The diversity-invasibility hypothesis

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models, field studies and the importance of scale

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Outline

1) The diversity-inasibility hypothesis – Elton
2) A LV model assessing invasibility
3) Spatial pattern studies
4) The influence of extrinsic factors in an experimental study
5) An extended model accounting for scale and resources
6) Conclusions

Community Invasibility

- One component of **community stability** is "resistance" to abiotic and biotic disturbances.
- **Invasion success** =
  propagule pressure + invasiveness + invasibility
- **Invasibility** = ease at which invasive species from low numbers become established members of a community
- Is there influence of community diversity on invasibility?
  What kind of influence?

Elton 1958

"the balance of **relatively simple communities** of plants and animals is more easily upset than that of richer ones; that is more subject to destructive oscillations in populations ... and **more vulnerable to invasions**"

"oceanic islands and crop monocultures are simple ecosystems that show high vulnerability to invasions ... and frequent outbreaks of population subsequently"

The diversity-invasibility hypothesis

High native diversity decreases community invasibility

The diversity-invasibility hypothesis

SUPPORT

- **classical niche theory** (MacArthur):
  - strongly structured (interconnected) communities
  - **competition** for resources
  - limited niche space
- "**sampling effect**" for strong competitor in community

The diversity-invasibility hypothesis

CAUTION

- indirect **facilitation**
- loosely structured non-equilibrium communities
- diversity is **correlated** with disturbance, isolation, resource availability, physical stress, competitors, consumers, that also directly influence invasibility
- diversity increases micro**heterogeneity**
  → more invasible
- **diversity-stability** (May)
- no influence if invader with very different traits

Modelling Invasibility

Invasion resistance deals with **great perturbations**: no asymptotic stability but community in new state-space with added species

<u>Assumptions</u>

- resident community at **equilibrium**
- **finite species pool** (characteristics limited)
- invading species similar to residents
- small **spatial scale** (LV assumes mixed pop.s)

How to quantify invasion success?

Questions from niche theory

- Invasibility into **vacant niches**
- **Niche saturated** communities are only invasible by competitive displacement.
- Is there **priority** of residents over invaders? Why?
- Do species **replacement** rates decline with species richness?

Model

- Examine **invasibility** of
  - stable model communities
  - varying in diversity and average strength of species competition
  - single trophical level
- Lotka-Volterra comptetion equations

$$\frac{dN_i}{dt} = \frac{r_i N_i}{K_i}\left(K_i - \sum_{j \neq i}^{n} \alpha_{ij} N_j\right)$$

Case 1990

Resident communities I

- α_{ij} chosen **random**ly from uniform distribution
- $r_i = 0.5$ for all i
- choose K_i so that the equilibrium densities of all species are feasible $(n_i > 0)$
- test for stability (small perturbations) of core community → discard if fails
- selection may bias properties of α_{ij}, however, unimportant here

Case 1990

Resident communities II

- **resource utilization overlap matrix** $U_{N \times M}$ gives rates of utilization of resident i on resource k
- u_{ik} from log-normal distribution
- community matrix A with

$$\alpha_{ij} = \frac{\sum_{k=1}^{M} u_{ik} u_{jk}}{\sum_{k=1}^{M} u_{ik}^2}$$

- K_i and r_i selected as before

➔ A is positive definite

➔ resulting core community is globally stable if feasible

Case 1990

Community invasion

- (I) α_{ij} for invader drawn from same distribution as residents
- (II) add new row to resource utilization matrix $\boldsymbol{U}$
- $\boldsymbol{K}$ of invader is average of resident $\boldsymbol{K}_{\boldsymbol{i}}$
- simulate invasion by introducing the invader at low numbers ($\boldsymbol{K}_{\boldsymbol{i}}/1000$) into equilibrium resident community
- **follow community trajectory** until it settles into a new equilibrium (not just look at equil. densities)

Case 1990

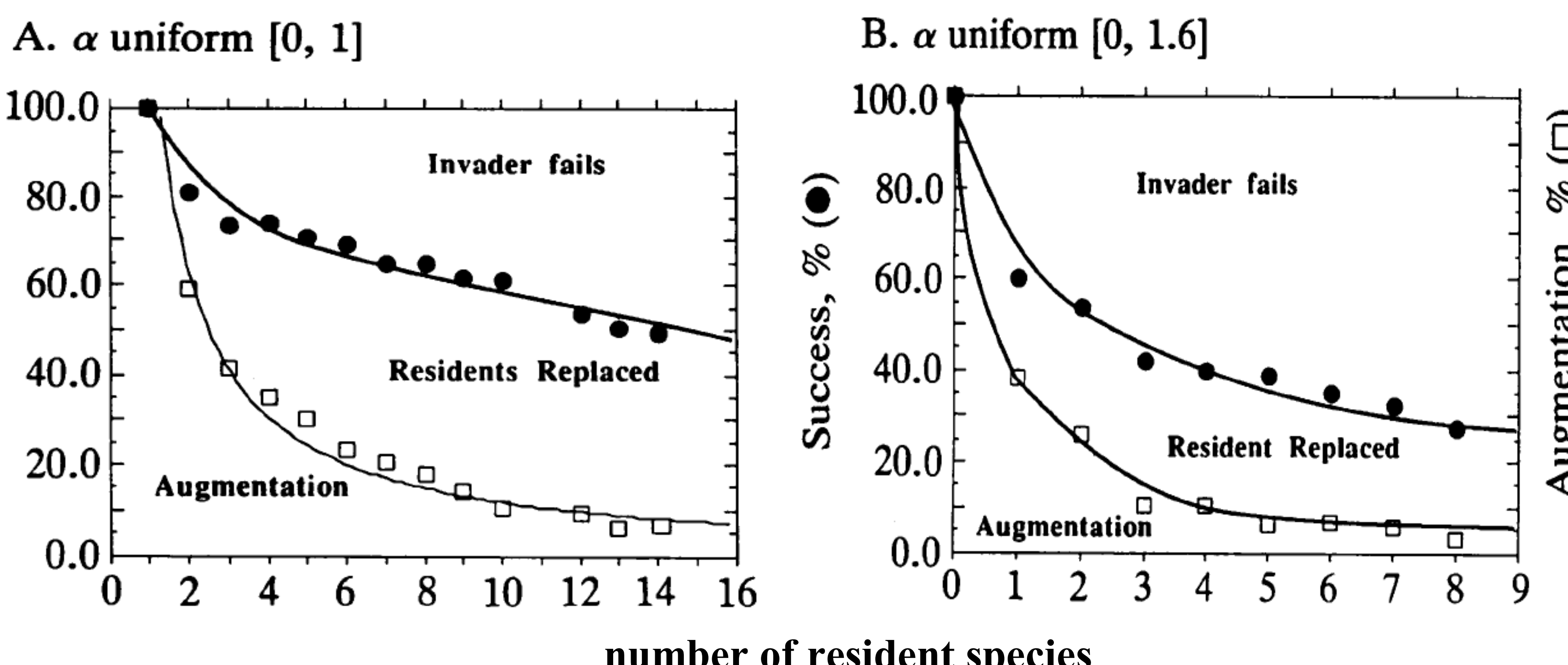
Simulation results

- **invasion success** = persistence at equilibrium
- **4 possible outcomes**
  - community augmentation
  - replacement
  - rejection failure
  - indirect failure (only variant I)

