# Traits of Invaders: Similar, but Different

David Chan

# What makes a successful invader?

- Most invaded habitats are ones that have been subject to disturbance
  - Leads to release of resources (food, light, space, etc.)
- Invaders need to capitalize on these resources quickly

- Which traits enable success?

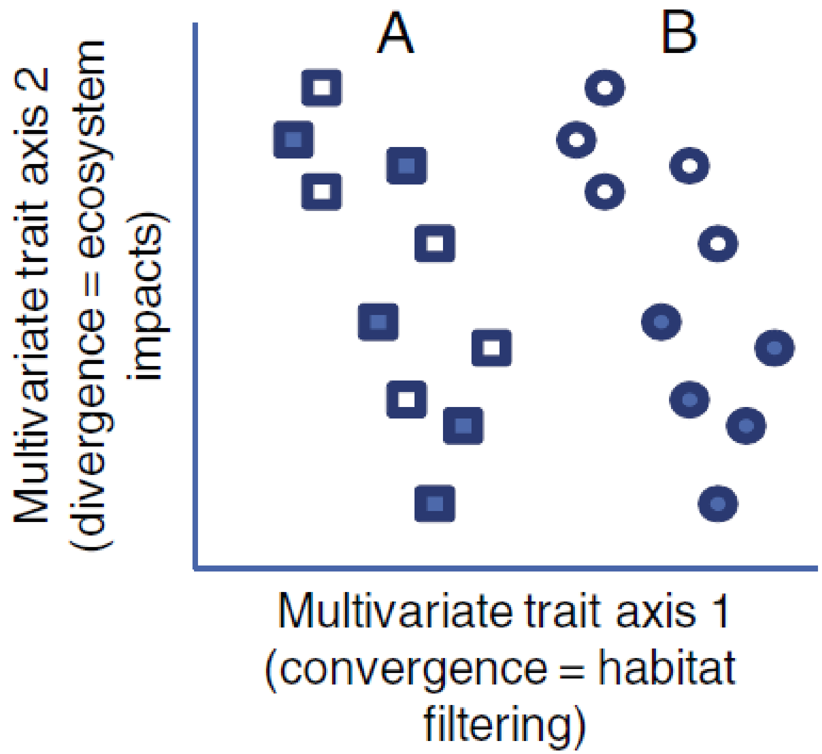
Grotkopp et al. 2002

# Cleland 2011

- What is the relationship between native and invasive species in a community?
- Competing theories:
  - Neutral theory: there should be few functional differences between native and invasive species as long as traits are similar
  - Niche-based community assembly theory and the concept of limiting similarity: invasives should have different traits and use resources differently than natives, otherwise they would experience competitive exclusion

# Similar, but Different

- "…while invading species differed from native species in a few ways, they were remarkably similar to the native species in these communities." – Scharfy et al. 2011




Cleland 2011

# Funk et al. 2008

- “…the specific functional composition of the native community is likely to be more important that community diversity (e.g. species richness).”

# The role of ecological filters

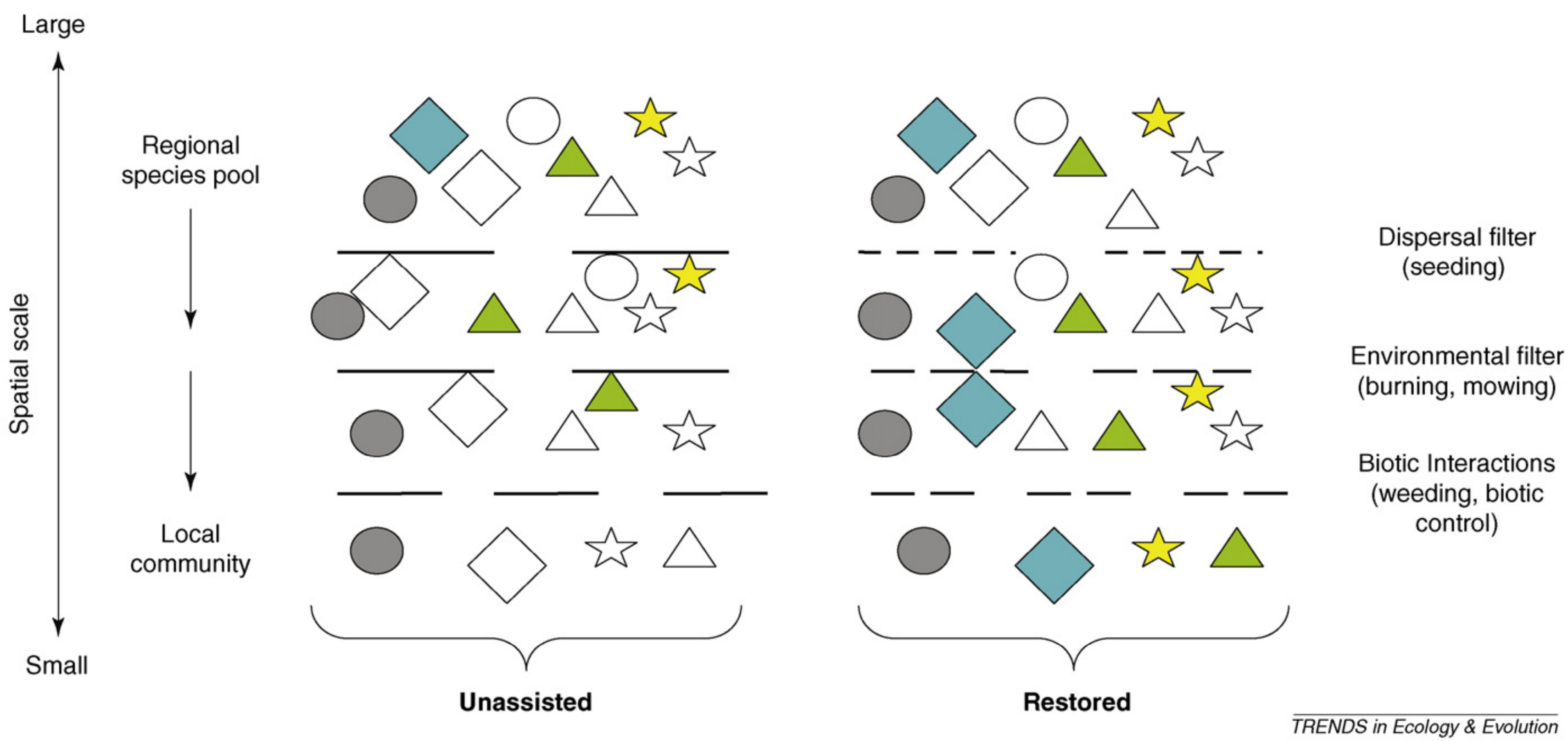



Figure I. Ecological filters act at multiple spatial scales to determine community composition (axis left). By influencing filters, restoration can guide community assembly (restoration strategies shown in parentheses on the right of the figure). Similar species are indicated using the same symbol; in each case, native species are shown in closed colored symbols and invasive species are in open white symbols.

