4. Metacommunities and Assembly Rules

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4. Metacommunities and Assembly Rules

Metacommunity concept – Spatially structured communities

Dynamics influenced by:

- regional species pools
- colonization (dispersal)
- disturbance regimes
- local extinctions
- local species interactions

Origins of the metacommunity concept –

Hutchinson, G. E. 1941. Ecological aspects of succession in natural populations. *American Naturalist* 75:406-418.

Hutchinson, G. E. 1948. Circular causal systems in ecology. *Annals of the New York Academy of Science* 50:221-246.

Hutchinson, G. E. 1951. Copepodology for the ornithologist. *Ecology* 32:571-577.

Hutchinson, G. E. 1953. The concept of pattern in ecology. *Proceedings of the Academy of Natural Sciences of Philadelphia* 104:1-12.

Hutchinson, G. E. 1961. The paradox of the plankton. *American Naturalist* 95:137-145.

Meta<u>population</u> Paradigm

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15, 237–240.

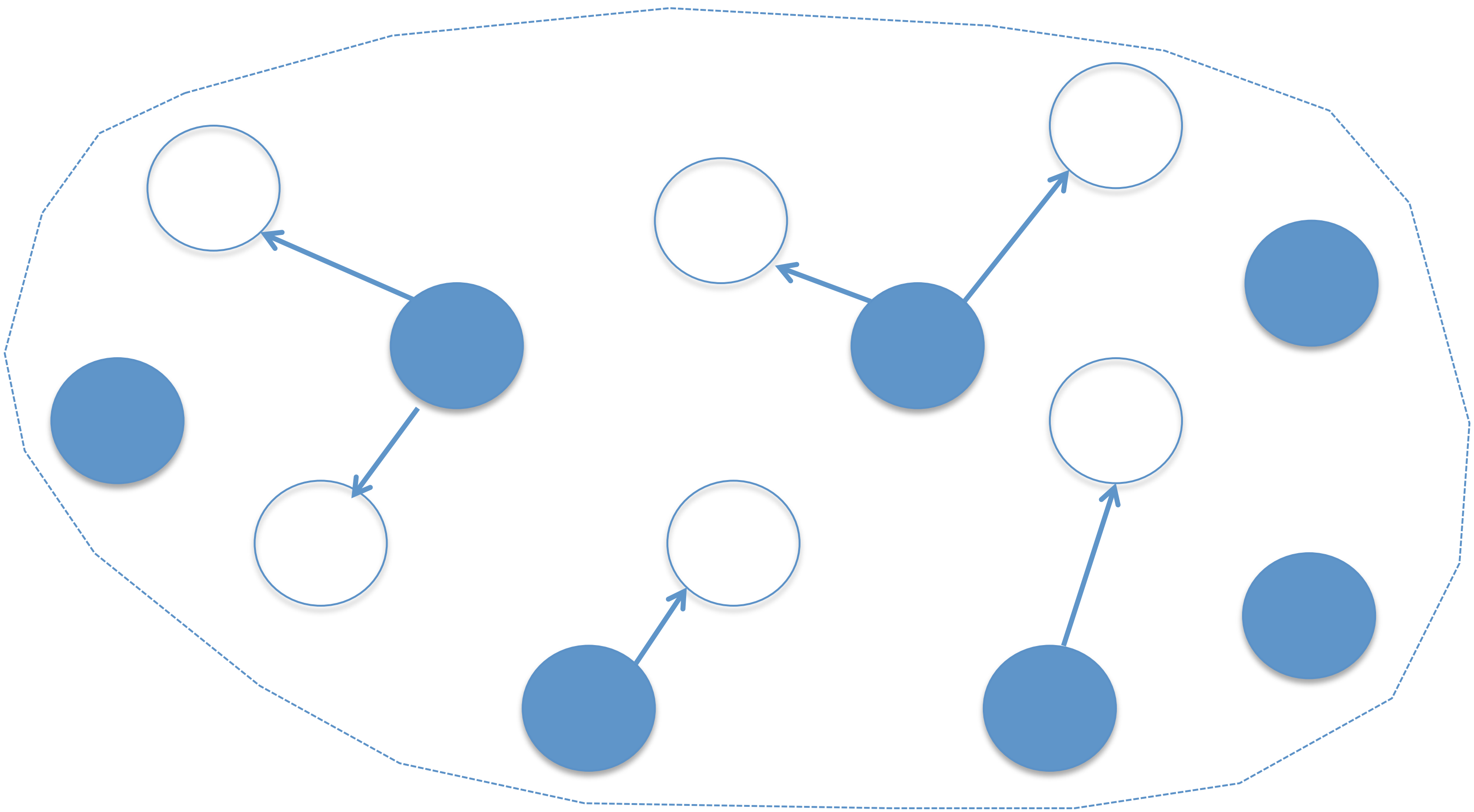
Levin, S. A. 1974. Dispersion and population interactions. American Naturalist 108:207–228.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist*, 132, 652–661.

Hanski, I. 1998. *Metapopulation Ecology*. Oxford University Press, Oxford, UK.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, 15, 237–240.

metapopulation – patch extinctions, patch recolonizations



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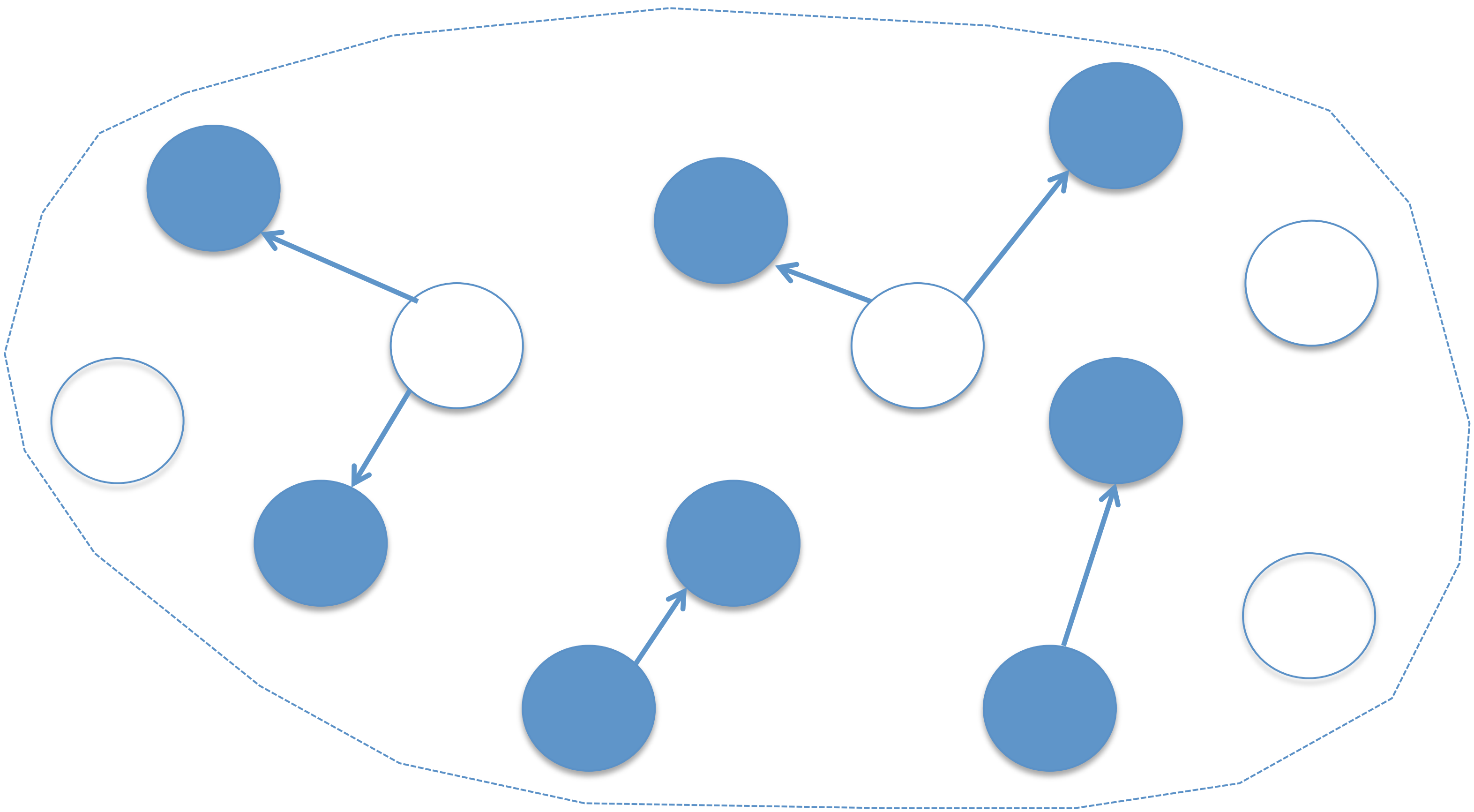

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Colonization rate, m, is proportional to fraction of patches occupied, p, and the fraction of patches vacant, 1-p

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$$dp/dt = mp(1-p) - ep$$

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metapopulation – patch extinctions, patch recolonizations

Colonization rate, m, is proportional to fraction of patches occupied, p, and the fraction of patches vacant, 1-p

Assume all local subpopulations (on patches) have the same constant extinction probability, e

$$dp/dt = mp(1-p) - ep$$

At equilibrium, $\hat{p} = 1 - e/m$

For p to remain positive, m must be > e

What is the effect of decreasing patch area on extinction rate?

What is the effect of decreasing patch area on extinction rate?

e increases

What is the effect of decreasing patch area on extinction rate?

e increases

What is the effect of increasing patch isolation on colonization rate?

What is the effect of decreasing patch area on extinction rate?

e increases

What is the effect of increasing patch isolation on colonization rate?

m decreases

What is the effect of decreasing patch area on extinction rate?

e increases

What is the effect of increasing patch isolation on colonization rate?

m decreases

$$\hat{p} = 1 - e/m$$

(p is fraction of patches occupied)

Pulliam, H.R. (1988). Sources, sinks, and population regulation. *American Naturalist*, 132, 652–661.