Case 1990

Invasibility vs. diversity

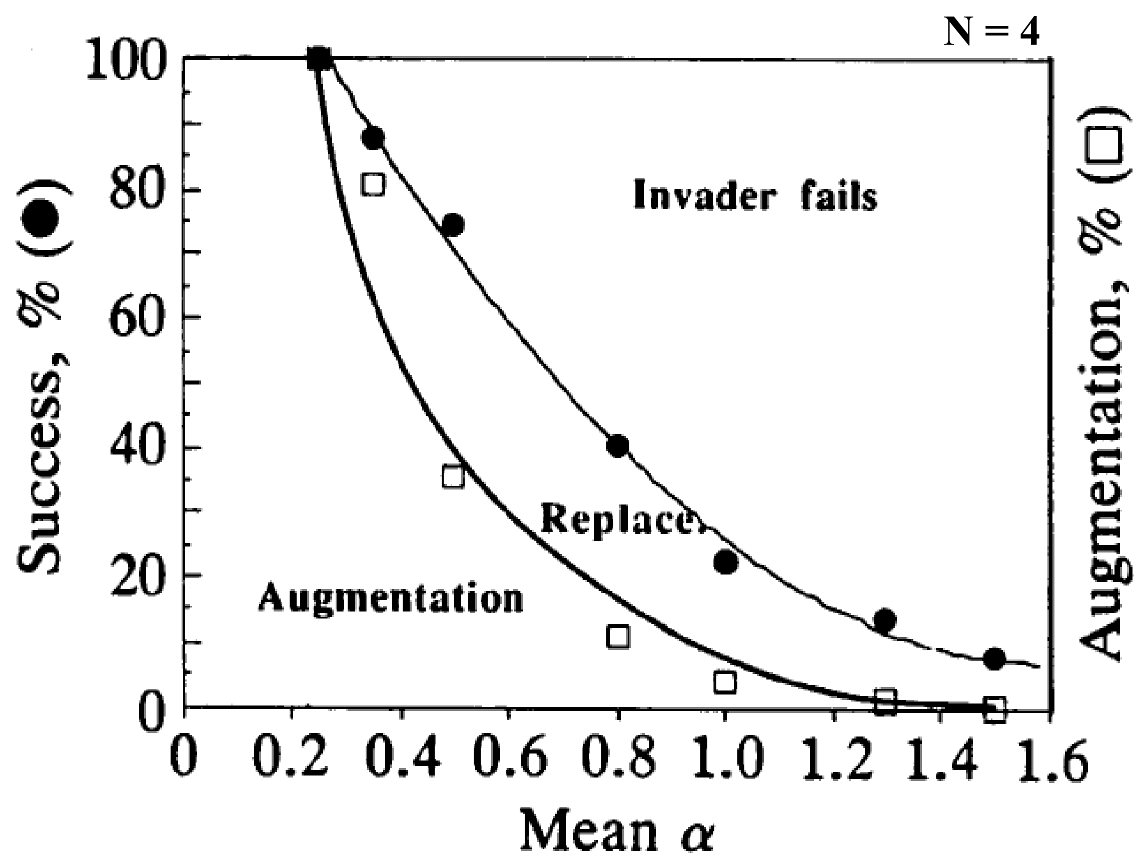
- Invasion outcome as a function of **community size** (random α_{ij}, similar for overlap matrices (II))



Case 1990

Invasibility vs. interactions

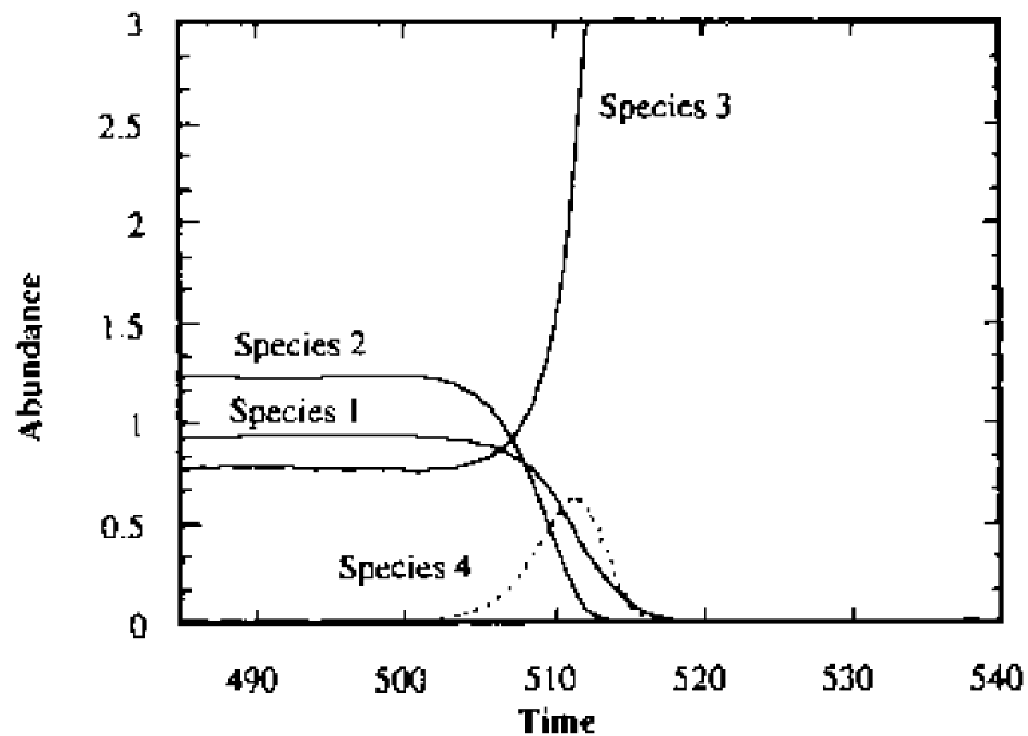
- Invasion outcome as a function of **interaction strengths**



Case 1990

Community fracturing

- positive growth does not imply invasion success
- feasibility and **multiple domains of local attraction** for random α_{ij}
- only for random α_{ij} (I)