Funk et al. 2008

# Invasion Pathways

- Limiting similarity theory- successful invaders will differ functionally from species already present in the community
- Ecological filter changes that lead to the alteration of the potential trait breath of the community
- Uneven dispersion of traits across available niche space

Funk et al. 2008

# Invasion Resistance

- Increasing functional diversity fills empty niche space
- Redundancy protects against perturbations that may remove species

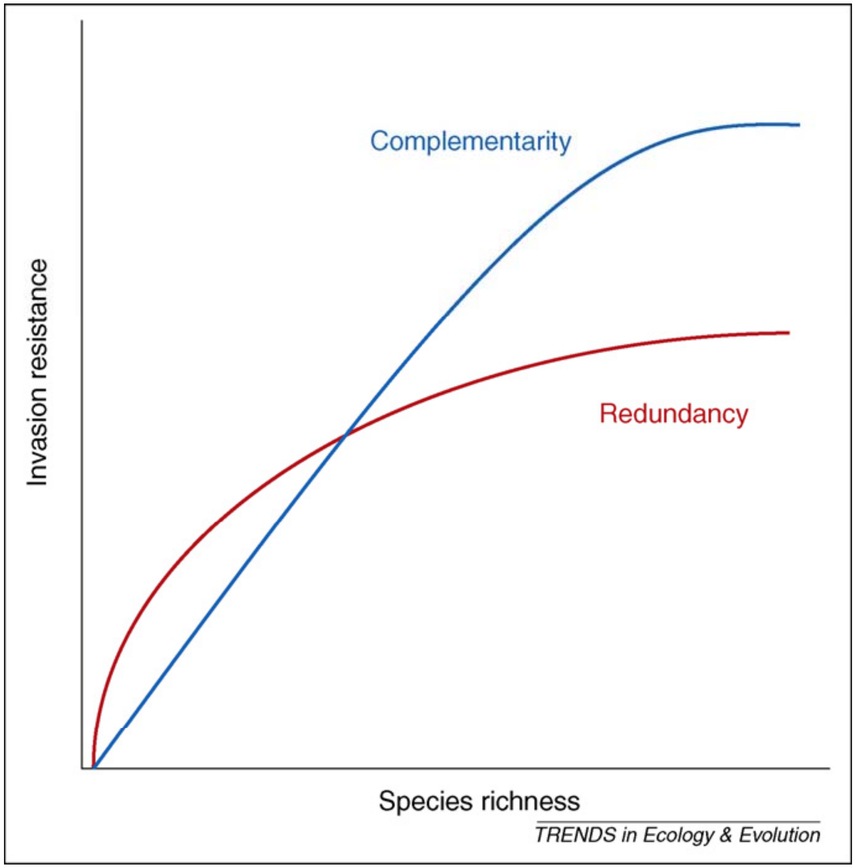



**Figure 1.** Functional redundancy and complementarity can influence invasion resistance in different ways. Increasing functional diversity (complementarity) can increase invasion resistance by reducing vacant niches available to new invaders. However, increasing the relative abundance of a few key functional types (redundancy) ensures that some level of invasion resistance will be met if species are eliminated from the system. Increasing functional redundancy, as opposed to functional diversity, could lead to higher resistance at low species richness if the invader is of the same functional type.

Funk et al. 2008

# Brym et al. 2011

- Looked at the invasion of a shade-intolerant shrub, *Elaeagnus umbellata,* in the understory of a Michigan forest
- Propose the following mechanisms for success:
  - Enemy Release
  - Association with N-fixing bacteria
  - Use of an empty temporal niche
  - Bird dispersal

# Distinct Trait Ranges

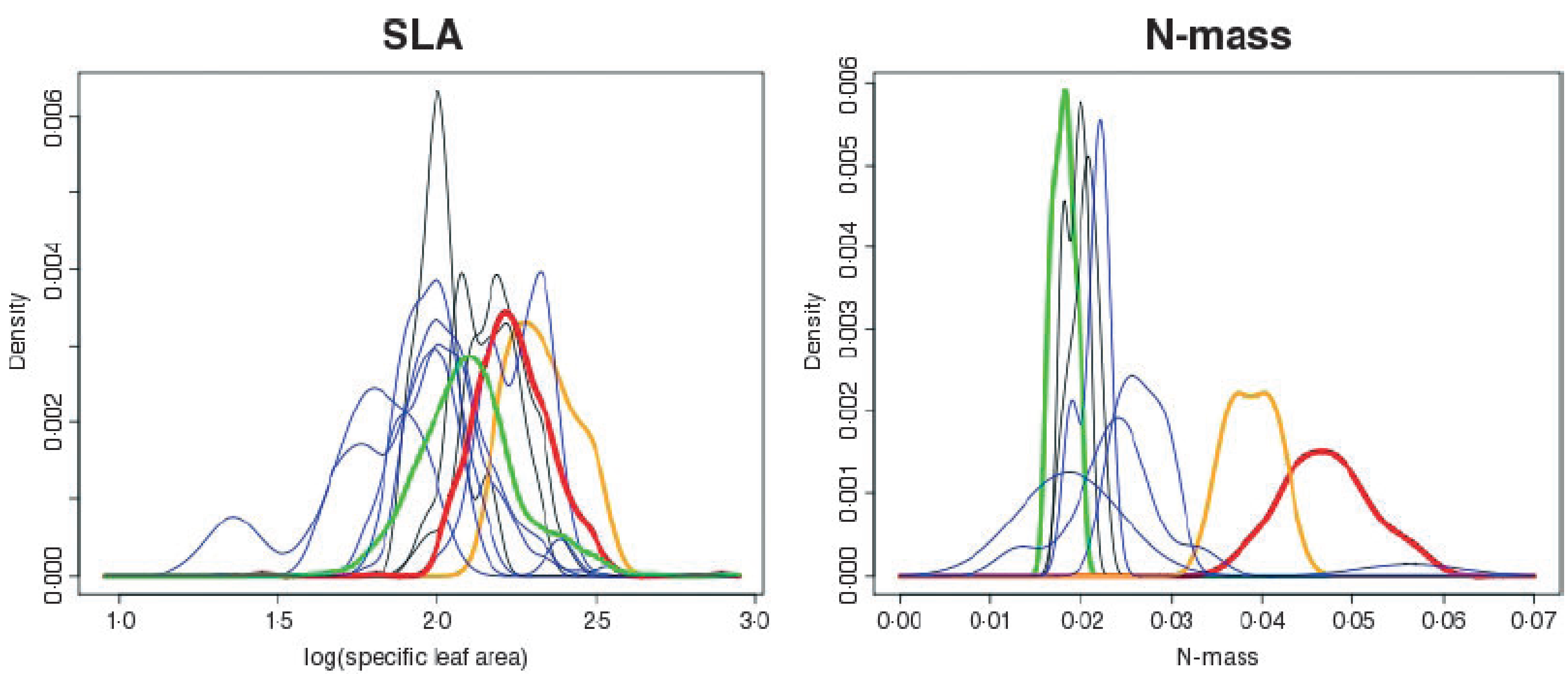



**Fig. 1.** Community trait axis constructed by the kernel density, shown as a proportion, (*y*-axis) of trait values (*x*-axis) for each species. Colour legend: *Elaeagnus umbellata*, red; *Hamamelis virginiana*, green; *Sassafras albidum*, gold; native canopy trees, navy blue; and native understorey trees, black. Note the similarity between *Elaeagnus* and *Sassafras* for many of these traits, and the dissimilarity between the two shrub species.