B I D E model of metapopulation dynamics

$$N_{t+1} = N_t + B + I - D - E$$

N_t is initial population size

B is total births

I is net immigration

D is total deaths

E is net emigration

BIDE model metapopulation subunits

$B = \sum b_j$ for $j = 1$ to m

$D = \sum d_j$ for $j = 1$ to m

$I = \sum i_j$ for $j = 1$ to m

$E = \sum e_j$ for $j = 1$ to m

$i_j = \sum i_{jk}$ for $k = 0$ to m

$e_j = \sum e_{jk}$ for $k = 0$ to m

$e_{kj} = i_{jk}$ for all $j \neq 0$

Within this framework, one can define:

a *source* subunit, or patch $b_j > d_j$ and $e_j > i_j$

a *sink* subunit, or patch $b_j < d_j$ and $e_j < i_j$

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a *source* subunit, or patch $b_j > d_j$ and $e_j > i_j$

a *sink* subunit, or patch $b_j < d_j$ and $e_j < i_j$

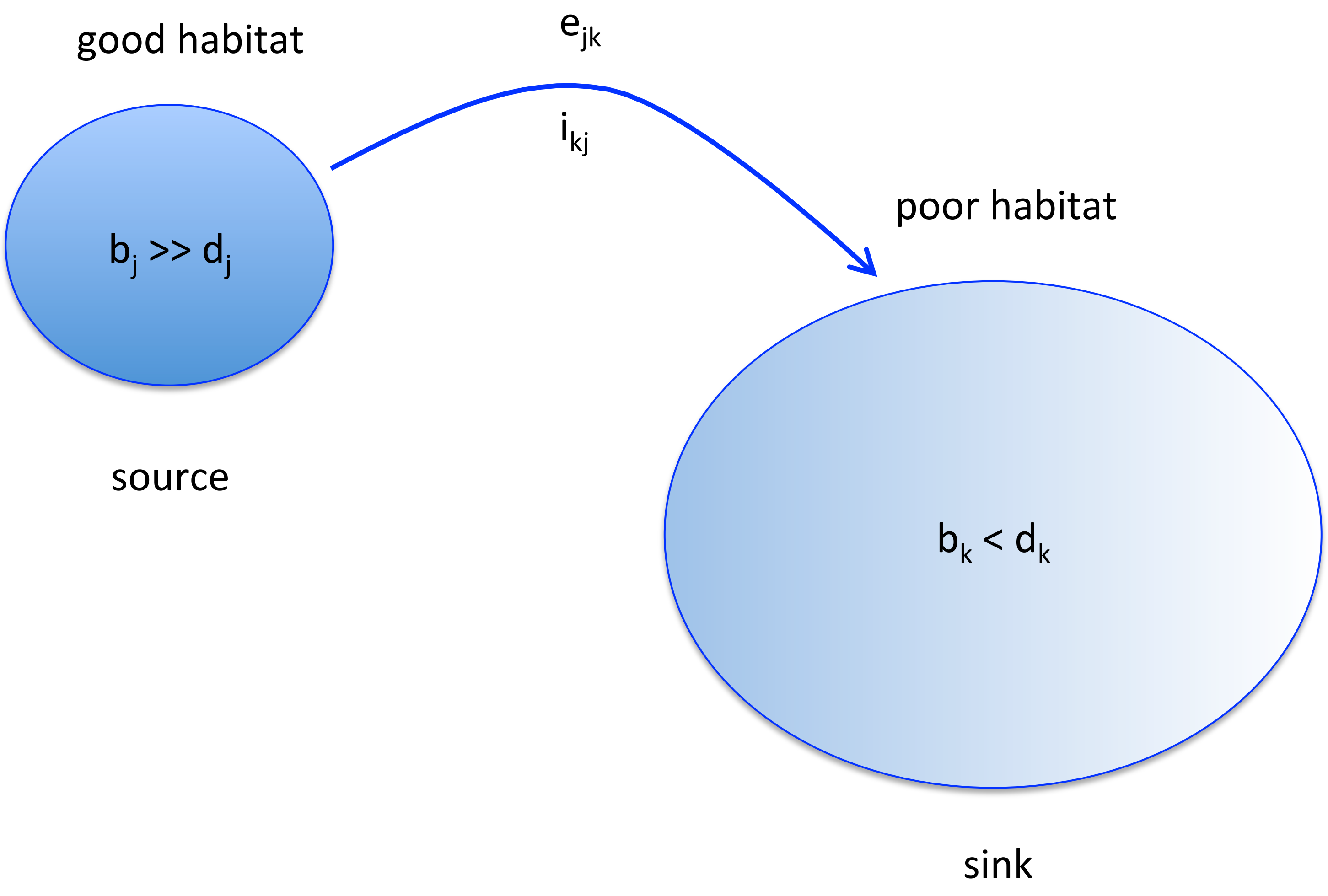
Sources are “net exporters”

Sinks are “net importers”

Sinks depend on the status of sources (e.g., donor control)

The model can be made more complex by making i_{jk} and e_{jk} *density dependent* based on the donating or receiving subunit’s abundance (n_j or n_k)

or by having fixed *thresholds* for emigration.



good habitat
e_{jk}
i_{kj}
$b_j >> d_j$
source
poor habitat
$b_k < d_k$
sink

CATASTROPHIC EXTINCTION OF POPULATION SOURCES IN A BUTTERFLY METAPOPULATION

CHRIS D. THOMAS,[1,*] MICHAEL C. SINGER,[2] AND DAVID A. BOUGHTON[2]

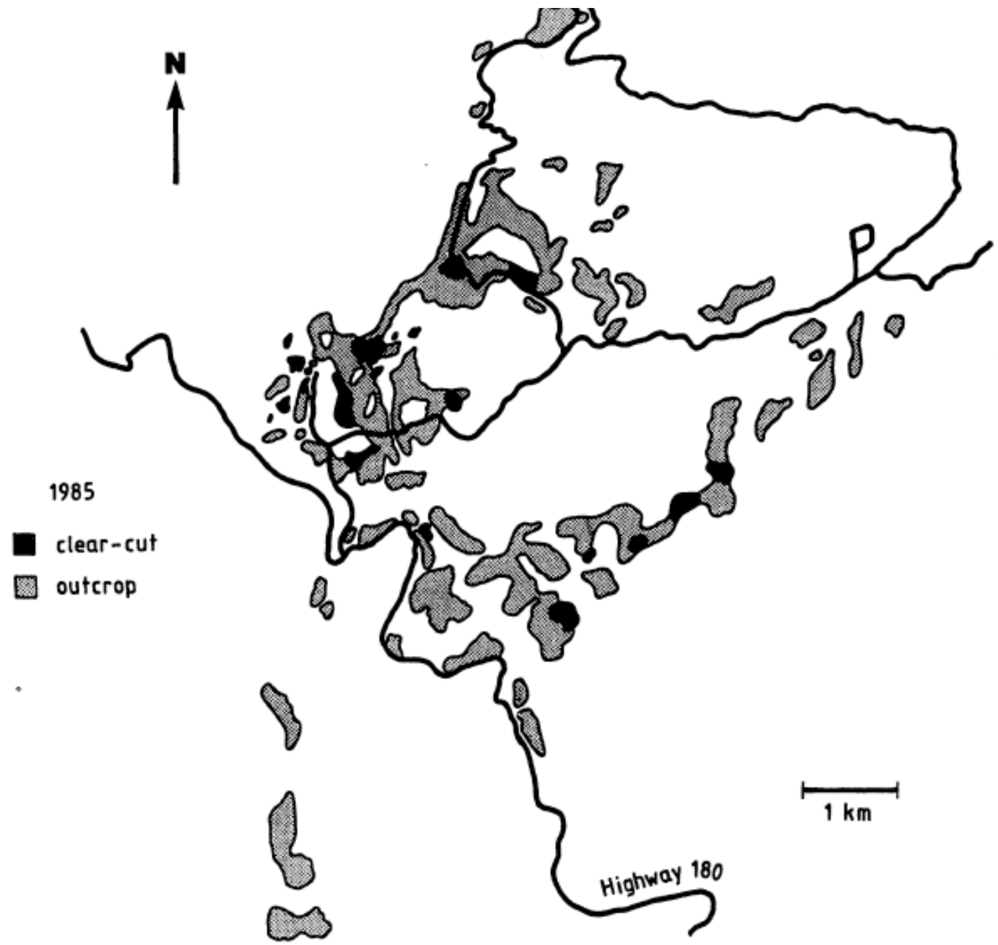


FIG. 1.—Distribution of *Euphydryas editha* population sources (clear-cut habitat) and pseudosinks (outcrops) at Generals' Highway. The 1985 distribution of eggs/young larvae is shown. Four additional outcrops are located 8.5–15 km southeast of the southernmost site shown. Thick lines indicate roads.

Euphydra editha, checkerspot butterfly in Sequoia National Forest, California

Rocky outcrops with historic host plants for butterfly = **pseudosinks**
(With deforested patches on the landscape, breeding success was poor in rocky outcrops under enhanced immigration rates)

Deforested "clear cuts" with novel host plant (*Collinsia*) for butterfly = **sources**

After a severe summer frost, *Collinsia* were killed, but butterflies on rocky outcrops did not go extinct, they persisted on their native host plants (*Pedicularis semibarbata* and *Castilleja disticha*).

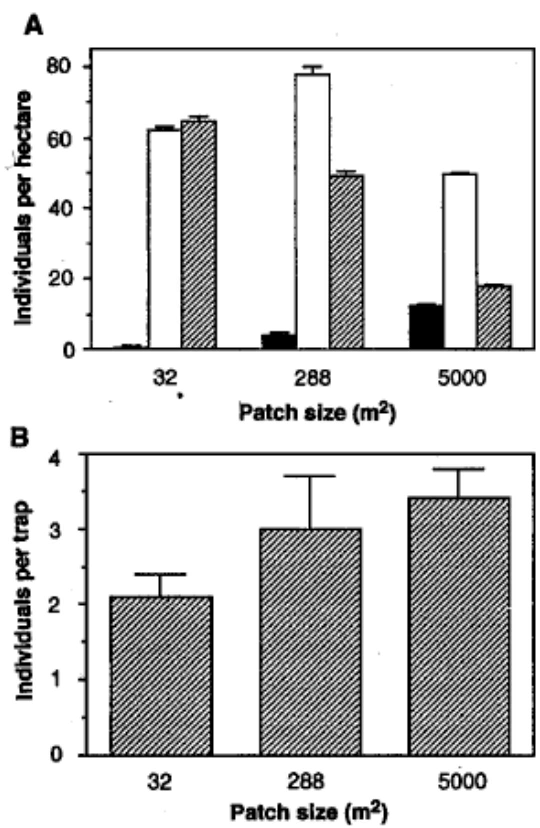
Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. J. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* 257:524-526.