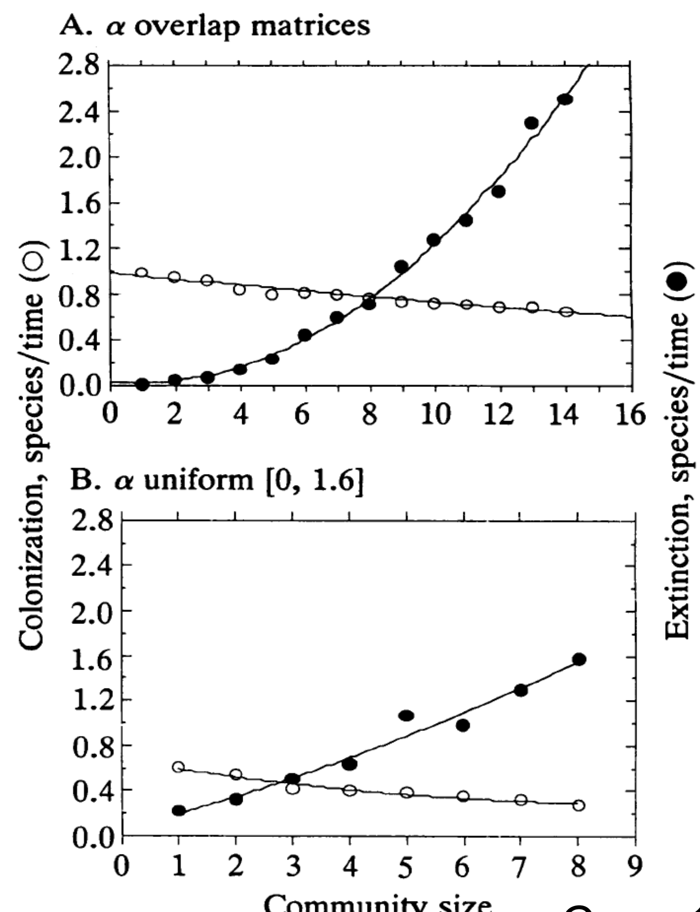


Case 1995

Colonization / extinction

colonization = invasion success (augmentation, replacement)
extinction (invasion caused) = resident species loss
(replacement, indirect failure)

- **equilibrium community size** where species extinction rate balances colonization rate
- **species turnover** at equilibrium lower with increased average interaction strength



Case 1990

Role of community vs. invader

- ANOVA of replicated invasion attempts (random $\boldsymbol{K}$) into different core communities
- i.e. compared between-community differences to between-invader (within-community) differences in invasion success/augmentation success
- $\boldsymbol{F} > 5 \; (\boldsymbol{p} < 0.001)$
- **between community differences** are more important than invader characteristics

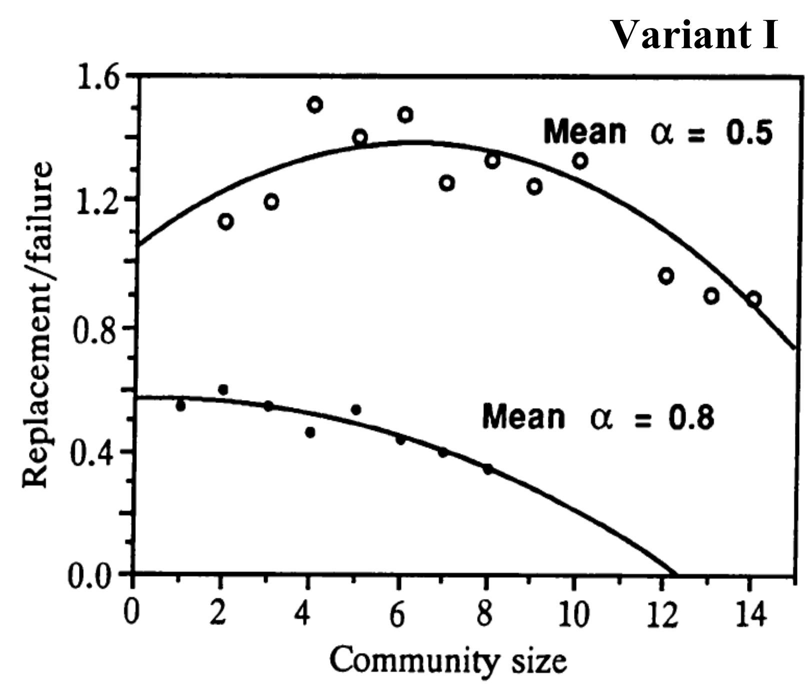
Case 1990

Invasion repelling

- **Augmentation** rates decline with community diversity (May)

- **Priority effect:** ability to repell invaders by emergence of multiple domains of attraction in large/strongly connected communities

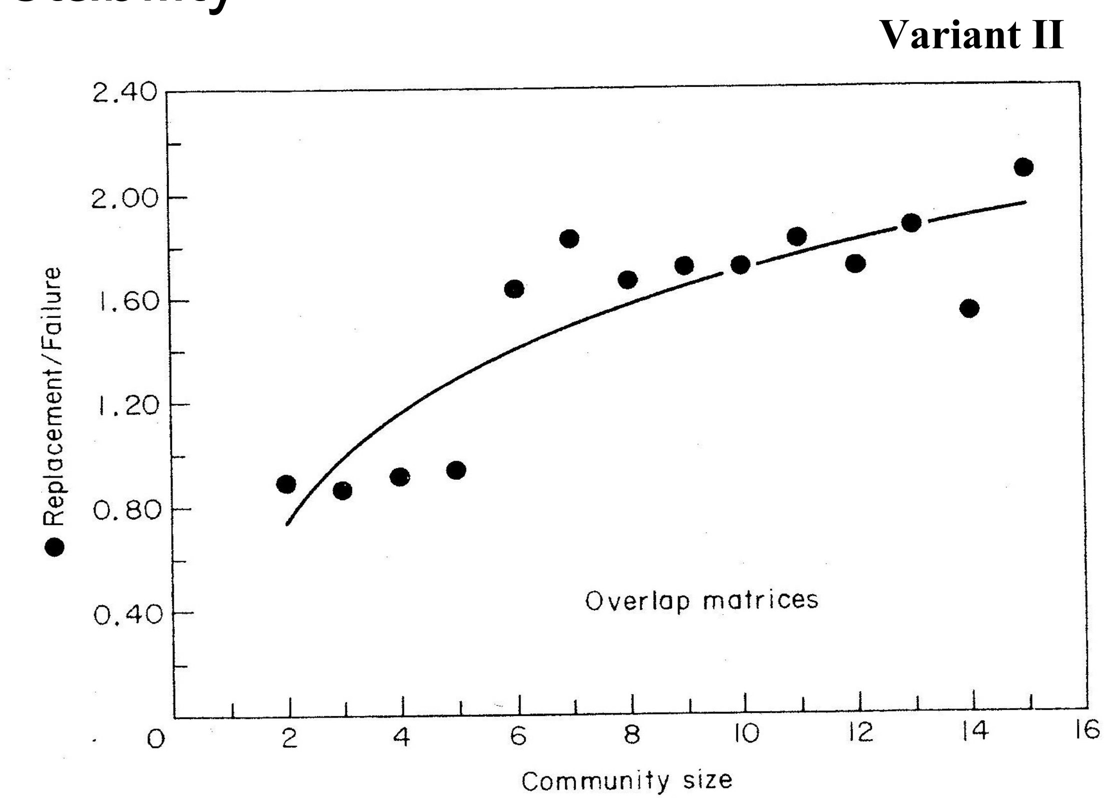
→ disadvantage of **low frequency** and **late-coming** species into diverse system (even if equivalent competitor)