Brym et al. 2011

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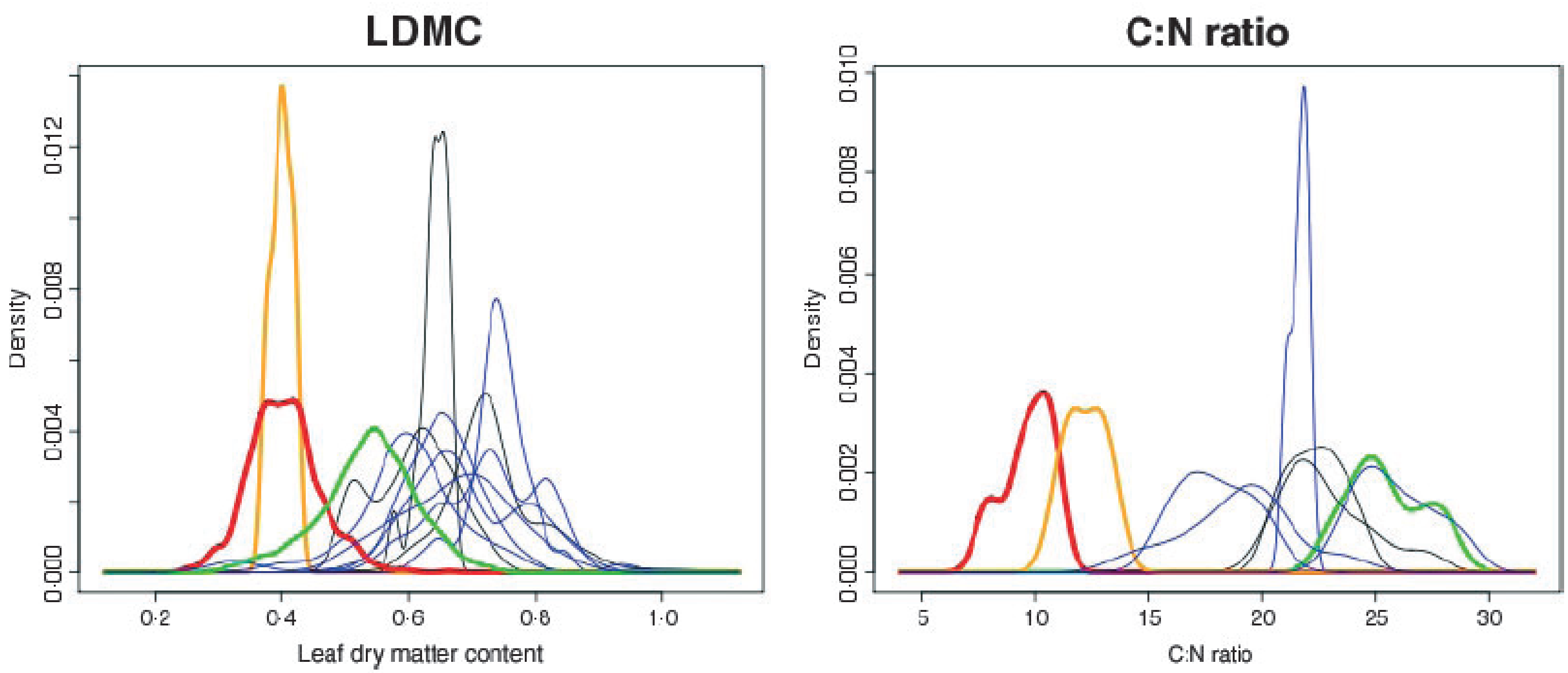


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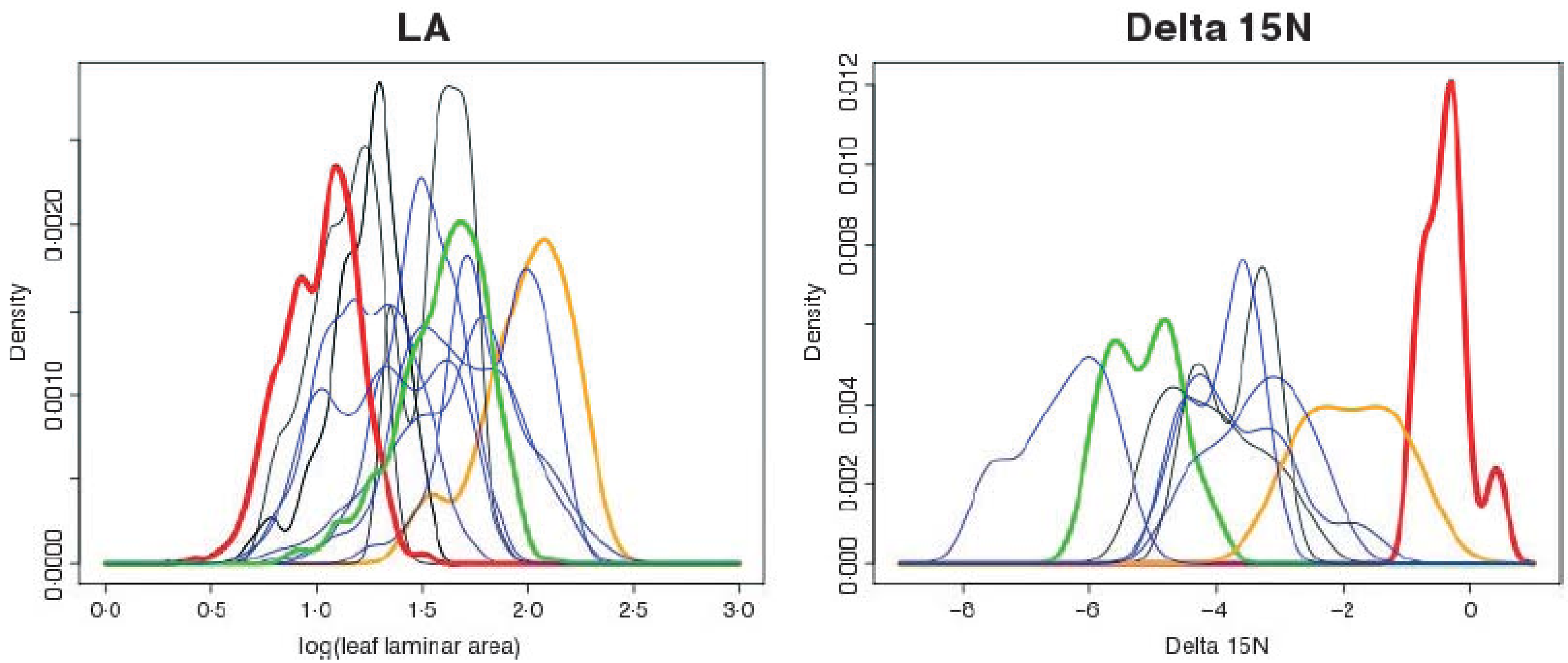


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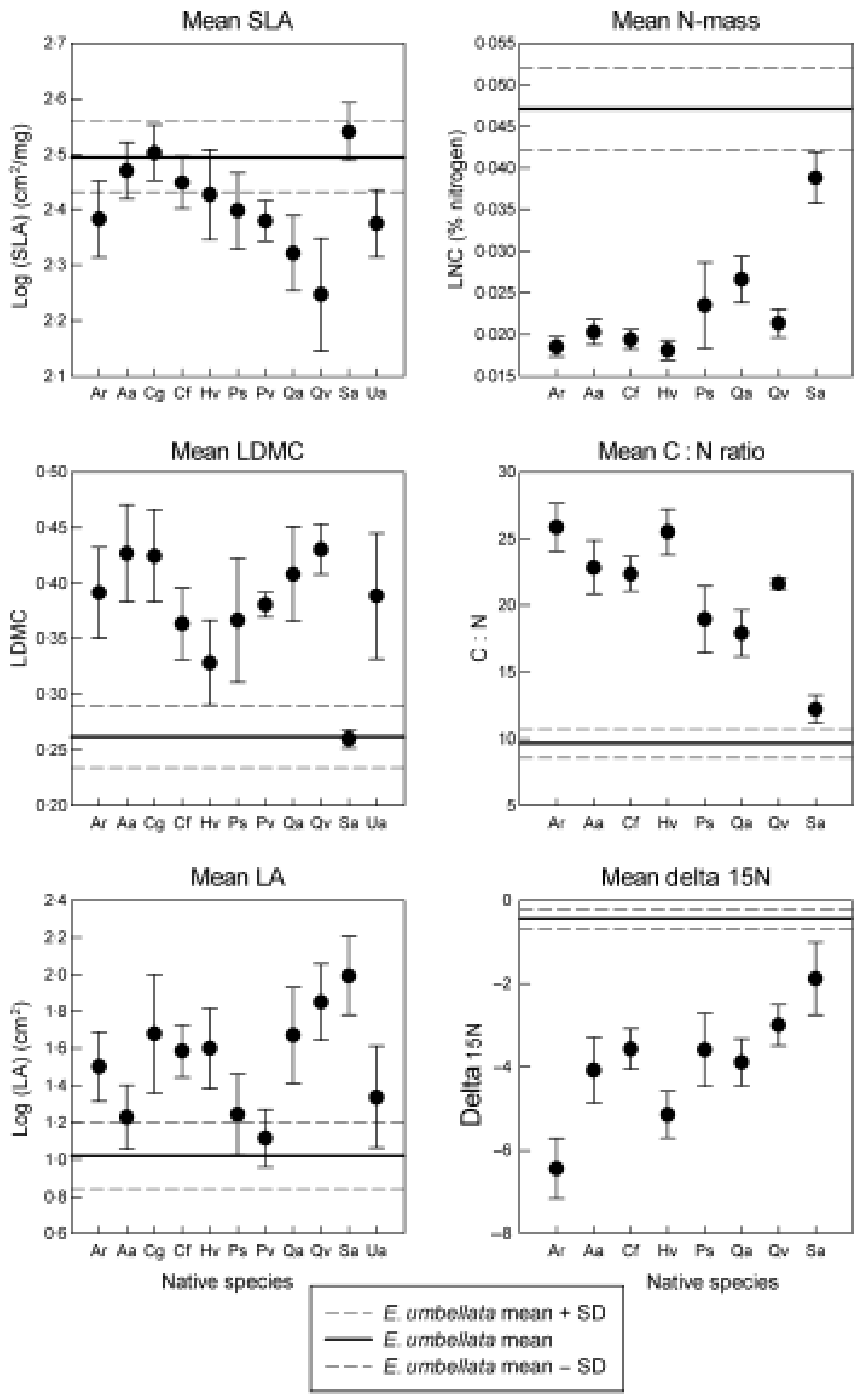
Brym et al. 2011