Degree of fragmentation (patch size holding total area constant) had *no effect* on:

soil properties, rate of plant succession, community species richness & diversity

But it *did affect*:

- population densities of several plant and animal species (greater on larger patches)
- persistence of clonal plants
- persistence of individual rodents (based on mark-recapture study)
- rodent age structure (smaller patches dominated by young, non-reproductive individuals



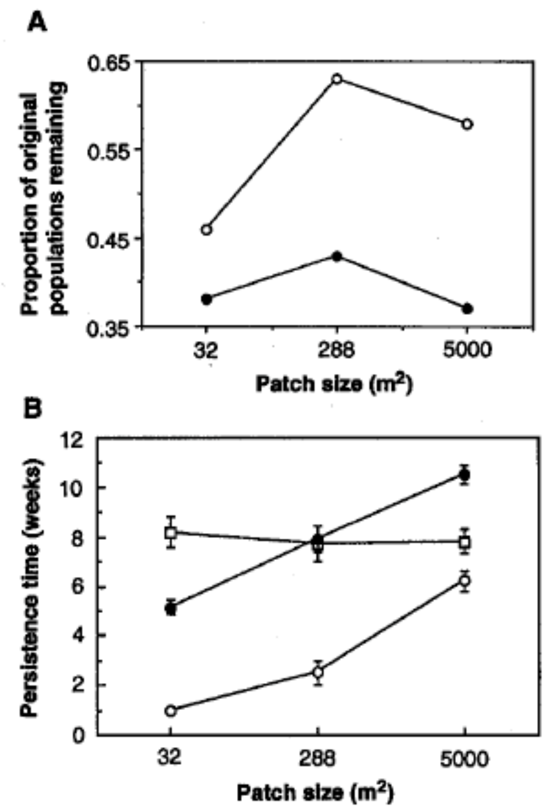


Fig. 3. (**A**) Proportion of local plant populations

Ecology, 79(6), 1998, pp. 2032–2040

RAIN FOREST FRAGMENTATION AND THE DYNAMICS OF AMAZONIAN TREE COMMUNITIES

WILLIAM F. LAURANCE, LEANDRO V. FERREIRA, JUDY M. RANKIN-DE MERONA,[1] AND SUSAN G. LAURANCE

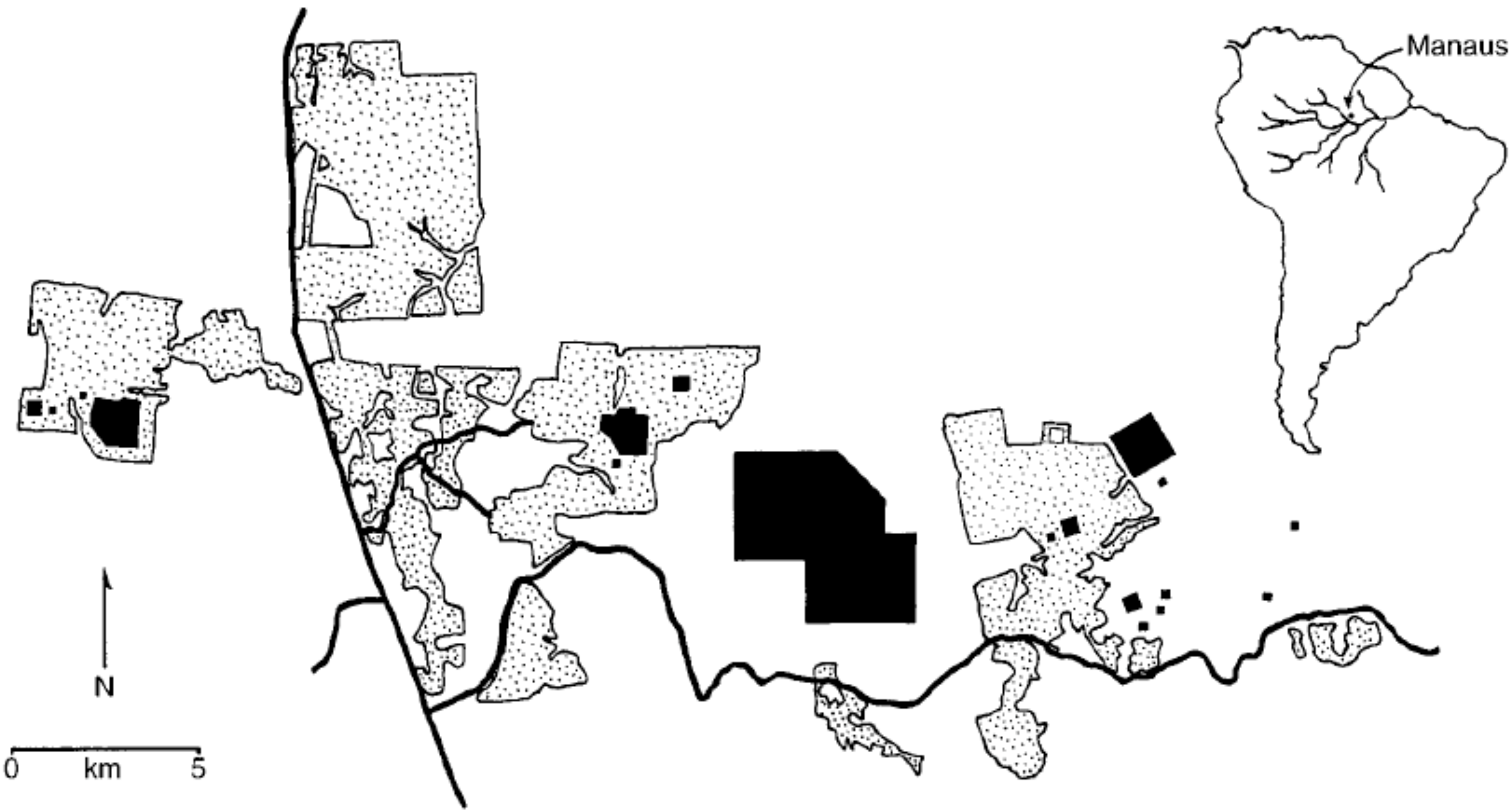
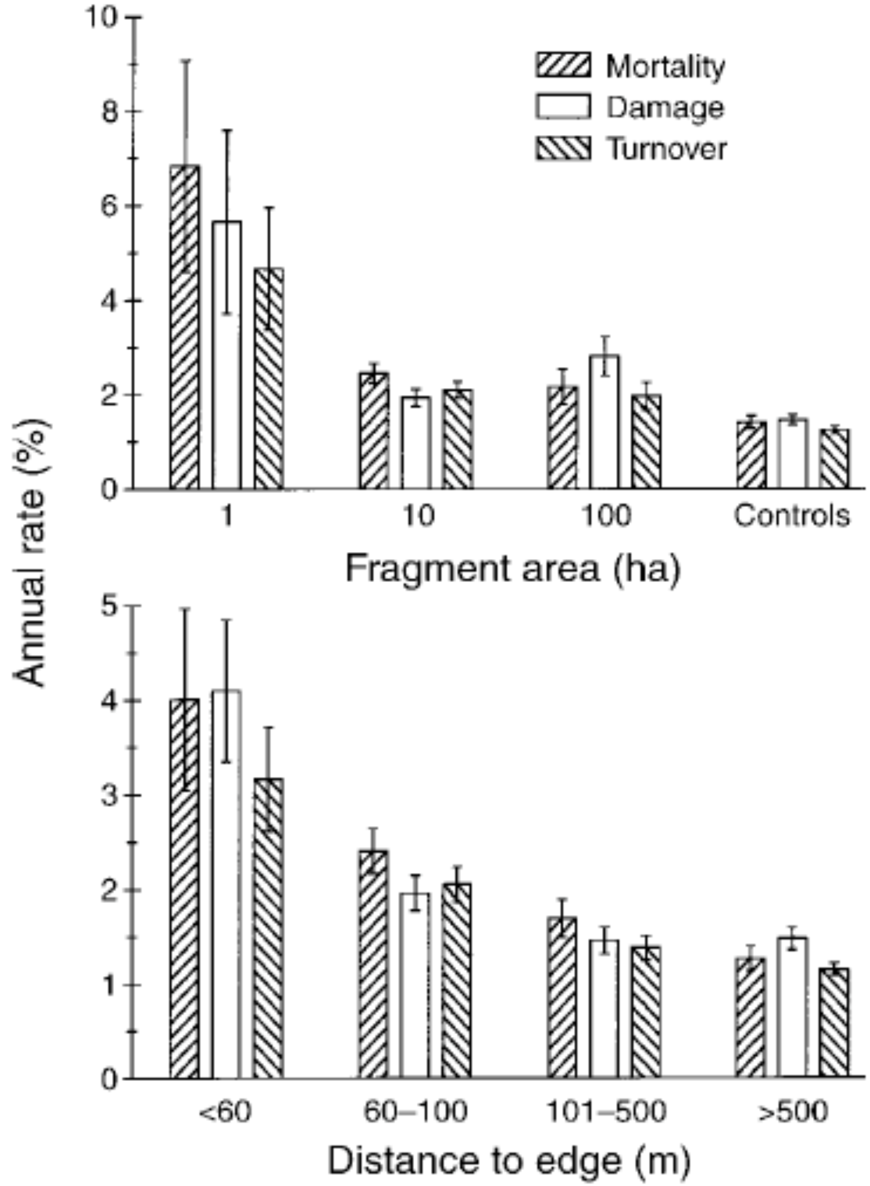


