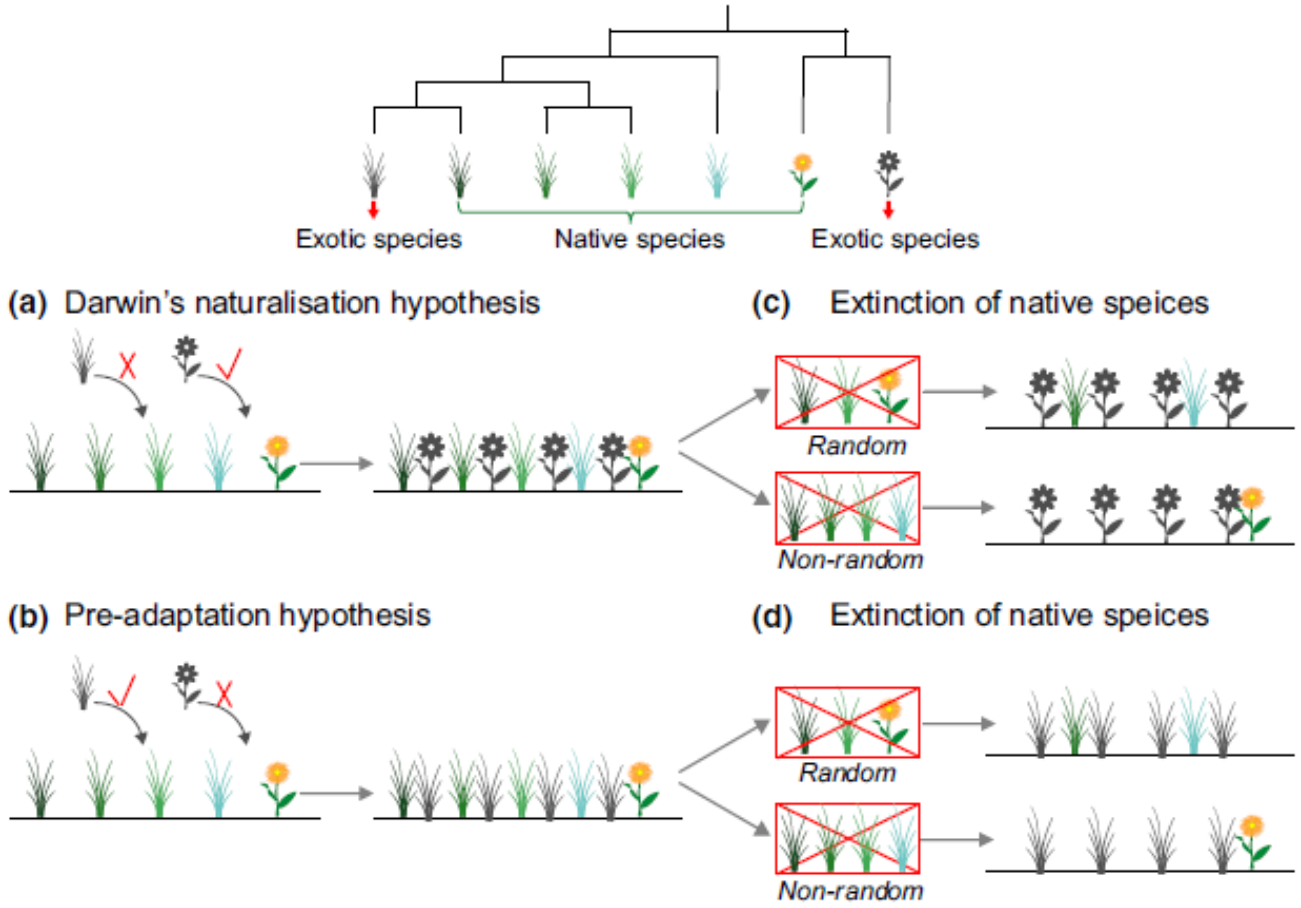
1. Single-year observation underestimate the negative effects of exotic–native phylogenetic distances on invasion success.
2. Native species displacement should be incorporated into Darwin's phylogenetic framework.

Native species displacement

Native residents more closely related to successful exotics were more likely to go extinct. This pattern becomes stronger at each stage.



A new framework of Darwin's naturalization conundrum

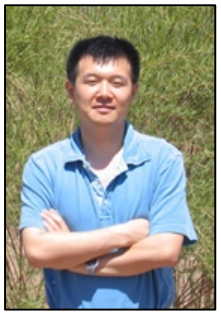


Li *et al.* 2015. *Ecol. Lett.*

Summary

- Darwin’s naturalization conundrum is stage and scale dependent.
- The strong competition among close relatives may not necessarily repel invaders, but instead may result in the loss of native species.
- It is only possible to reconcile Darwin’s conundrum by incorporating native species displacement into Darwin's framework.

Acknowledgements



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