Brym et al. 2011

# Burns and Winn 2006

- Looked at Phenotypic Plasticity and Invasiveness in *Commelinaceae* (spiderworts/dayflowers)
- Compared traits to Invasiveness and environment (with/without competition)
  - 2-way fixed effect ANOVA
- A significant interaction would signify difference in plasticity

*Table 2.* Results from two-way fixed effect ANOVA for the effects of Invasiveness, competitive environment, and their interaction on total biomass, stem elongation, the ratio of dry biomass of roots to shoots (root:shoot), and SLA.

| Trait | Total biomass | | | Elongation | | | Root:shoot | | | SLA | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | df | MS | *F* | df | MS | *F* | df | MS | *F* | df | MS | *F* |
| Invasiveness | 1 | 3.1 | 9** | 1 | 2.6 | 4.4* | 1 | 0.061 | 1.2 | 1 | 350 | 40*** |
| Environment | 1 | 68 | 210*** | 1 | 5.5 | 9.2** | 1 | 0.040 | 7.6** | 1 | 62 | 7.2** |
| I × E | 1 | 3.8 | 11*** | 1 | 0.003 | 0.01 | 1 | 0.14 | 2.6 | 1 | 3.8 | 0.44 |
| Error | 155 | 0.33 | | 155 | | | 155 | 0.05 | | 155 | 8.5 | |

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

# Support for the Empty Niche Hypothesis

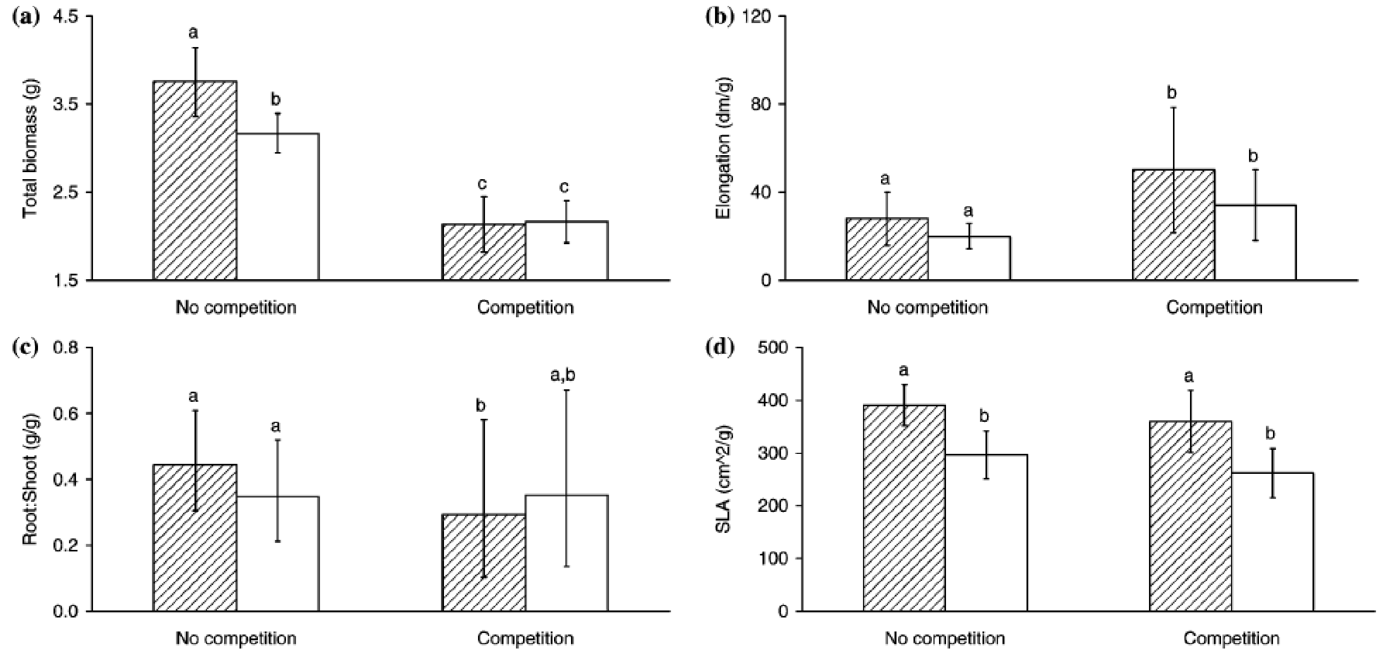



*Figure 1*. Means (95% CI) by environment and invasiveness for (a) final dry biomass (corrected for initial cutting size), (b) stem elongation, (c) root-to-shoot dry biomass ratio, and (d) SLA of invasive (hatched bars) and non-invasive (open bars) congeners. Means that share a lower-case letter do not differ significantly by *post hoc* comparisons among all possible pairs.

- Specialization for invading non-competitive environments

Burns & Winn 2005

# Drenovsky and James 2010

- Resource Use and Efficiency

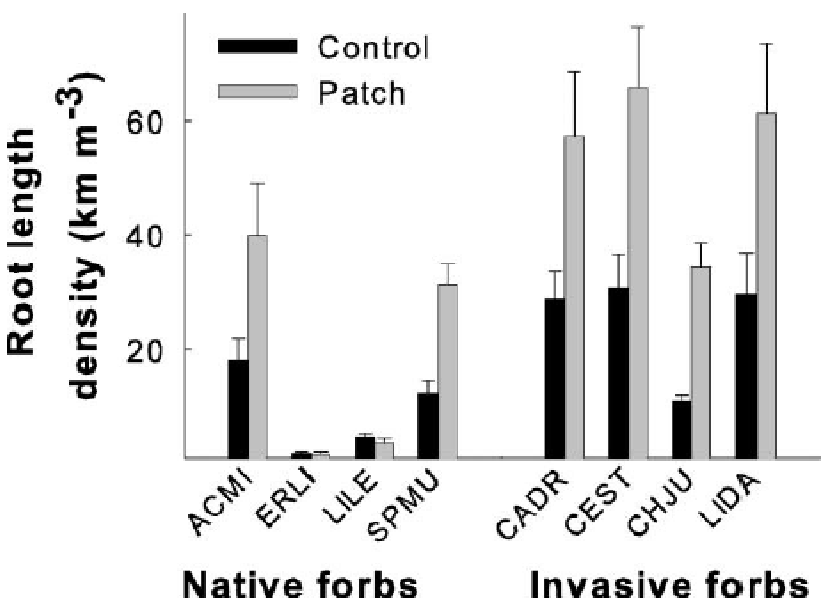



**Figure 6.** Root length density of native and invasive forbs grown in pots with nutrients distributed evenly in a low concentration (control) or with nutrients concentrated in small patches (patch; mean ± SE). Species abbreviations follow Table 1. Figure reprinted with permission from the Botanical Society of America. Data are from Drenovsky et al.[10]