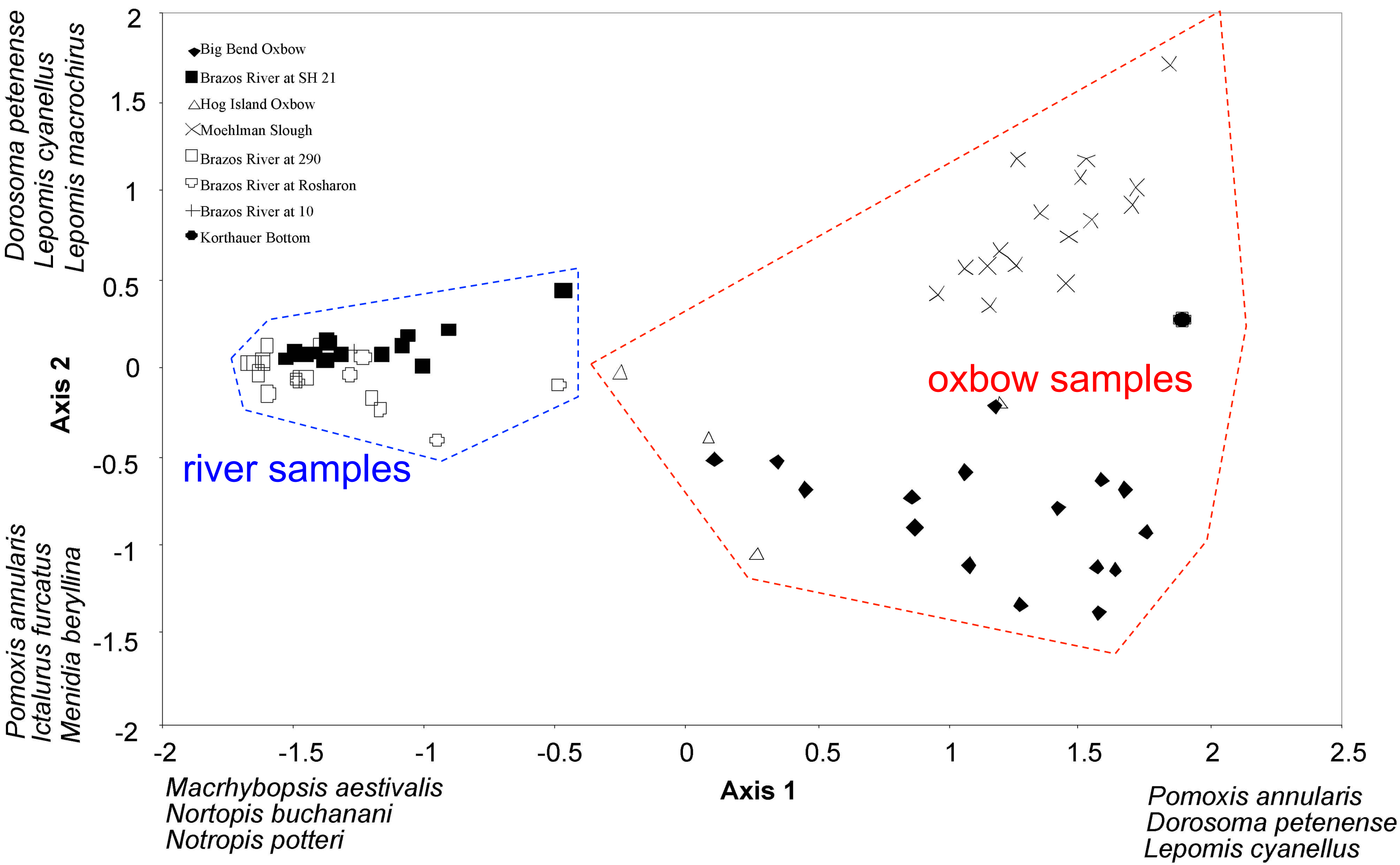
FIG. 1. Study area in central Amazonia, showing locations of forest fragments and controls (shaded blocks) used in the study. Stippled areas are cattle pastures or regrowth forest, while unstippled areas are rain forest. Thick, solid lines are roads.



Annual rate (%)
10
8
6
4
2
0
Mortality
Damage
Turnover
1
10
100
Controls
Fragment area (ha)
5
4
3
2
1
0
<60
60–100
101–500
>500
Distance to edge (m)


Brazos River, Texas

During floods, there is exchange of fishes between river and oxbow lakes.



Correspondence Analysis (CA) using seine net CPUE data for fishes

Some species are more abundant in the river channel following floods.

Correlation between monthly peak discharge and CPUE in channel with a time lag of 1 month:

- White crappie, *Pomoxis annularis* +0.67

- Gizzard shad, *Dorosoma petenense* +0.58

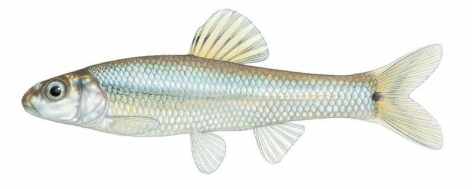
Flood connections result in exportation of fish to the river channel.

source-sink metapopulation dynamics

Flood connections also result in entry of fish abundant in the river channel into oxbow lakes where they perish within a few months.

Red shiner, *Cyprinella lutrensis*

Bullhead minnow, *Pimephales vigilax*



Exploration of the Metacommunity Concept–

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601-613.

Holyoak, M. A. Leibold, and R. D. Holt (editors). 2005. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago.

Leibold et al. 2004. *Ecology Letters* 7:601-613.

Table 1 Terms used to define scales of organization and population dynamics in metacommunities

Term	Definition
Ecological scales of organization	
Population	All individuals of a single species within a habitat patch
Metapopulation	A set of local populations of a single species that are linked by dispersal (after Gilpin and Hanski 1991)
Community	The individuals of all species that potentially interact within a single patch or local area of habitat
Metacommunity	A set of local communities that are linked by dispersal of multiple interacting species (Wilson 1992)
Descriptions of space	
Patch	A discrete area of habitat. Patches have variously been defined as microsites or localities (Levins 1969; Tilman 1994; Amarasekare & Nisbet 2001; Mouquet & Loreau 2002). In this paper we use the term analogously to localities, which are capable of holding populations or communities
Microsite	A site that is capable of holding a single individual. Microsites are nested within localities
Locality	An area of habitat encompassing multiple microsites and capable of holding a local community
Region	A large area of habitat containing multiple localities and capable of supporting a metacommunity. This corresponds to the 'mesoscale' of Holt (1993)
Types of dynamics	
Spatial dynamics	Any mechanism by which the distribution or movement of individuals across space influences local or regional population dynamics. Different types of dynamics are discussed by Holyoak & Ray (1999)
Mass effect	A mechanisms for spatial dynamics in which there is net flow of individuals created by differences in population size (or density) in different patches (Shmida & Wilson 1985)
Rescue effect	A mechanism for spatial dynamics in which there is the prevention of local extinction of species by immigration (Brown & Kodric-Brown 1977)
Source–sink effects	A mechanism for spatial dynamics in which there is the enhancement of local populations by immigration in 'sink' localities due to migration of individuals from other localities where emigration results in lowered populations
Colonization	A mechanism for spatial dynamics in which populations become established at sites from which they were previously absent

Leibold et al. 2004. *Ecology Letters* 7:601-613.

Term	Definition
Dispersal	Movement of individuals from a site (emigration) to another (immigration)
Stochastic extinctions	A mechanism whereby established local populations of component species become extinct for reasons that are independent of the other species present or of deterministic change in patch quality. Among other possibilities these include stochastic components associated with small populations and extinctions due to stochastic environmental changes (i.e. disturbances) that can affect large populations
Deterministic extinctions	A mechanism whereby established local populations of component species become extinct due to deterministic aspects of patch quality or in the composition of the local community
Metacommunity dynamics	The dynamics that arise within metacommunities. Logically, these consist of spatial dynamics, community dynamics (multispecies interactions or the emergent properties arising from them within communities), and the interaction of spatial and community dynamics. The term is best avoided because its use detracts from the dynamical mechanisms
Types of model population or community structure	
Classic (Levins) metapopulation	A group of identical local populations with finite and equal probabilities of extinction and recolonization – no rescue effects occur
Source–sink system	A system with habitat-specific demography such that some patches (source habitats) have a finite growth rate of greater than unity and produce a net excess of individuals which migrate to sink patches. Populations in sink habitats have finite growth rates of less than one and would decline to extinction in the absence of immigration from sources (based on Holt 1985; Pulliam 1988)
Mainland–island system	A system with variation in local population size which influences the extinction probability of populations. Systems are usually described as consisting of extinction-resistant mainland populations and extinction-prone island populations (Boorman and Levitt 1973).
Open community	A community which experiences immigration and/or emigration
Closed community	A community that is isolated, receiving no immigrants and giving out no emigrants
Patch occupancy model	A model in which patches contain either individuals or populations of one or more species and where local population sizes are not modelled
Spatially explicit model	A model in which the arrangement of patches or distance between patches can influence patterns of movement and interaction

Leibold et al. 2004. *Ecology Letters* 7:601-613.

Patch-dynamics paradigm

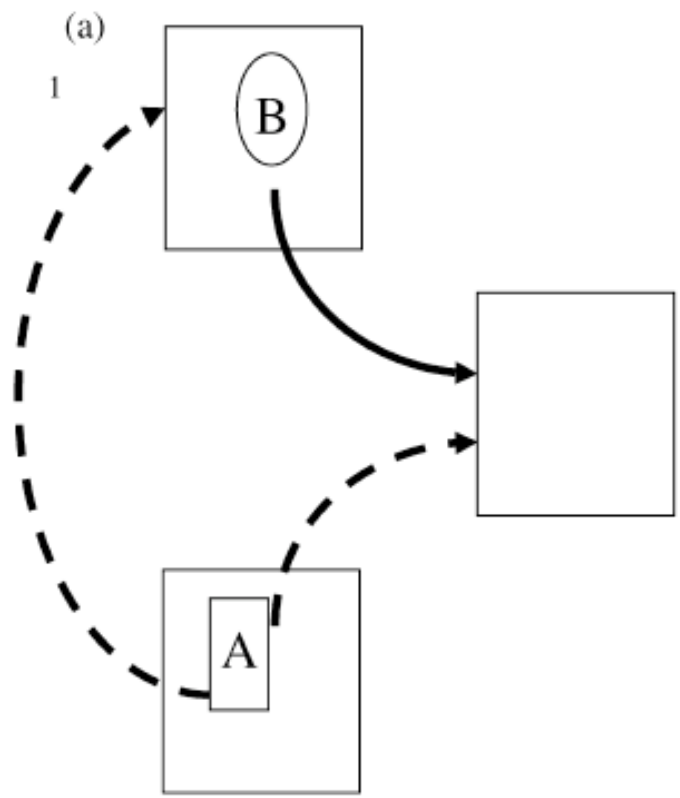


Figure 1 Schematic representation of the four paradigms for metacommunity theory for two competing species with populations A and B. Arrows connect donor populations with potential colonization sites, shown as large boxes or ovals. Solid arrows indicate higher dispersal than dashed arrows and either unidirectional movement (single-headed arrows) or bidirectional movement (double-headed arrows). The degree to which a species is the competitive dominant in a site is shown by the matching of the smaller box or oval (denoting its habitat type niche) with the site symbol. The four paradigms illustrated are (a) patch-dynamics, (b) species-sorting, (c) mass-effects and (d) neutral. In (a) the patch-dynamics paradigm is shown with conditions that permit coexistence: a competition-colonization trade-off is illustrated with species A being a superior competitor but species B being a superior colonist; the third patch is vacant and could become occupied by either species. In (b) species are separated into spatial niches and dispersal is not sufficient to alter their distribution. In (c) mass effects cause species to be present in both source and sink habitats; the smaller letters and symbols indicate smaller sized populations. In (d) all species are currently present in all patches; species would gradually be lost from the region and would be replaced by speciation.