Case 1990

Invasion repelling

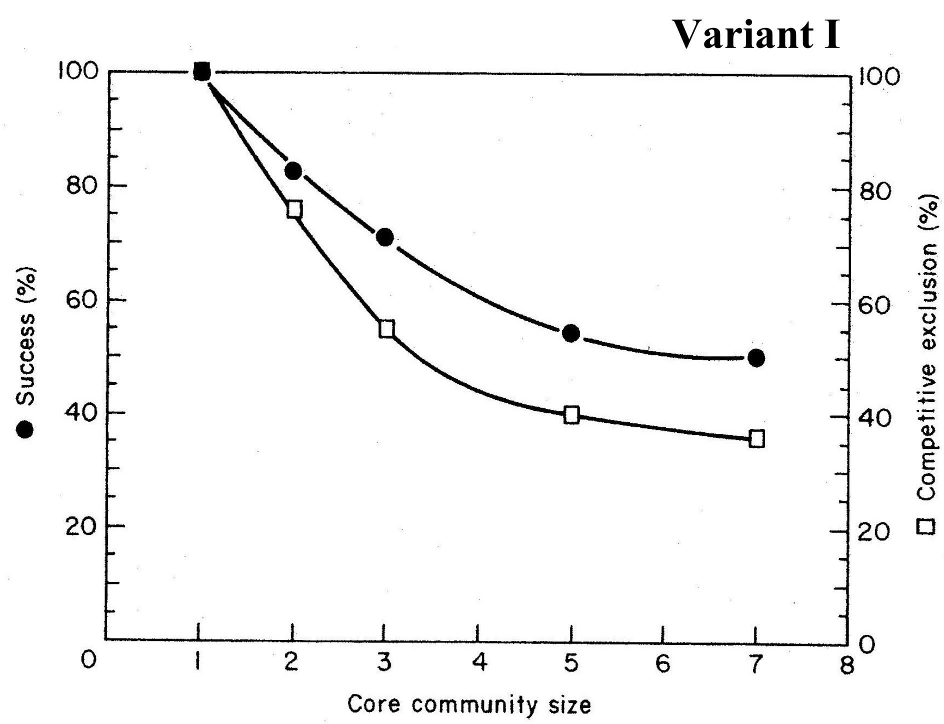
- using resource utilization overlap matrices
  no multiple domains of attraction
- diversity-stability



Case 1991

Indirect interactions

- **species' enemy's enemy is ally**
- inferior competitors are protected from competitive exclusion by invading superior



→ species rich communities protect themselves from invasion

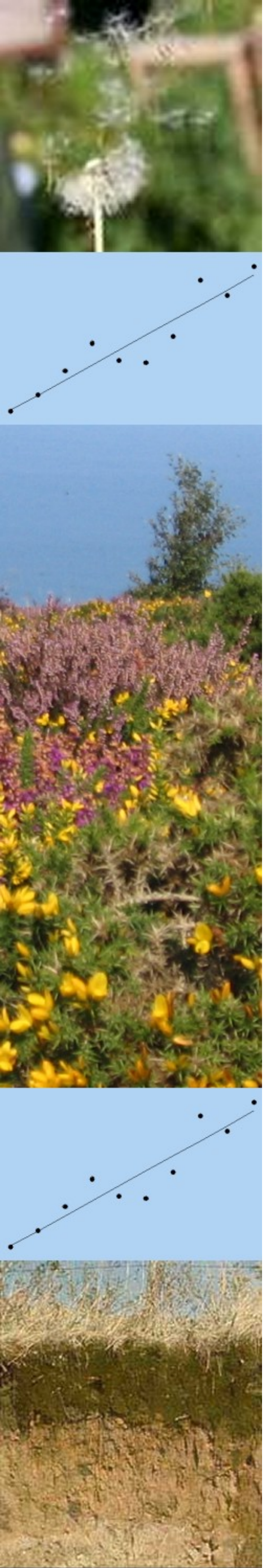
Case 1991

Summary

"species-interactive theory of island biogeography"

- large, tightly interacting community resistant to invasion without invoking
  - coevolution
  - adaptation (Lack)
  - *a priori* resident priority
- **multiple stable domains** of the diffuse competition system yield invasion resistance
- **However, interaction is just part of the story!**