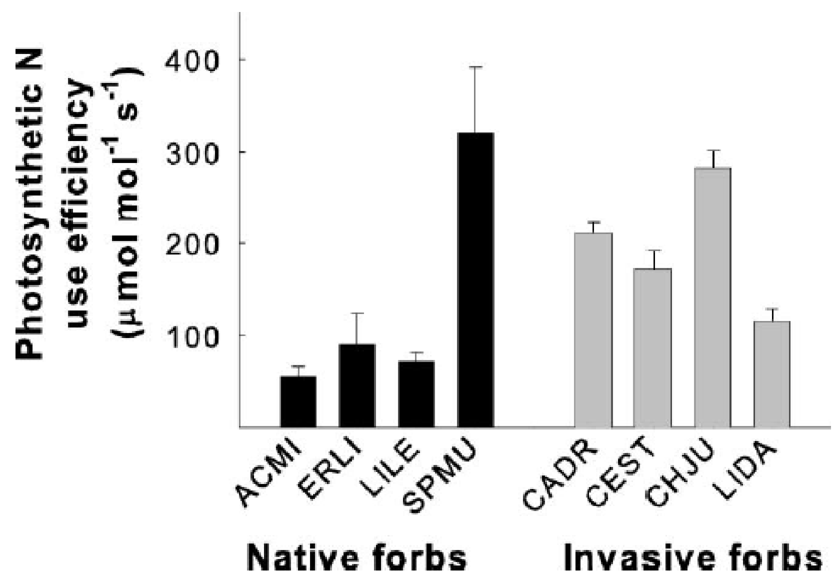



**Figure 7.** Photosynthetic nitrogen use efficiency of native and invasive forbs (mean ± SE). Species abbreviations follow Table 1. Redrawn figure reprinted with permission from the Botanical Society of America. Data are from Drenovsky et al.[10]

# Importance of SLA

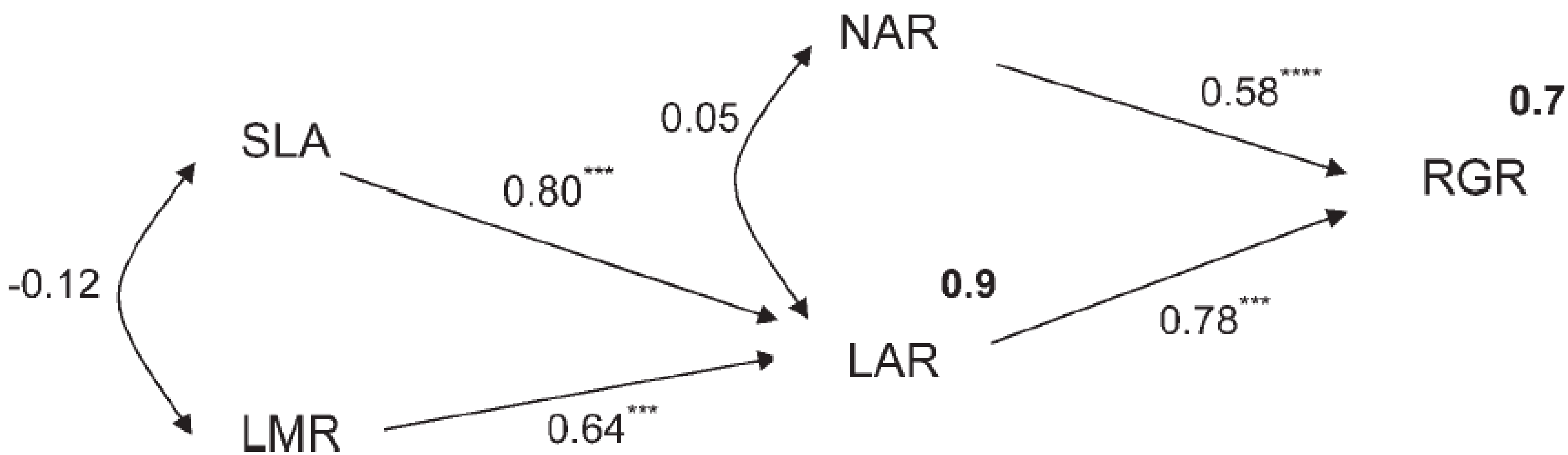



**Figure 3.** Path model describing how variation in net assimilation rate (NAR), leaf area ratio (LAR), specific leaf area (SLA), and leaf mass ratio (LMR) influences variation in relative growth rate (RGR) of native and invasive forbs. For each path effect, the standardized partial regression coefficient is given and the significance of the path is indicated as $^{***}P < 0.0001$. Numbers in bold are the total variance explained ($r^2$) for each dependent variable. Measurements were quantified across four harvests spaced in 2-week intervals. Figure reprinted with permission from SRM. Data are from James and Drenovsky.[9]

Drenovsky and James 2010

# Variation in traits

- Variation is greater in the native plants for 7 of the 9 traits.
- Implications for trait space and invasion resistance

**Table 2. Coefficients of variation for RGR, SLA, and nutrient use and acquisition traits measured for native and invasive forbs. Species replicates for RGR and SLA were based on values for each harvest interval. Data reprinted with permission from the Botanical Society of America. Data are from Drenovsky et al.[10]**

| Trait | Native CV | Invasive CV |
|---|---|---|
| RGR (g/g/day) | 50.1 | 26.7 |
| SLA ($m^2$/kg) | 23.8 | 22.6 |
| Total aboveground biomass (g) | 120.4 | 35.4 |
| Total belowground biomass (g) | 132.1 | 52.9 |
| Root mass ratio (%) | 28 | 37.4 |
| Root length density (km/$m^3$) | 90.5 | 58.3 |
| Leaf nitrogen (g/kg) | 16.2 | 21.2 |
| Leaf phosphorus (g/kg) | 25.3 | 47.2 |
| Photosynthetic assimilation rate (μmol/$m^2$/s) | 65.1 | 23.5 |
| Photosynthetic nitrogen use efficiency (μmol/mol/s) | 106.6 | 36.9 |

CV indicates coefficient of variation; RGR, relative growth rate; and SLA, specific leaf area.

Drenovsky and James 2010

# Hamilton et al. 2005

- **Regional**- Royal National Park **Continental**- Australia
- **Single** is from a simple regression between trait and abundance
- **Control** is from the independent effect of each trait after controlling for residence time
- **Multiple** is from a multiple regression
- Note **Seed Mass** and **SLA**

| | Single | | Control (rt) | | Multiple | |
|---|---|---|---|---|---|---|
| Trait | $r_{(d.f.)}$ | $P$-value | $r_{p\ (d.f.)}$ | $P$-value | $r_{p\ (d.f.)}$ | $P$-value |
| (a) Regional | | | | | | |
| SLA | $0.17_{(1,138)}$ | **0.04** | $0.14_{(2,133)}$ | 0.11 | $0.07_{(4,108)}$ | 0.49 |
| Height | $-0.21_{(1,150)}$ | **0.009** | $-0.21_{(2,145)}$ | **0.01** | $-0.07_{(4,108)}$ | 0.46 |
| Seed mass | $-0.27_{(1,118)}$ | **0.003** | $-0.26_{(2,116)}$ | **0.004** | $-0.19_{(4,108)}$ | **0.04** |
| (b) Continental | | | | | | |
| SLA | $0.30_{(1,137)}$ | **< 0.001** | $0.23_{(2,132)}$ | **0.007** | $0.21_{(4,108)}$ | **0.03** |
| Height | $-0.17_{(1,149)}$ | **0.03** | $-0.21_{(2,144)}$ | **0.01** | $0.00_{(4,108)}$ | 0.97 |
| Seed mass | $-0.29_{(1,118)}$ | **0.001** | $-0.32_{(2,116)}$ | **< 0.001** | $-0.23_{(4,108)}$ | **0.02** |

Hamilton et al. 2005

# Issues of Scale

- Why is Seed Mass significant at multiple scales, while SLA drops out at regional scales?
  - Colonization (seed mass) vs. Establishment (SLA) opportunities
- At Local scales, small seed mass does not correlate with invasion success, while SLA does (Lake & Leishman 2004)
  - However, did not control for cross-correlation with other life history traits
- Temporally, abundance of a non-native species increases with increasing time (Hamilton et al. 2005)
  - Slope significantly greater at continental vs. regional scale

# Grotkopp et al. 2002

- In addition to assigning invasiveness based on actual reports, the following equation was used to quantify invasiveness (derived from Rejmanek and Richardson 1996):

$$Z = 19.77 - 0.51\sqrt{M} - 3.14\sqrt{J} - 1.21S$$

- M = mean seed mass
- J = minimum juvenile period
- S = mean interval between large seed crops