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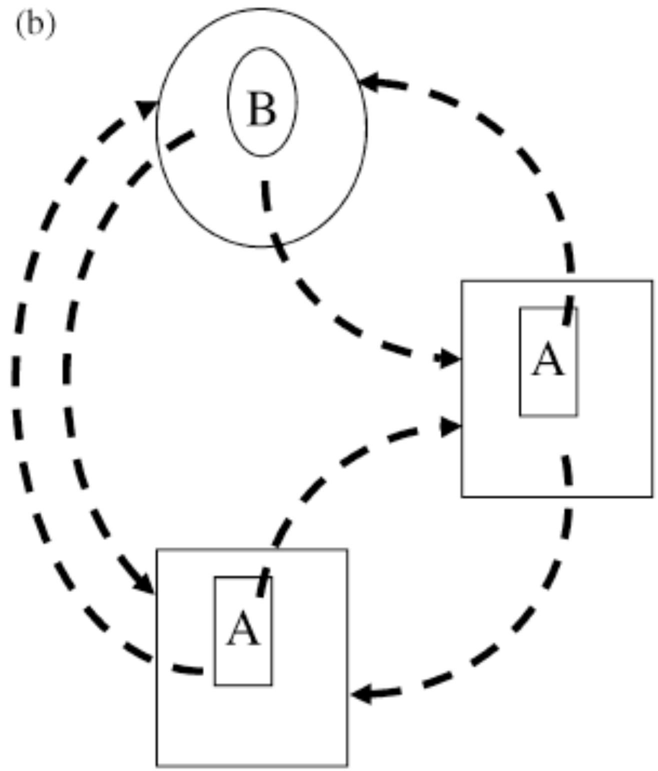
Species-sorting paradigm



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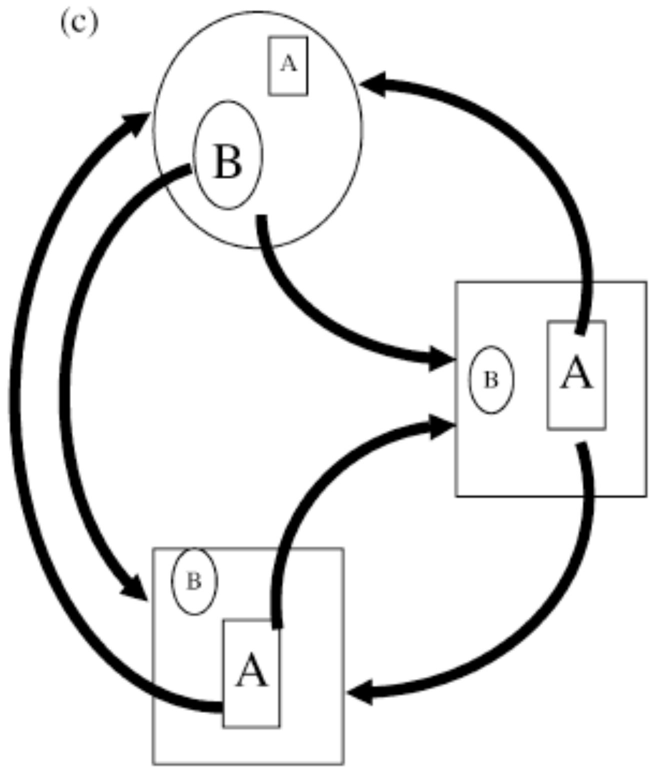
Mass-effects paradigm



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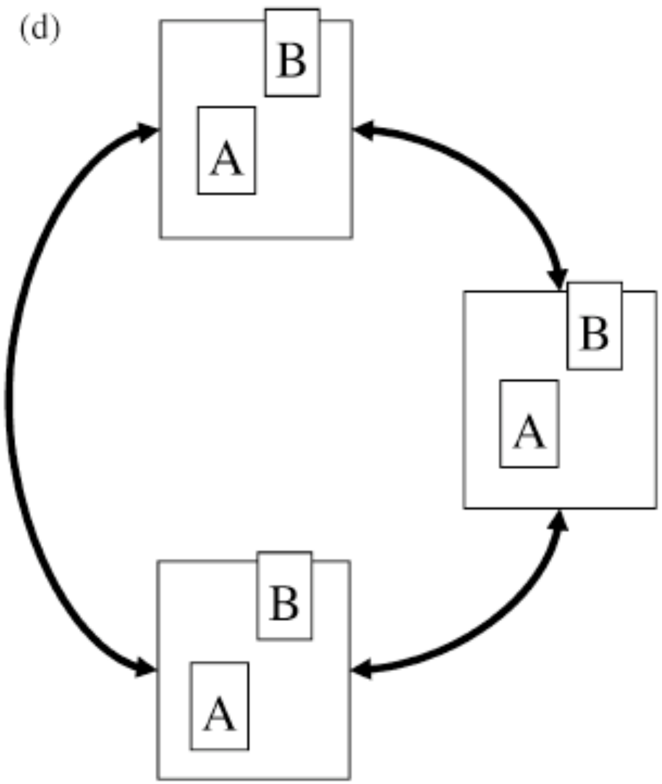
Neutral paradigm



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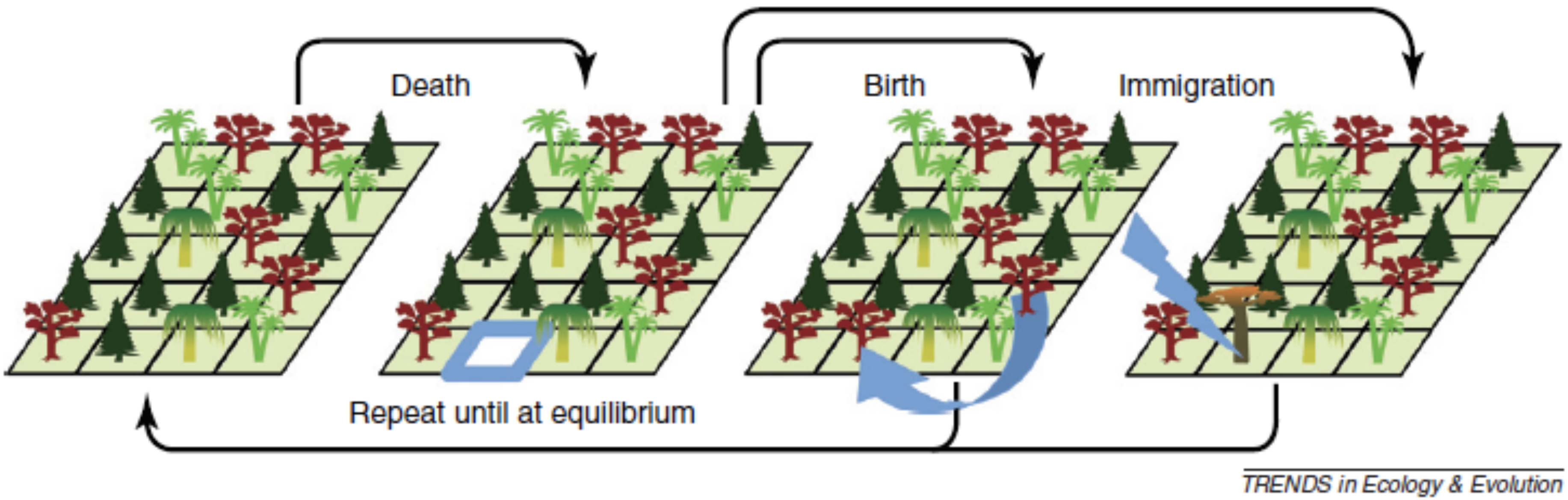
Hubbell, S.P. 2001. *The Unified Theory of Biodiversity and Biogeography*. Princeton University Press.



$$\Pr(n_1, n_2, \ldots, n_S|\theta, J) = \frac{J!\theta^S}{1^{\phi_1}2^{\phi_2}\cdots J^{\phi_J}\phi_1!\phi_2!\cdots\phi_J!\Pi_{k=1}^{J}(\theta+k-1)}$$

where $\theta = 2J\nu$ is the fundamental biodiversity number (ν is the speciation rate), and φ_i is the number of species that have *i* individuals in the sample.

This equation shows that the UNTB implies a nontrivial dominance-diversity equilibrium between speciation and extinction.

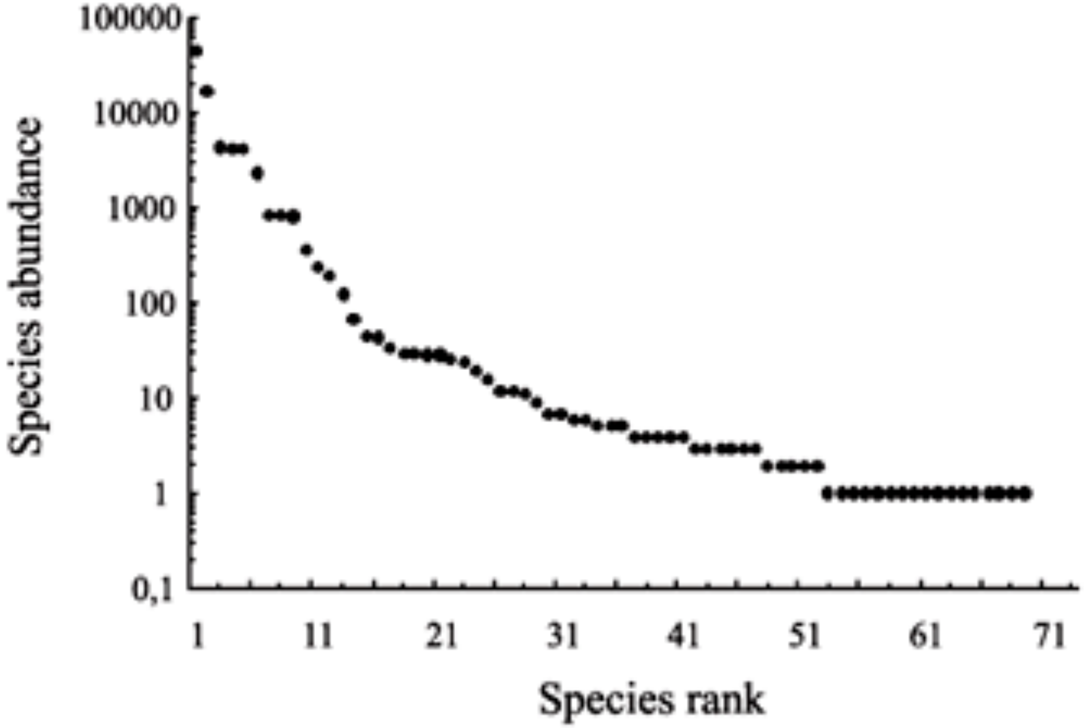


Figure 1. Rank-abundance distribution for the total data of drosophilids in mangrove forests of Santa Catarina Island.