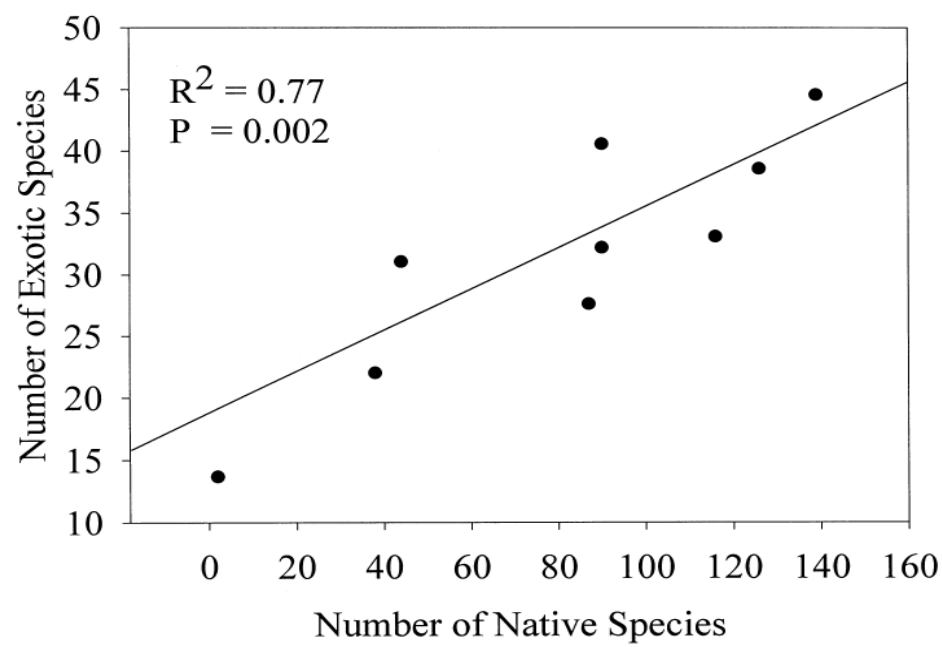
Case 1990



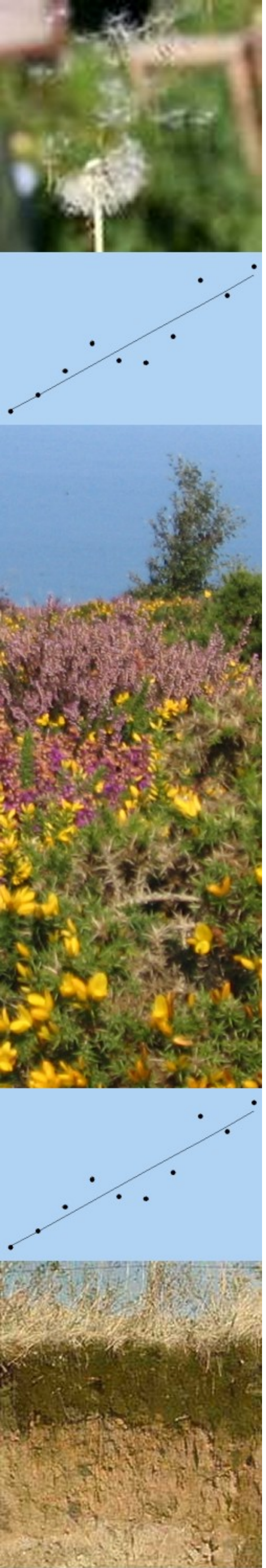
Spatial pattern studies

- correlate invader abundance (as **indicator for invasibility**) with community diversity
- many studies find **positive relationship** between diversity and invasibility (which is explained in various ways)

e.g. Australian heath- and shrubland reserves



Levine and D'Antonio 1999



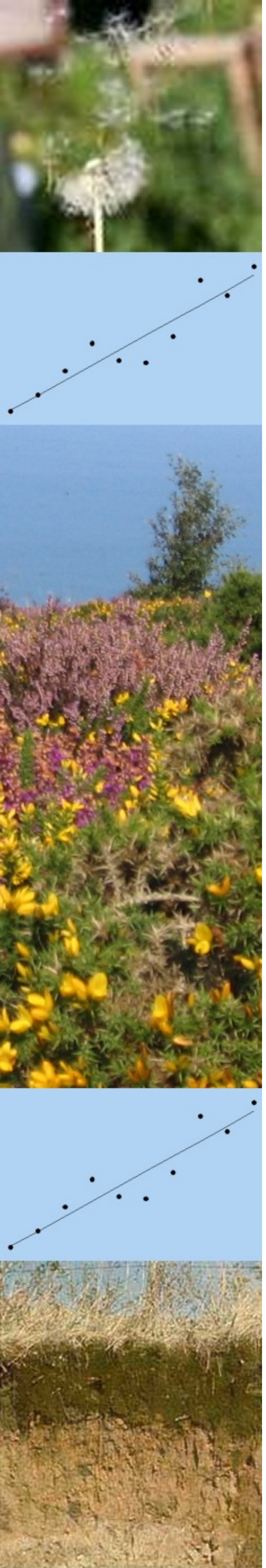
Why positive relationship?

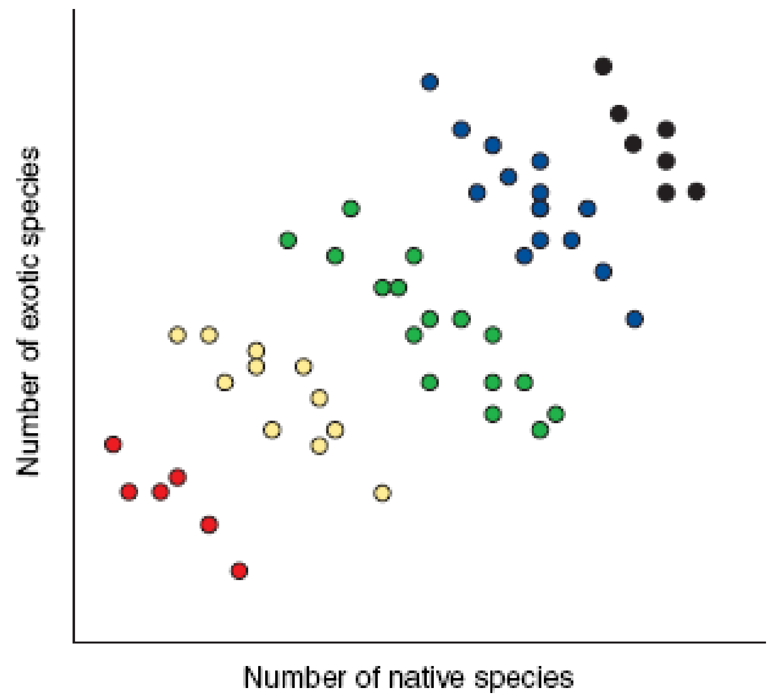
- **Environmental covariates** (similarity of natives and invasive species)
- **Propagule supply**, species pool size
- Environmental **heterogeneity**
- indirect **facilitation**
- community maturity stage
- Current vs. pre-invasion resident diversity (influence of invader on diversity)

Levine and D'Antonio 1999

The importance of scale and covarying factors

- **Scale dependence** and **extrinsic factors** drive diversity and invasibility
  - latitude
  - climate
  - soils
  - resource supply





Shea and Chesson 2002

The influence of extrinsic factors

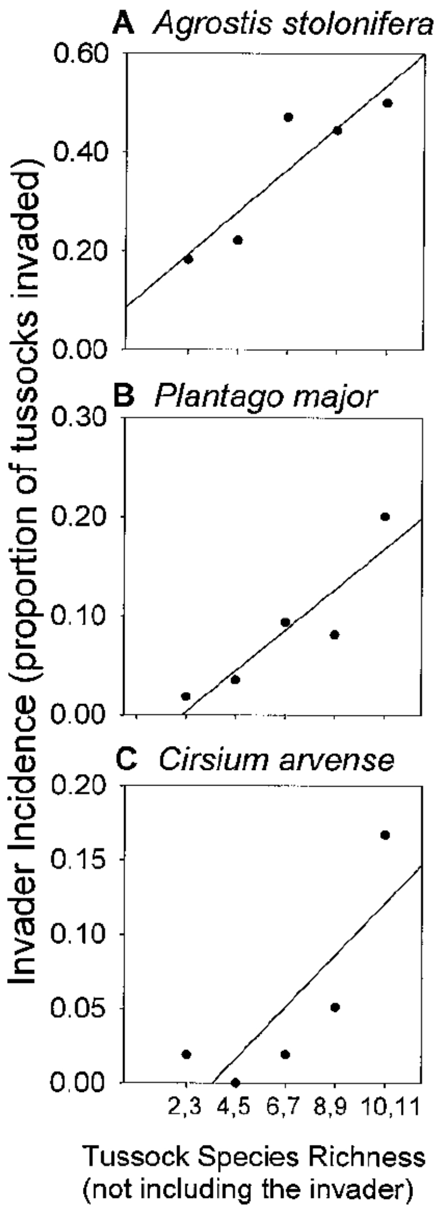
- **experimental study** about scale dependence of diversity-invasibility relationship
- *Carex nudata* tussocks (discrete micro-islands) in a California riparian system

