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?

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.
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

Exotic species

Native species

Exotic species

Resident community

Darwin’s naturalization hypothesis

Native species

Exotic species

Resident community

Darwin’s naturalization hypothesis

Competitive interactions

Native species

Exotic species

Resident community

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

Pre-adaptation hypothesis

Pre-adaptation hypothesis

Exotic species

Native species

Exotic species

Environmental filtering

 Resident community

Darwin’s naturalization conundrum

Recent studies produced mixed results...

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

Jones et al. 2011. *PNAS*
The validity of Darwin’s hypothesis is invasion stage dependent.

Species pool

- Ambrosia_artsimisiifolia
- Ageratum_aconitifolium
- Bidens_pilosus
- Dichondra_micrantha
- Mosla_dianthera
- Lespedeza_cuneata
- Medicago_sativa
- Senna_tora
- Senna_occidentalis
- Celosia_argentea
- Corchorus_capsularis
- Phyllanthus_serpgalis
- Sida_mysorensis
- Urona_obata
- Pennisetum_alopecuroides
- Paspalum_notatum
- Dactyloctonion_aegyptiun
- Magnolia_grandiflora
- Amborella_trichopoda

Invasive species
Experimental design

114 plots → 81 plots → 81 plots → 63 plots

Species richness
Phylogenetic relatedness on **Invader Density**

(a) Monocultures

(b) 4-species polycultures

(c) 9-species polycultures

(d) Monocultures + polycultures

$p = 0.002$

$p = 0.002$

$p = 0.119$

$p < 0.001$
Phylogenetic relatedness on Invader Density

Pre-adaptation hypothesis

- (a) Monocultures
  - Invader proportion established (sqrt-transformed)
  - Nearest phylogenetic distance (NPD)
  - $p = 0.002$

- (b) 4-species polycultures
  - Invader establishment
  - Phylogenetic distance
  - $p = 0.002$

- (c) 9-species polycultures
  - $p = 0.119$

- (d) Monocultures + polycultures
  - $p < 0.001$
Phylogenetic relatedness on Invader Individual Size

(a) Monocultures

(b) 4-species polycultures

(c) 9-species polycultures

(d) Monocultures + polycultures

Nearest phylogenetic distance (NPD )

Invader size (g plant$^{-1}$) (log-transformed)
Phylogenetic relatedness on **Invader Individual Size**

Darwin’s naturalization hypothesis

(a) Monocultures
(b) 4-species polycultures
(c) 9-species polycultures
(d) Monocultures + polycultures

Nearest phylogenetic distance (NPD)

Invader size

Phylogenetic distance

$p = 0.018$

$p = 0.098$

$p = 0.203$

$p < 0.001$
The validity of Darwin’s hypothesis is invasion stage dependent.

Li et al. 2015. J. Appl. Ecol.
The validity of Darwin’s hypothesis is spatial scale dependent.

Environmental filtering

Competitive interaction

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Spatial scale

Small

Large

Pre-adaptation hypothesis

Darwin’s naturalization hypothesis

A meta-analysis of 87 data entries

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) Map of the study site showing Successional fields, Young forest, and Old growth forest.

(b) Grid of field C5 with a scale of 40 m.

(c) Grid of field E2 with a scale of 40 m.

Hutcheson Memorial Forest, Somerset County, New Jersey

Murray Buell, Helen Buell and John Small
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).
The Buell-Small Succession Study

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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.

Year 2009

- Failed exotics
- Successful exotics

<table>
<thead>
<tr>
<th>Stage</th>
<th>Failed Exotics</th>
<th>Successful Exotics</th>
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<tr>
<td>Introduction</td>
<td>280 (N = 480)</td>
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<tr>
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<td>Dominant</td>
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*** Significance Level
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.
Historical samples show consistent patterns

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

**Year 1989-2009**

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*** indicates a significant difference.
Historical samples show consistent patterns

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

Year 1989-2009

Pre-adaptation hypothesis!
Static vs. dynamic patterns?

2. Native species displacement should be incorporated into Darwin’s phylogenetic framework.
Static vs. dynamic patterns?

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.

Year 1989-2009
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.
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