Citation: Warren RJ II, Skelly DK, Schmitz OJ, Bradford MA (2011) Universal Ecological Patterns in College Basketball Communities. PLoS ONE 6(3): e17342. doi:10.1371/journal.pone.0017342

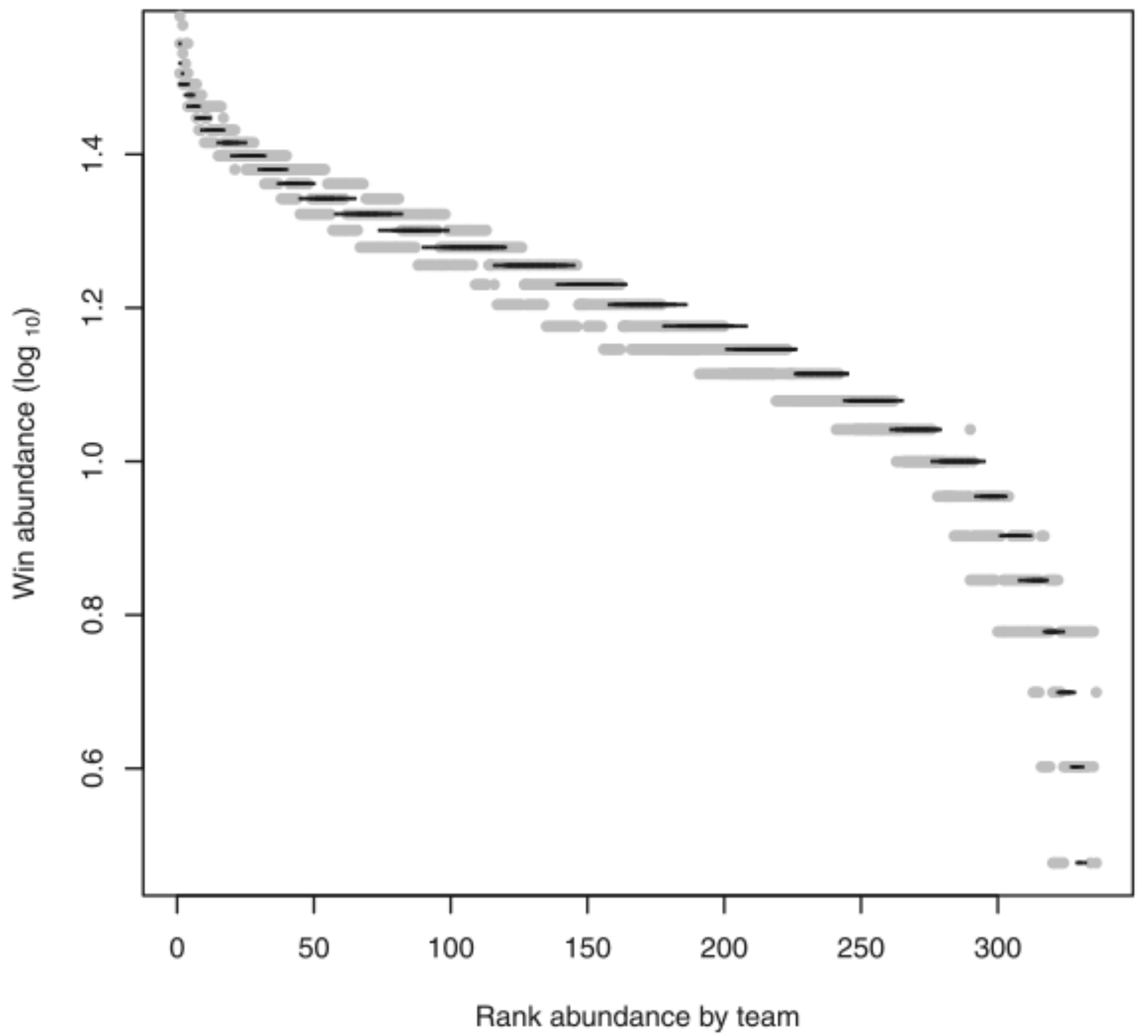
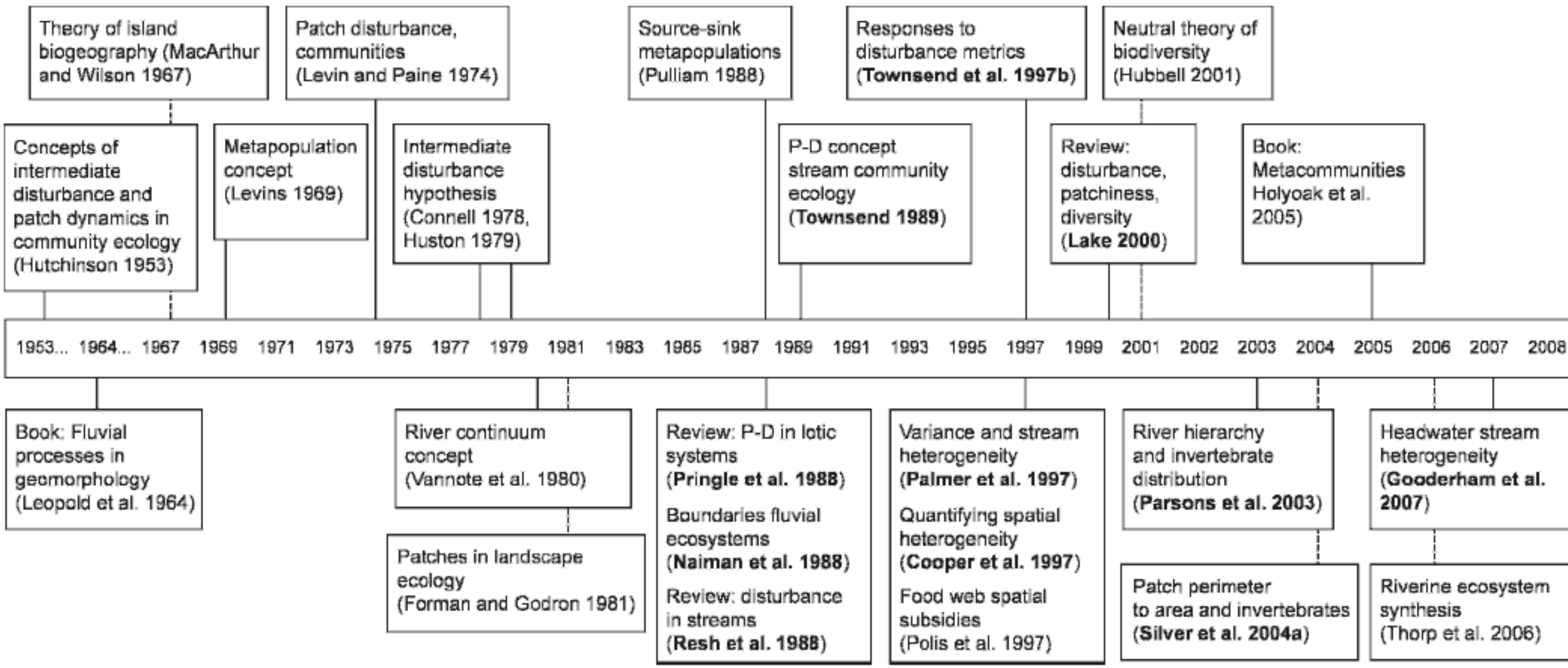


Figure 2. Rank abundance of college basketball wins by team. The abundance of wins in college basketball, a result of competition between teams of unequal abilities, creates the same pattern used by ecologists to infer mechanism from species abundance distributions (SADs). The $\log_{10}$ abundance of college basketball wins is ranked by team, just as the abundance of individuals is ranked by species for ecological communities. Mean wins (gray) across 2004 to 2008±95% CI are given along with random (*Normal*, $\mu = 16$, $\sigma = 6$) wins (black), and these random and observed patterns are not significantly different (see text).

Winemiller, K.O., A.S. Flecker & D.J. Hoeinghaus. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. *Journal of the North American Benthological Society* 29:84-99.



Winemiller et al. 2010. *Journal of the North American Benthological Society* 29:84-99.

TABLE 1. Summary of key features of 4 metacommunity models (adapted from Holyoak et al. 2005) and examples of studies published in *J-NABS* consistent with the models.

Characteristic	Patch dynamics	Species sorting	Mass effects	Neutral
Patch similarity	High	Low	Low	High
Interpatch movement	Variable[a]	Not specified	High	Variable
Species similarity	Variable	Low	Low	High
Tradeoffs among traits	Yes	Yes	Yes	No
Local species composition	Variable	Constant	Constant	Variable
Regional species composition	Constant	Constant	Constant	Variable
Spatial synchrony	Some	Not specified	High	Not specified
Local equilibrium dynamics	No	Yes	Depends on dispersal rates	No
J-NABS studies supporting model	Casas and Langton 2008	Palmer et al. 1991 Brunke and Gonser 1999 Suren and Duncan 1999 Kobayashi and Kagaya 2004 Arrington and Winemiller 2006	Englund 1991 Matthaei et al. 2000 Gjerløv et al. 2003 Silver et al. 2004a Tronstad et al. 2007	?

[a] According to Townsend (1989), dispersal between patches often can be rapid in stream community patch dynamics, whereas Holyoak et al. (2005) contend that interpatch movement is relatively low under the patch dynamics metacommunity model.

The patch-dynamics concept of metacommunities

Assumptions:

- **Tradeoff between colonizing ability and competitiveness**
  (r strategists vs. K strategists)

- Intermediate disturbance yields highest diversity
  (too high, and diversity is reduced)
  (too low, and competitive dominants exclude r strategists)

MacArthur, R. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press.