  (1) survey **invasion patterns** on similar sized tussocks

  (2) random ***in situ* manipulation** of local diversity in a natural context and seed addition of 3 different invasive plants

Levine 2000

The influence of extrinsic factors

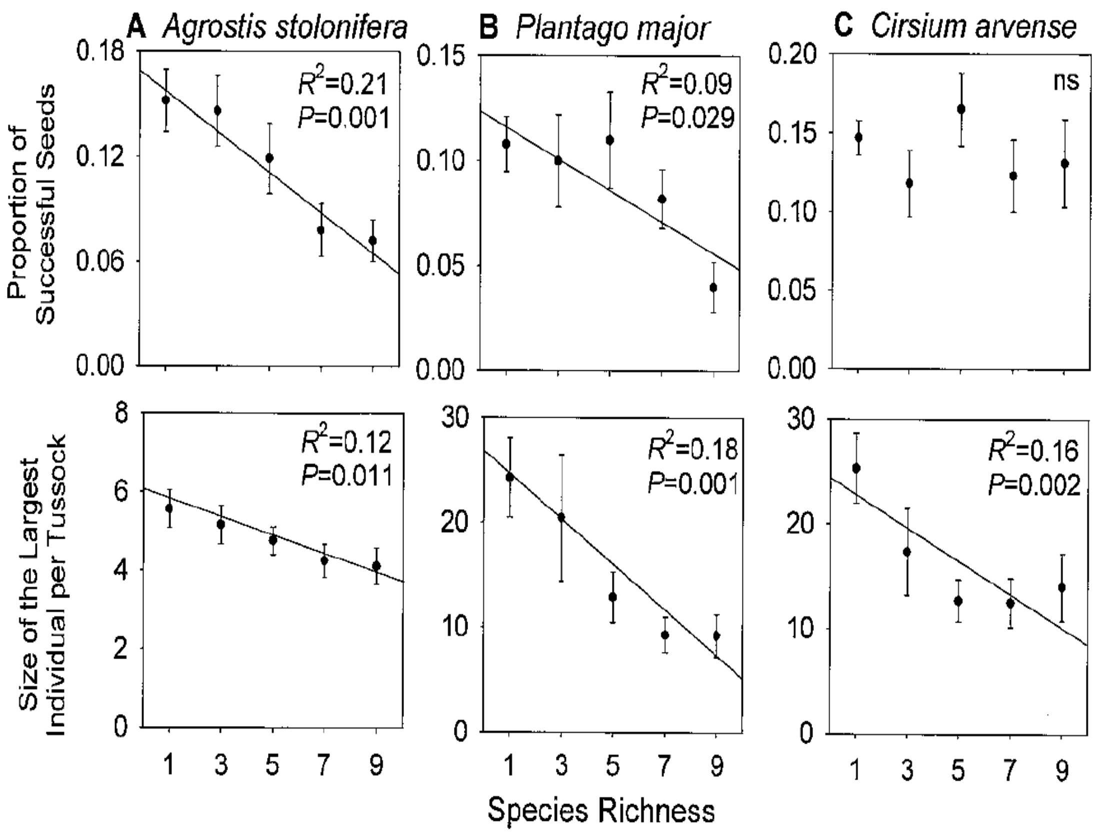


- **positive correlations** may not reflect intrinsic effects of diversity
- may result from similar response of natives and exotics to **environmental conditions** (soil nutrients, disturbance, prop. pressure)

Levine 2000

The influence of extrinsic factors

- results of **small scale** manipulation experiments



- **resident species cover**/diversity affects germination of invasive seeds
- on **large scale** covarying factors determine invasibility (small R^2 of diversity effect)

Levine 2000

Scale and resources

- **small-scale**:
  - constant environmental variables
  - only differing number of native species
- **large-scale**:
  - variation also in environmental factors that may covary with diversity and influence invasibility
- need to account for the effect of such covariates