# Links among traits

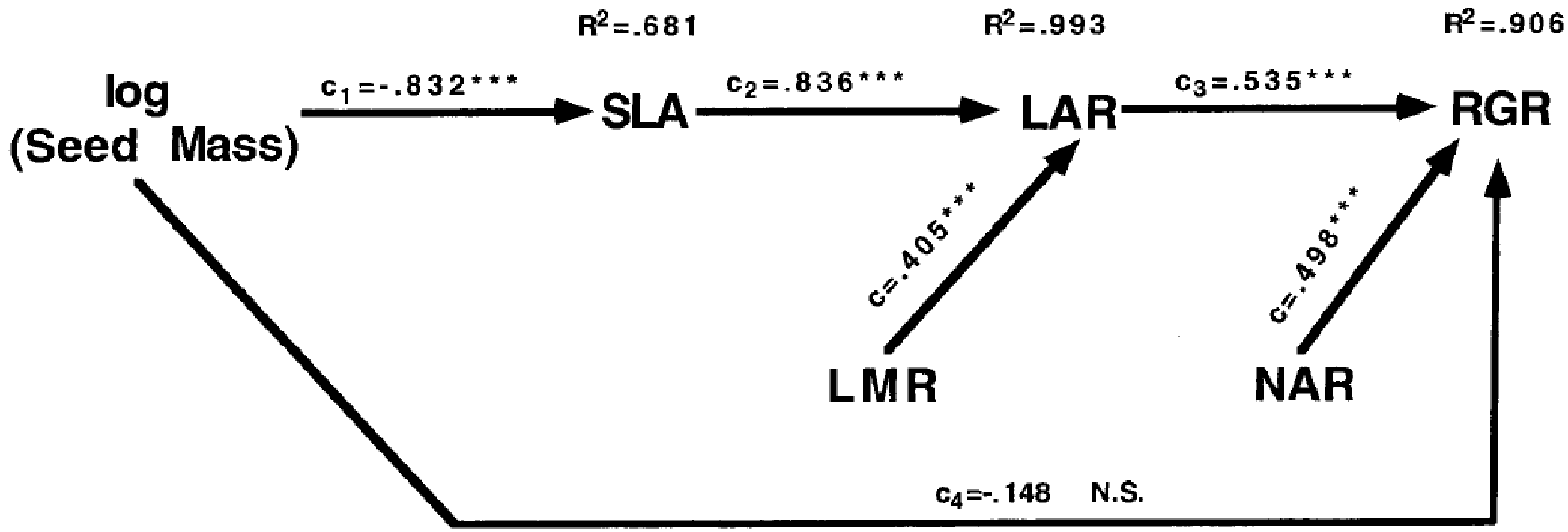



Figure 8: Path diagram and path coefficients ($c$) showing strengths of causal links between log (seed mass), specific leaf area ($SLA$), leaf area ratio ($LAR$), leaf mass ratio ($LMR$), net assimilation rate ($NAR$), and relative growth rate ($RGR$). Three asterisks indicate $P < .001$.

Grotkopp et al. 2002

# RGR and SLA compared to Seed Mass

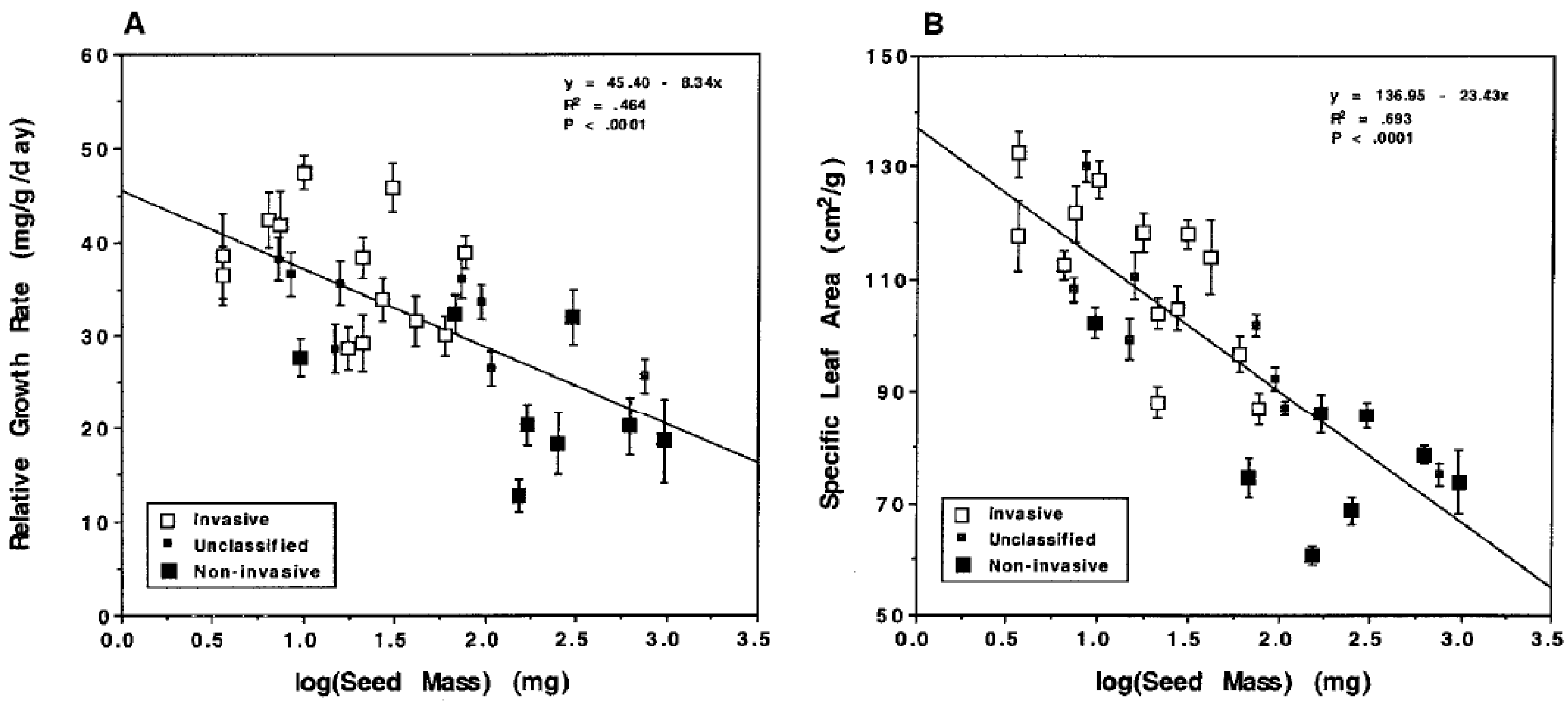



Figure 7: Relationships (*A*) between relative growth rate and log (seed mass) and (*B*) between specific leaf area and log (seed mass)