Pianka, E.R. (1970). On r and K selection. *American Naturalist* 104:592–597.

r strategist -- rapid maturation, small adult size, high reproductive effort, small investment per progeny, high fecundity => **good colonizing ability**

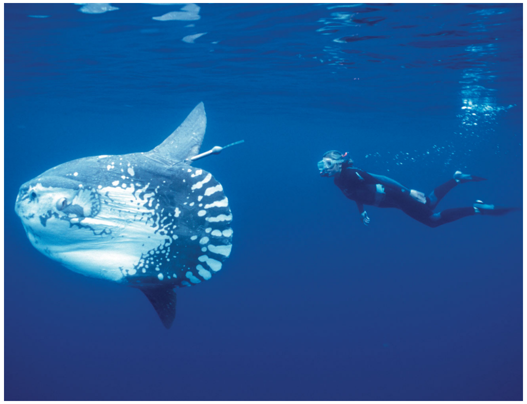
(mouse, zebra finch, guppy, diatom)

K strategist -- slow maturation, large adult size, low reproductive effort, large investment per progeny, low fecundity => **good competitive ability**

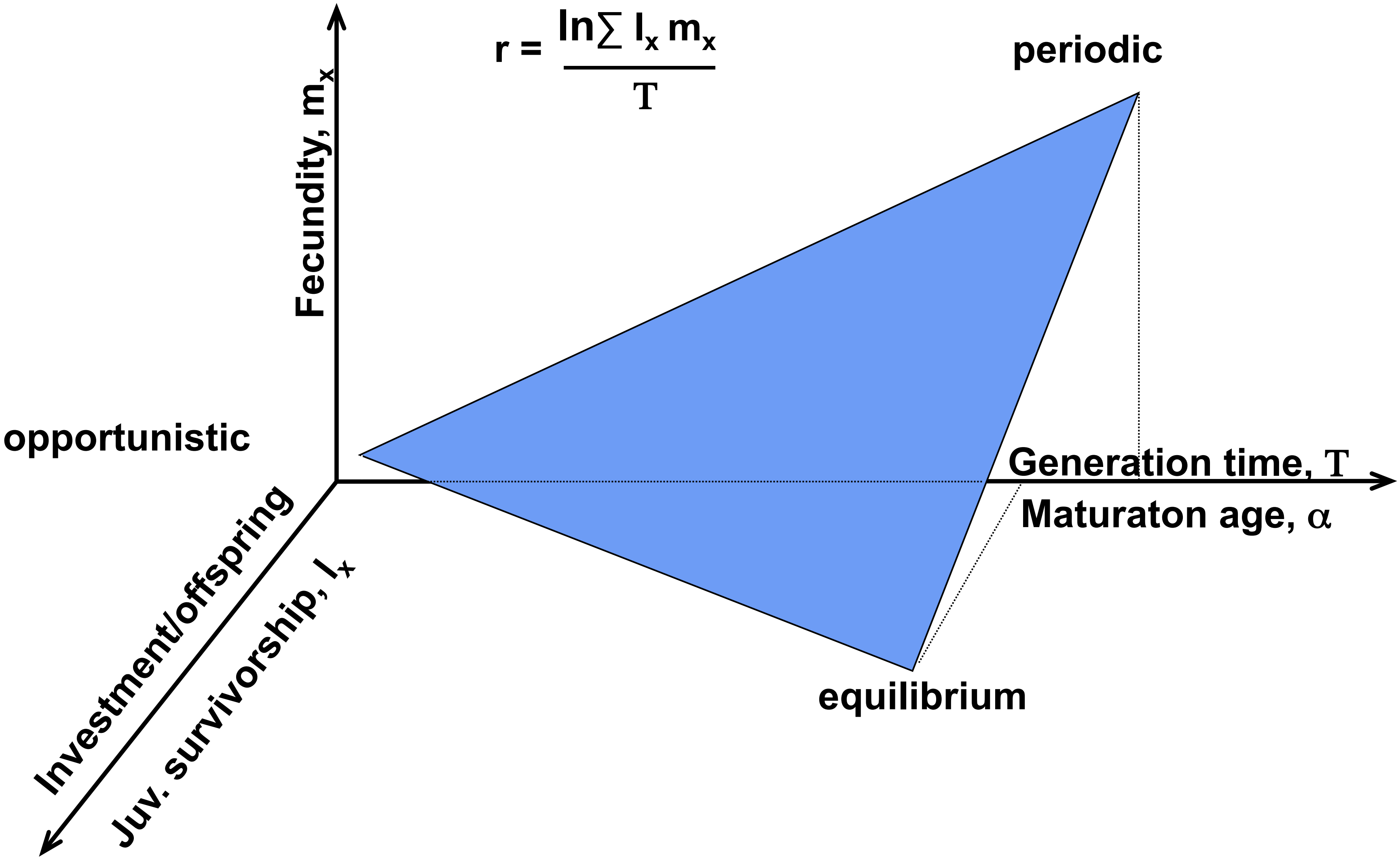
(gorilla, harpy eagle, coelacanth, redwood tree)

Problem – patterns of allocation in nature often do not match this set of predictions.

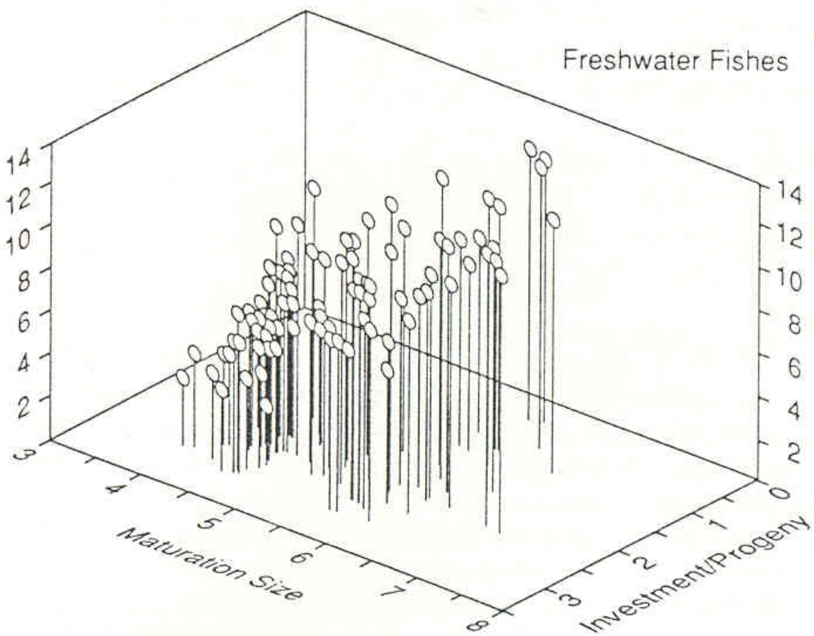
Fish species with divergent life history strategies



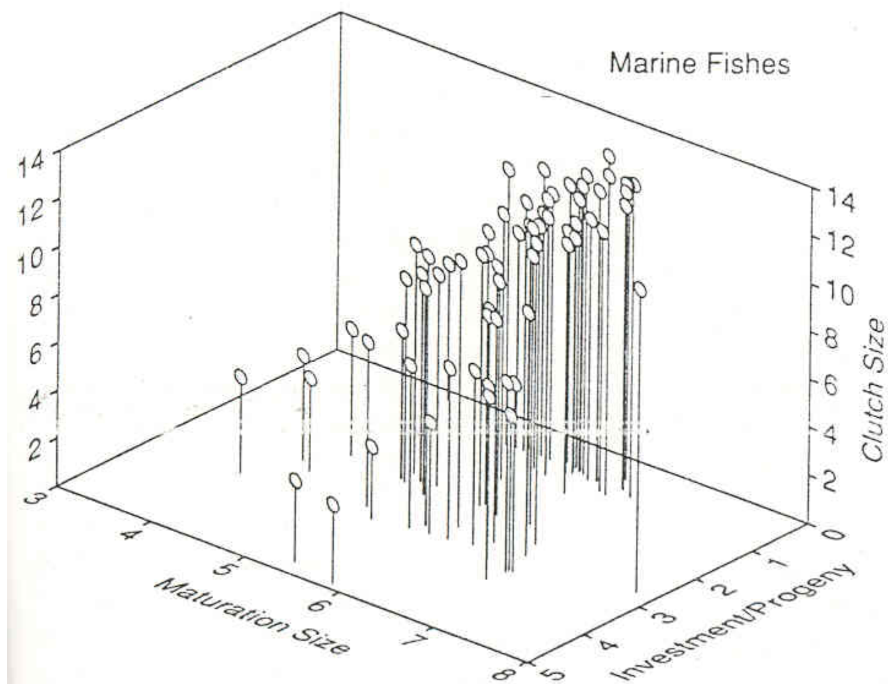
adaptive surface of primary life history strategies



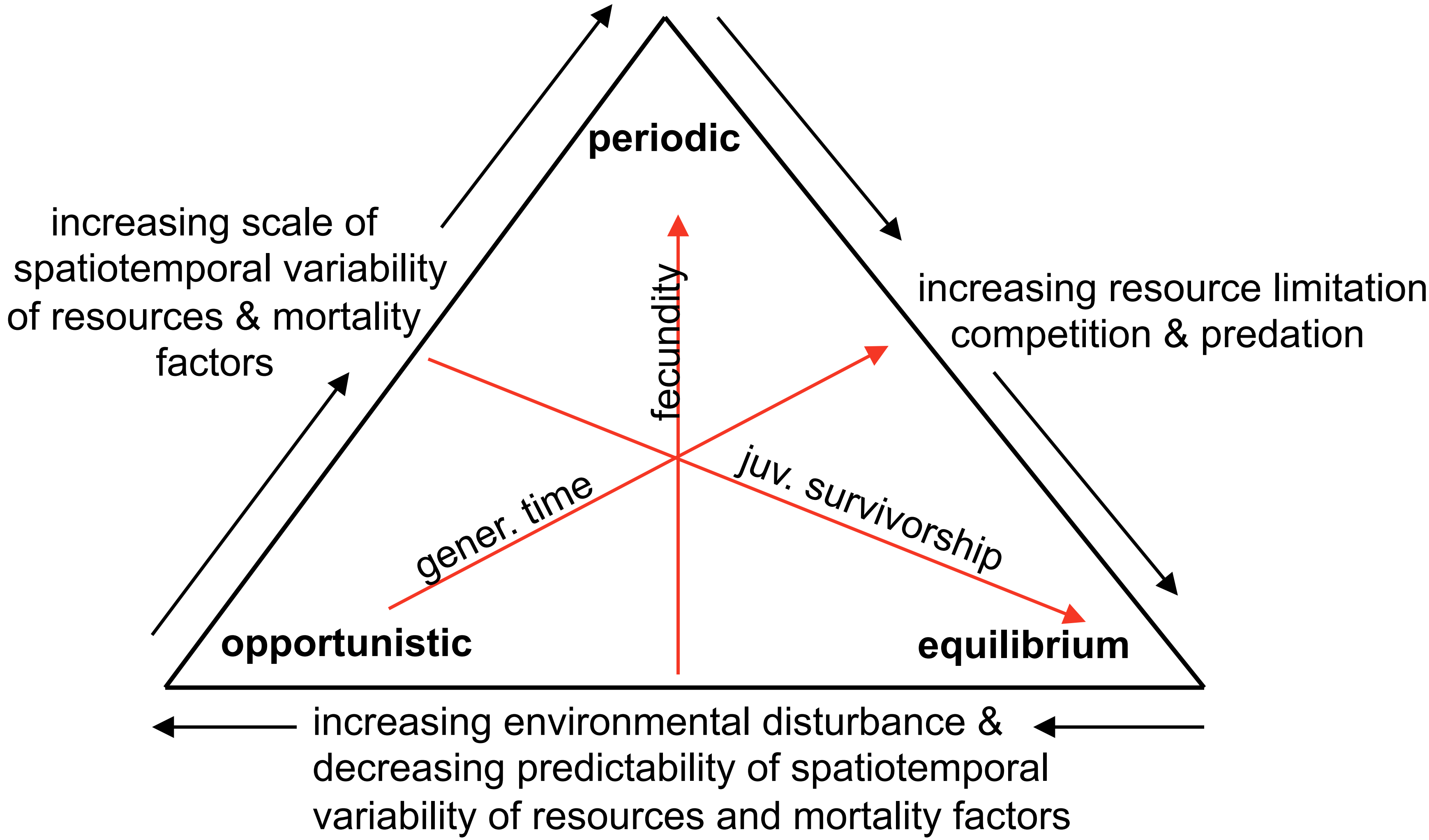
Winemiller, K.O. and K.A. Rose. 1992. Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* 49:2196-2218.