➔ **extension of Case's model** to account for resource availability

Byers and Noonburg 2003

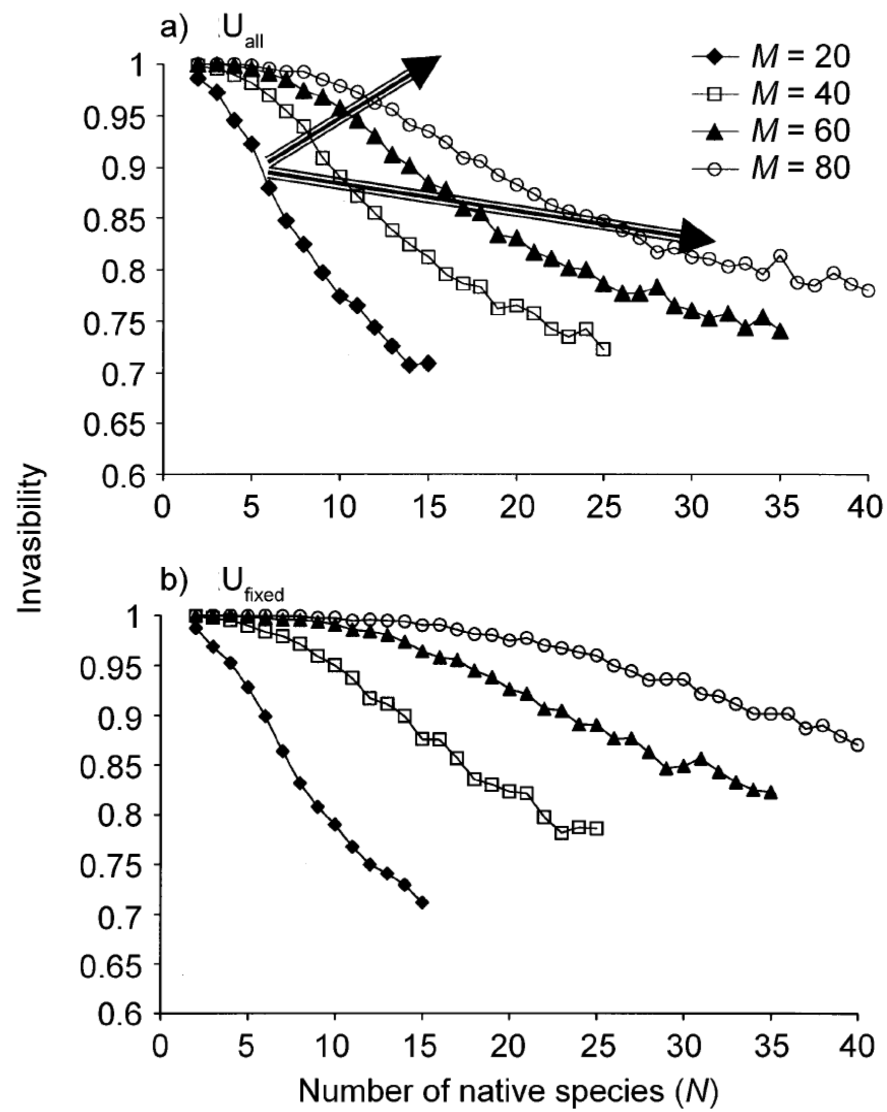
Model extension

- **resource utilization overlap method**
  - direct link of environmental differences with interaction strength
- modified algorithm for selection of u_{ij}
- for each species i select M uniformly distributed random numbers $x_{ik} \in [0,1]$ and add each to u_{ik} (k random) if $x_{ik} > $ threshold T
- U_{all}: niche breadth increases with M, $T = 0$
- U_{fix}: niche breadth independent of M, T varies with M, so that $M(1-T) = M_{util} = const.$

Byers and Noonburg 2003

Scale dependence

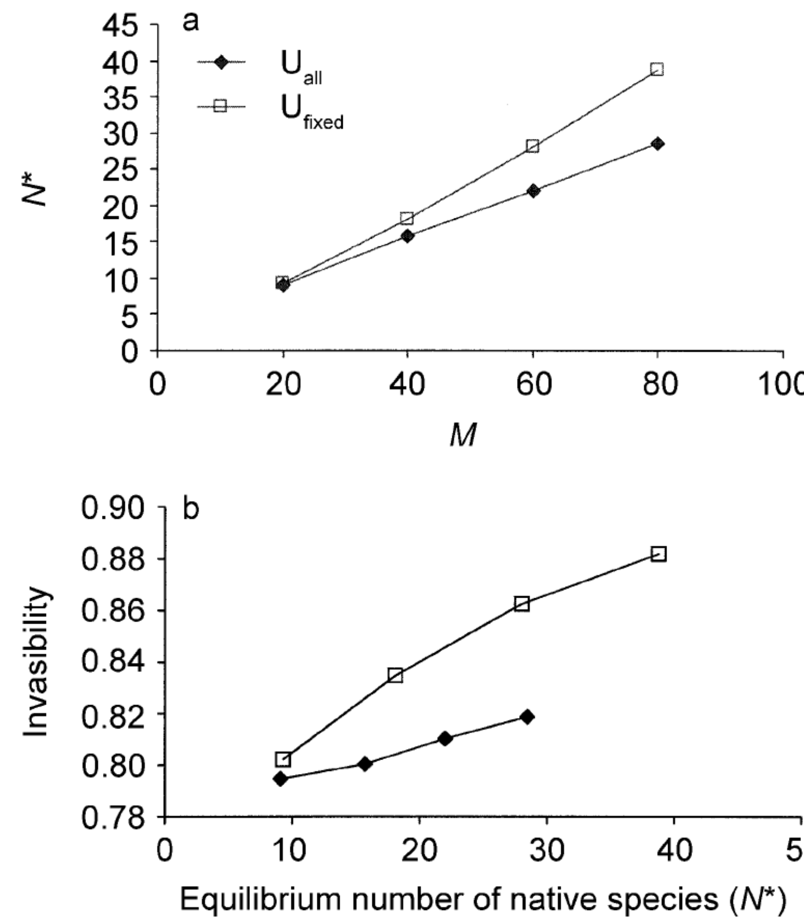
- Small scale
  - const M: invasibility ~ 1/N
- Large scale
  - N increases slowly with M: invasibiliy ~ N
  - N increases rapidly with M: invasibility ~ 1/N
- in field studies often N ~ M



Byers and Noonburg 2003

Resource dependence

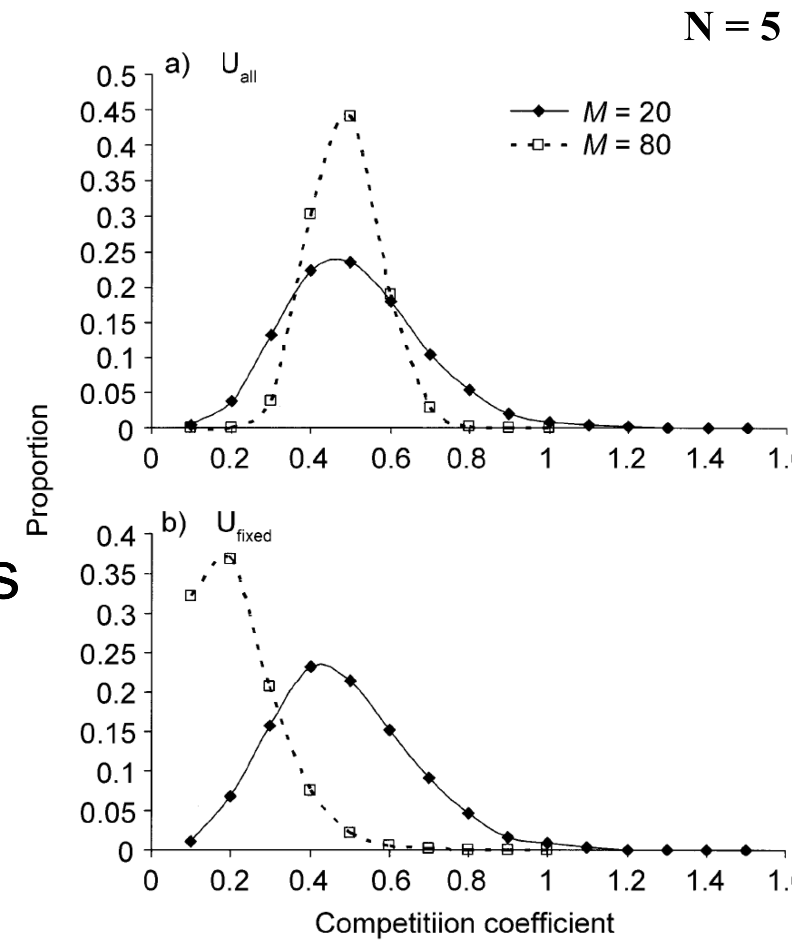
- increased N^* with M
- U_{fix} : divesity promotes invasibility (natives and invasives similarly regulated, resources available)
- U_{all} : invasibility not affected by N^*, but rather by factors covarying with M (e.g. disturbance)



Byers and Noonburg 2003

Competition strength

- $M \sim 1/Var(\alpha)$
- U_{fix} :
  - $M \sim 1/\bar{\alpha}$
  - proportionally less competition
    $\rightarrow$ more free resources
  - "specialist" community
  - invasibility rises more rapidly than for "generalists"