Grotkopp et al. 2002

# Minimum Generation Time

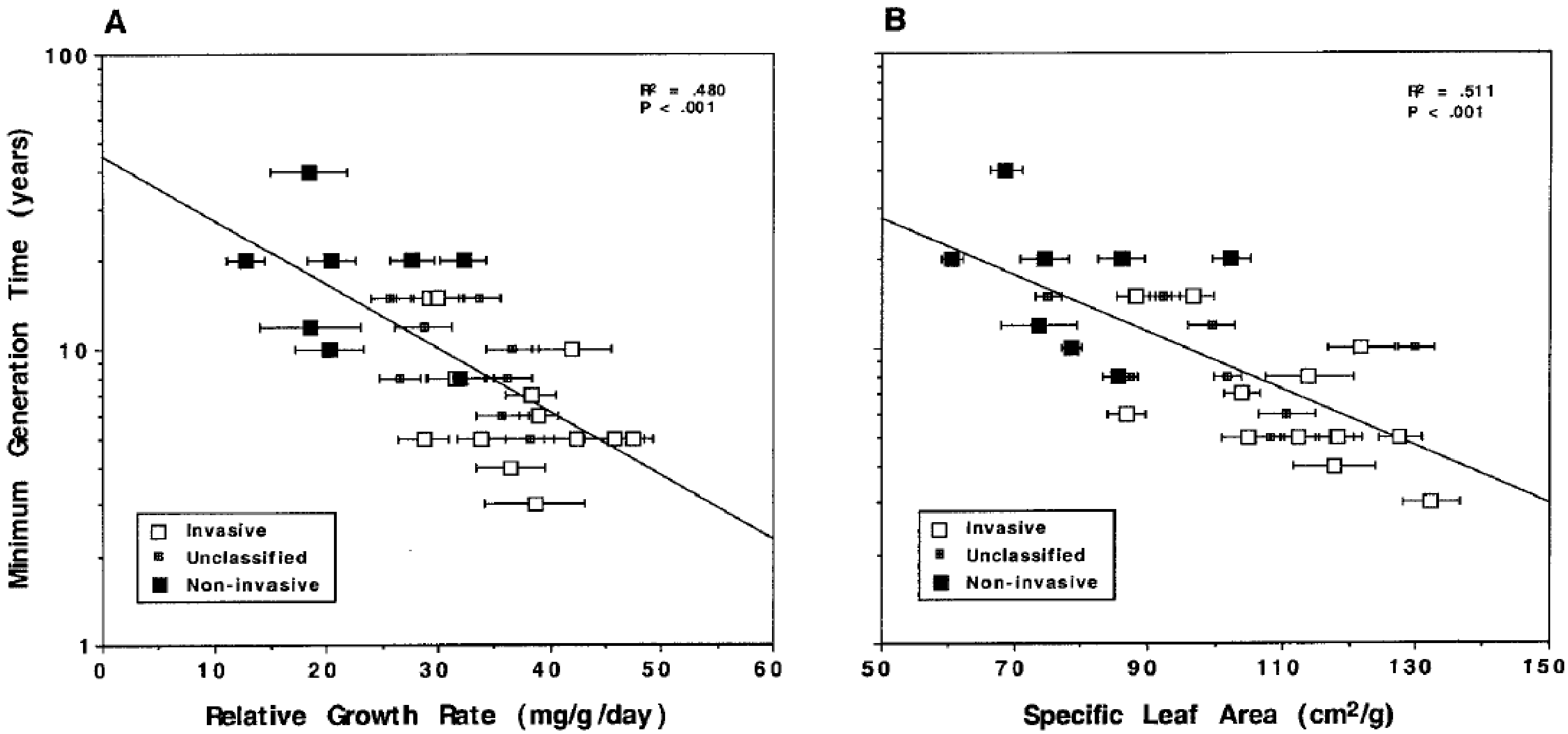



Figure 9: Relationships between log (minimum generation time) and (*A*) relative growth rate and (*B*) specific leaf area

Grotkopp et al. 2002

# Effect of Age

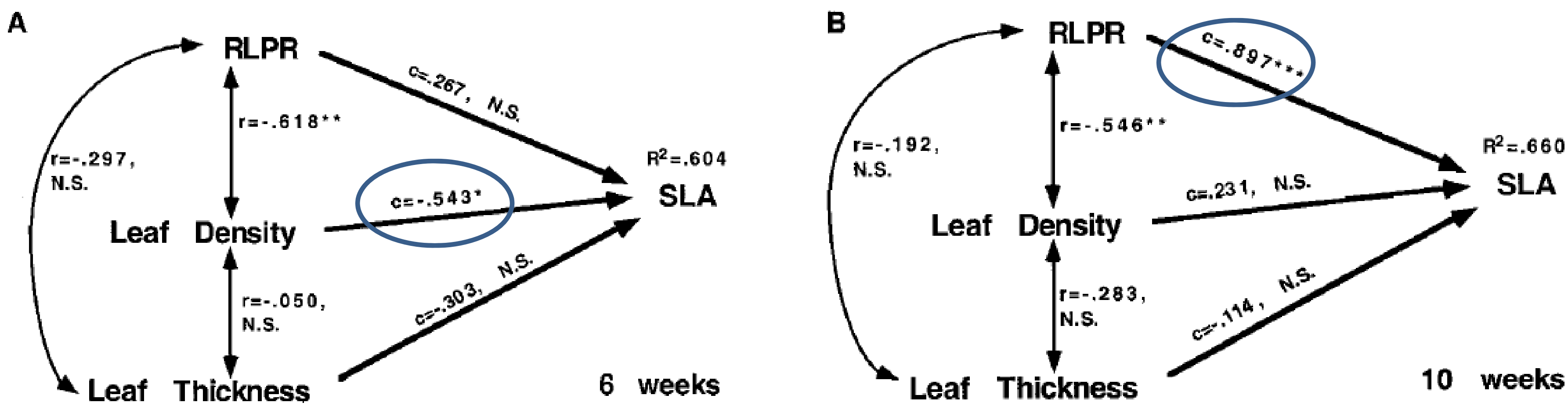



**Figure 6:** Path diagrams and path coefficients (*c*) showing strengths of causal links between relative leaf production rate (*RLPR*), leaf density, leaf thickness, and specific leaf area (*SLA*) in seedlings of 29 pine species at (*A*) 6 wk and (*B*) 10 wk. A single asterisk indicates $P < .05$; two asterisks indicate $P < .01$; three asterisks indicate $P < .001$.

Table 1: Abbreviation, name, and units of growth analysis quantities

| Abbreviation | Variable name | Units |
|---|---|---|
| RGR | Relative growth rate | $mg/g_{plant}/d$ |
| NAR | Net assimilation rate | $mg/cm^2/d$ |
| LAR | Leaf area ratio | $cm^2/g_{plant}$ |
| LMR | Leaf mass ratio | $g_{leaf}/g_{plant}$ |
| SLA | Specific leaf area | $cm^2/g_{leaf}$ |
| RLPR | Relative leaf production rate | leaf/leaf/d |

Grotkopp et al. 2002

# Which traits really matter (to pine trees)

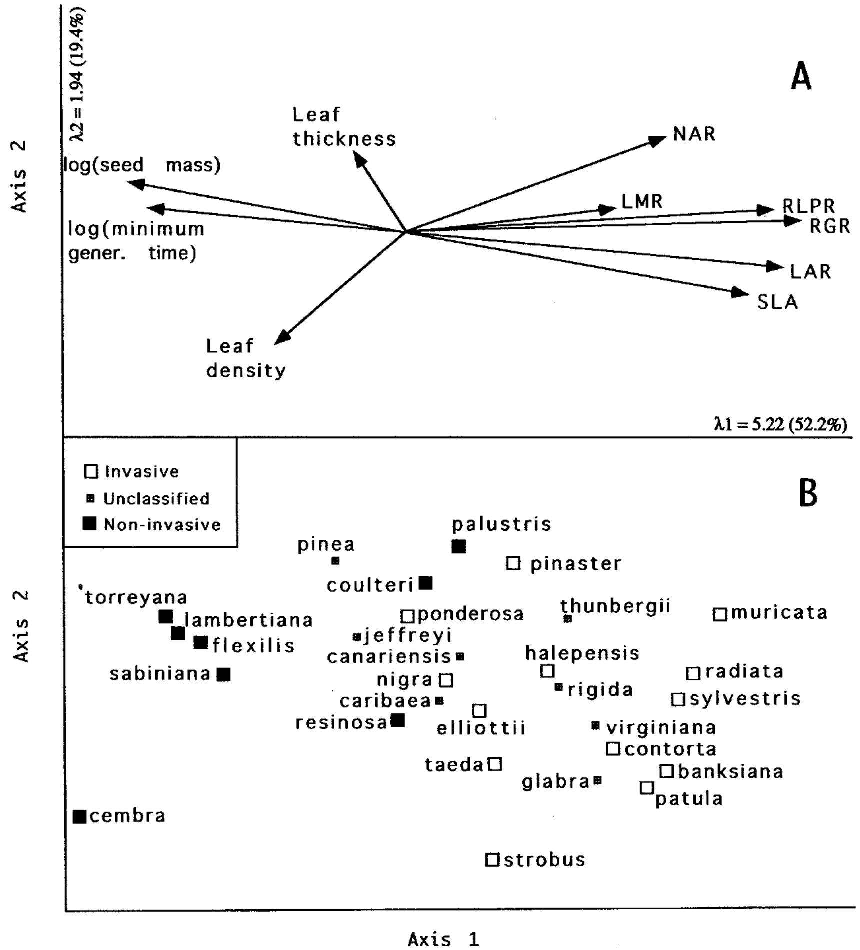
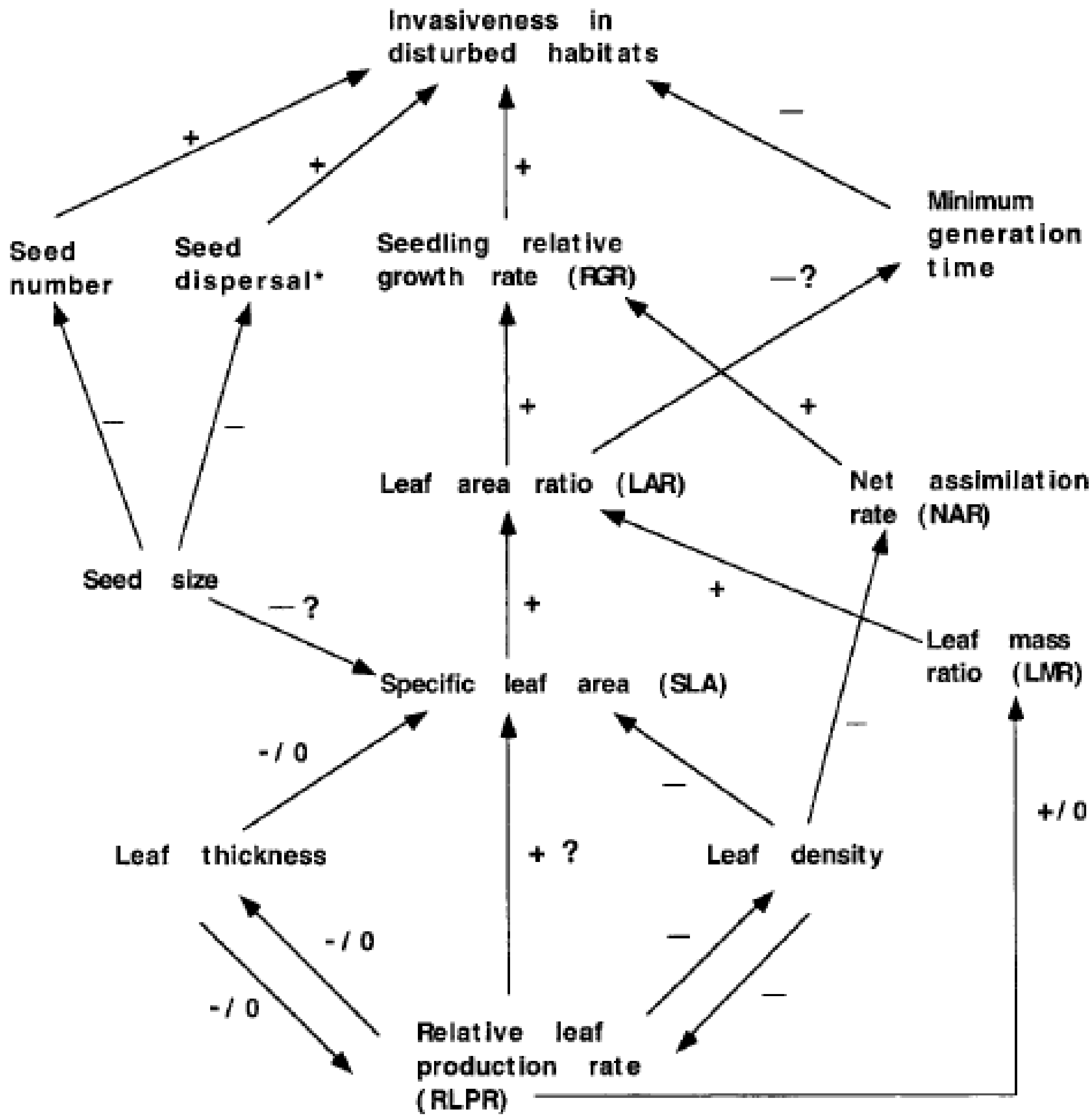



**Figure 11:** Biplot of 29 pine (*Pinus*) species and 10 life-history-related variables created by principal component analysis. For the sake of clarity, the variables (*A*) are plotted separately from species (*B*).

Grotkopp et al. 2002




Grotkopp et al. 2002

# Relating Invasiveness to Traits

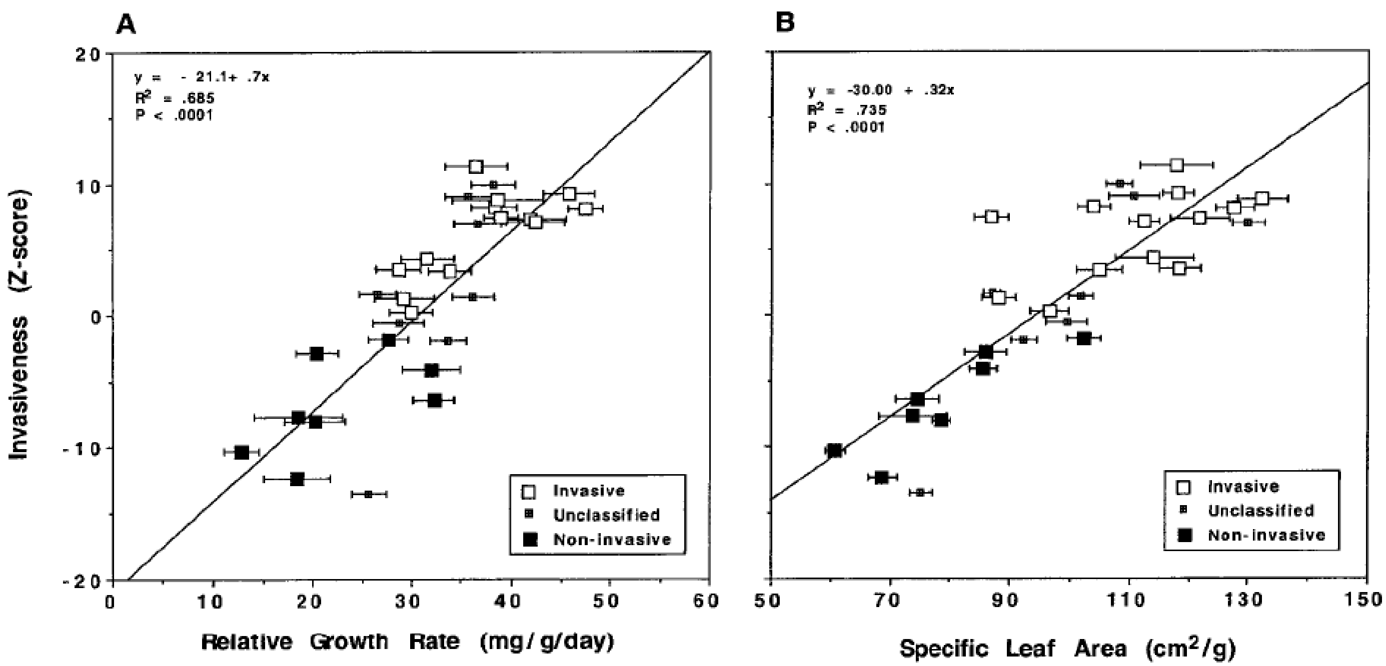



**Figure 10:** Relationships (*A*) between a measure of invasiveness (*Z* score) and relative growth rate and (*B*) between invasiveness (*Z* score) and specific leaf area. The *Z* scores are calculated from the discriminant function derived by Rejmánek and Richardson (1996).

Grotkopp et al. 2002

# What makes a successful invader?

- High RGR/SLA
- Low Seed Mass
- Short Generation times

- But do these traits mean much for persistence in the invaded environment?

# Citations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