Byers and Noonburg 2003

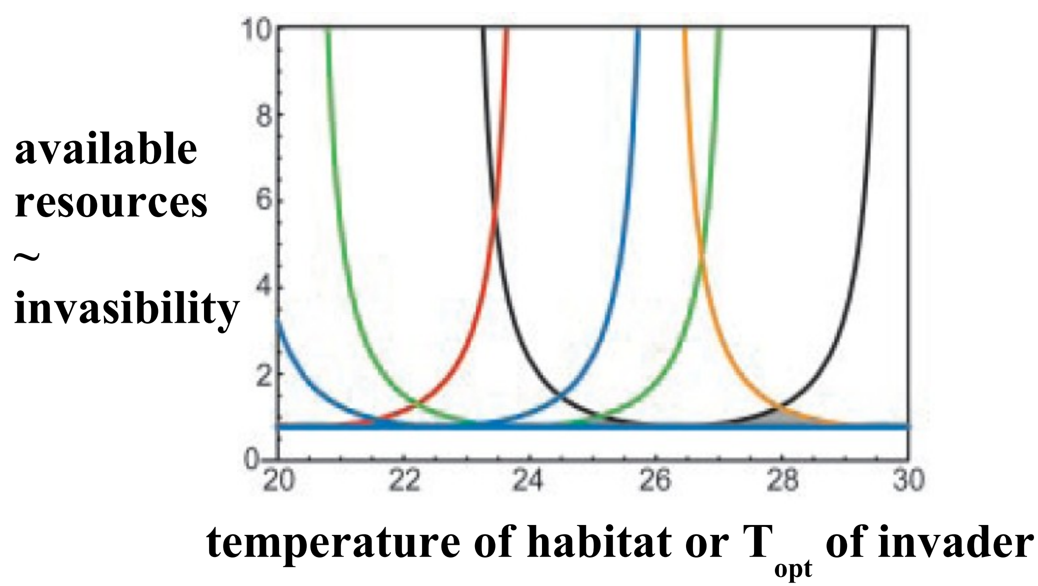
Summary

- **decreasing interaction strength** as resources increase → increasing invasibility with native diversity at **large scale**
- **niche breadth behaviour** of natives determines
  - strength of positive relationship between native and invasive species diversity
  - relative contribution of extrinsic factors to the community
- **increasing interaction strength** at constant resource numbers → decreasing invasibility with native richness at **small scale**

Byers and Noonburg 2003

Stochastic niche theory

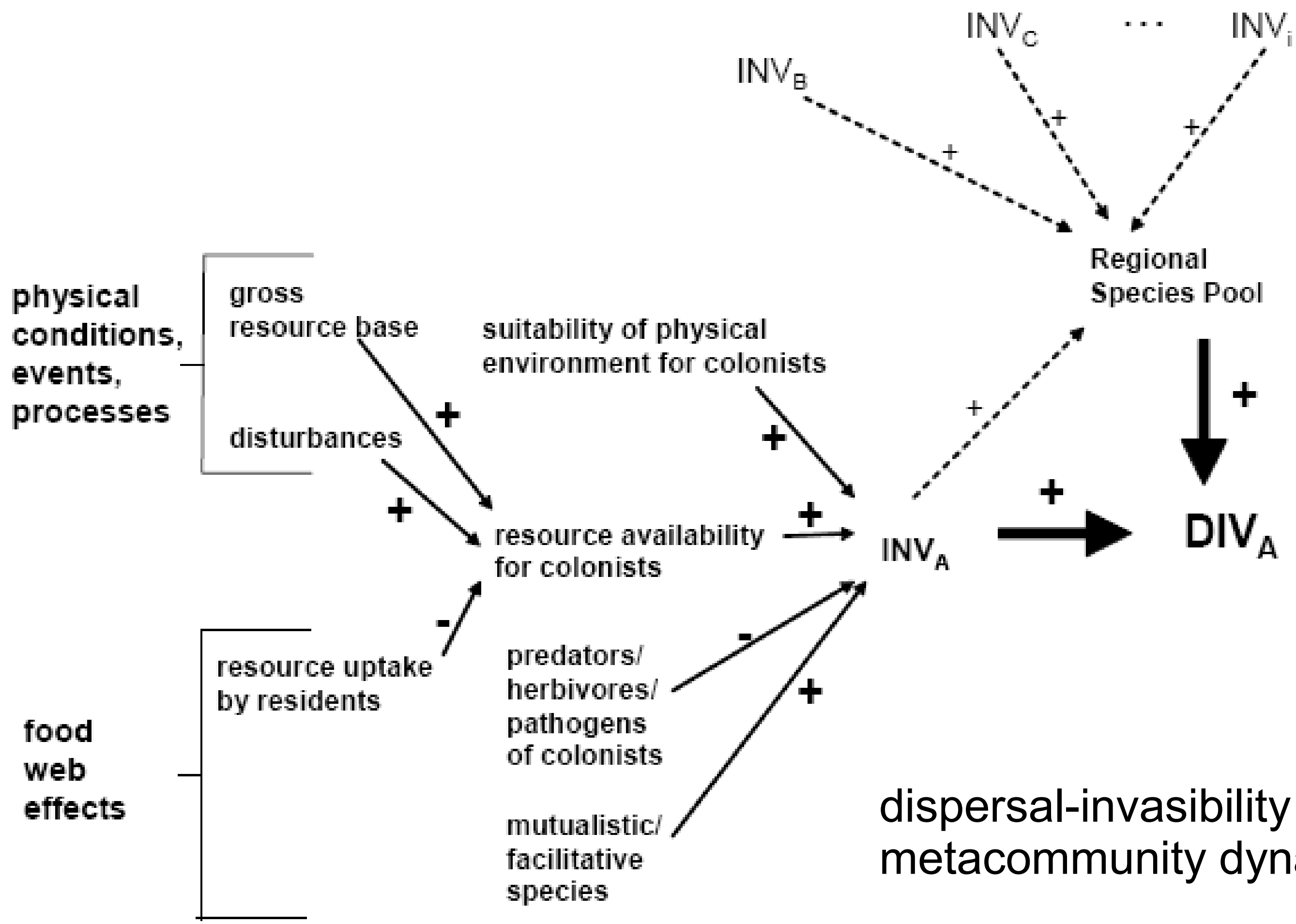
- similar conclusion:
  - invasibility depends on the degree to which native species exploit **habitat heterogeneity** in limiting resources
  - scale dependence of spatial heterogeneity



Tilman 2004

However

Does invasibility drive community diversity?



dispersal-invasibility model of metacommunity dynamics

Davis 2005

Conclusions

- Interactions at **different scales** and **covarying factors** (e.g. resource availability) drive patterns of diversity – invasibility.
- Most diverse communities are at great risk of invasion, and species loss affects neighbourhood-scale diversity and may erode invasion resistance.

➔ **We need to conserve diversity to repel invaders.**