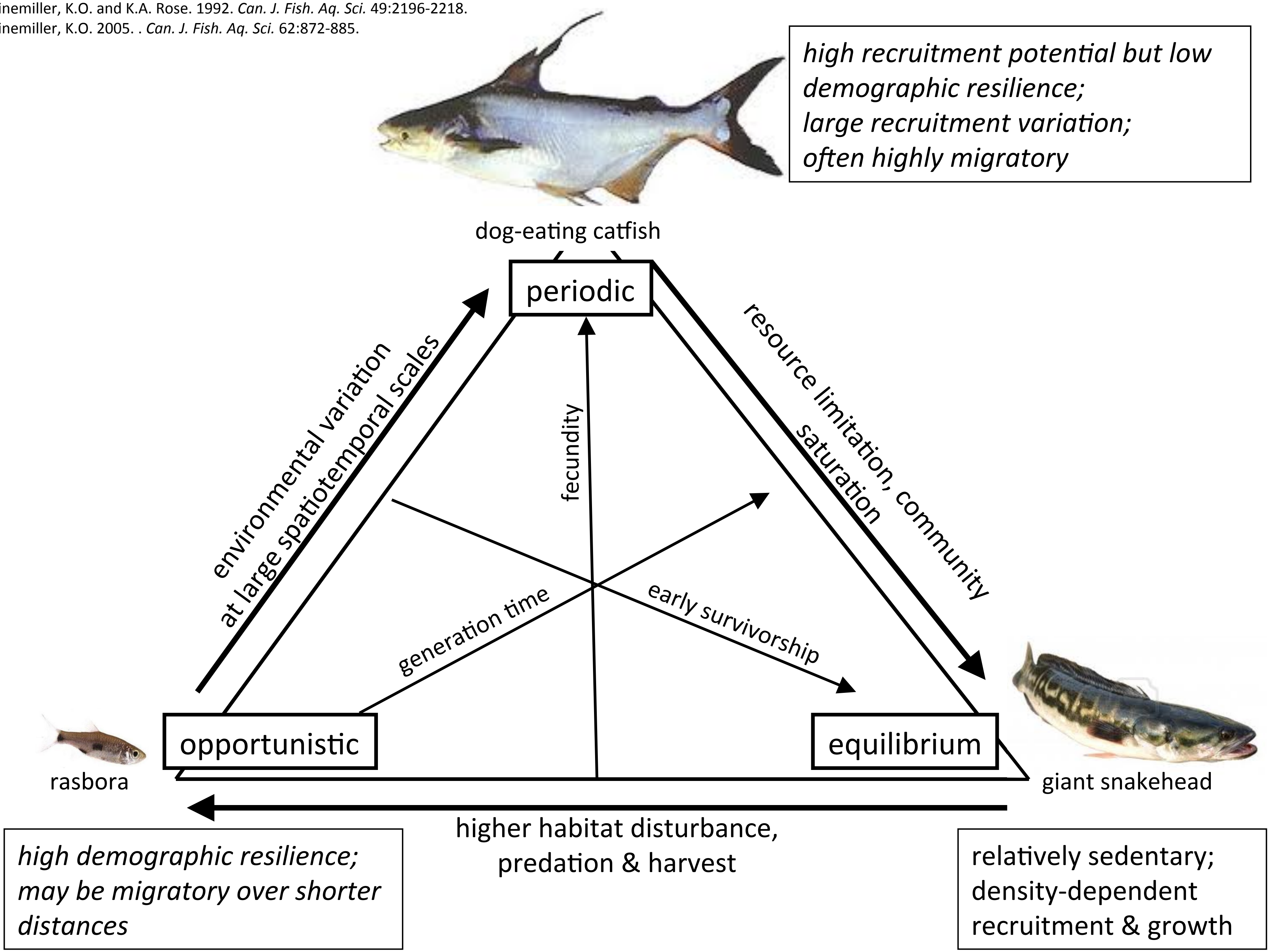
A remarkably consistent pattern of species ordination!



Life History Model **(Winemiller 1989, 1992, Winemiller & Rose 1992, 1993)**



Winemiller, K.O. 1989. *Oecologia* 81:225-241.
Winemiller, K.O. and K.A. Rose. 1992. *Can. J. Fish. Aq. Sci.* 49:2196-2218.
Winemiller, K.O. 2005. . *Can. J. Fish. Aq. Sci.* 62:872-885.



Environmental Variation, Life History Strategies, & Species Interactions:

"The Storage Effect"

Vol. 125, No. 6 The American Naturalist June 1985

COEXISTENCE MEDIATED BY RECRUITMENT FLUCTUATIONS: A FIELD GUIDE TO THE STORAGE EFFECT

ROBERT R. WARNER AND PETER L. CHESSON

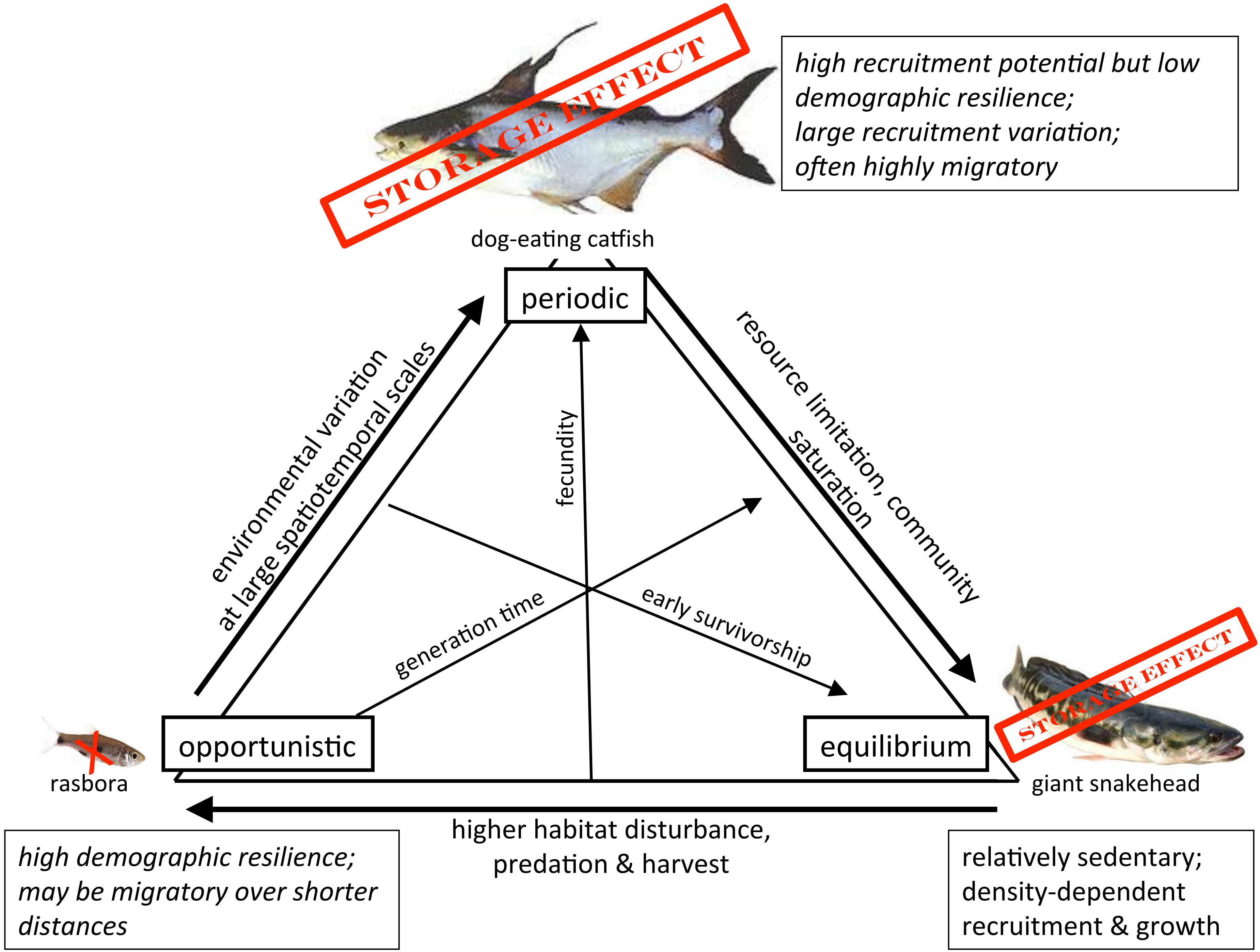
Functional tradeoffs determine species coexistence via the storage effect

Amy L. Angert[a,b,1], Travis E. Huxman[b,c], Peter Chesson[b], and D. Lawrence Venable[b]

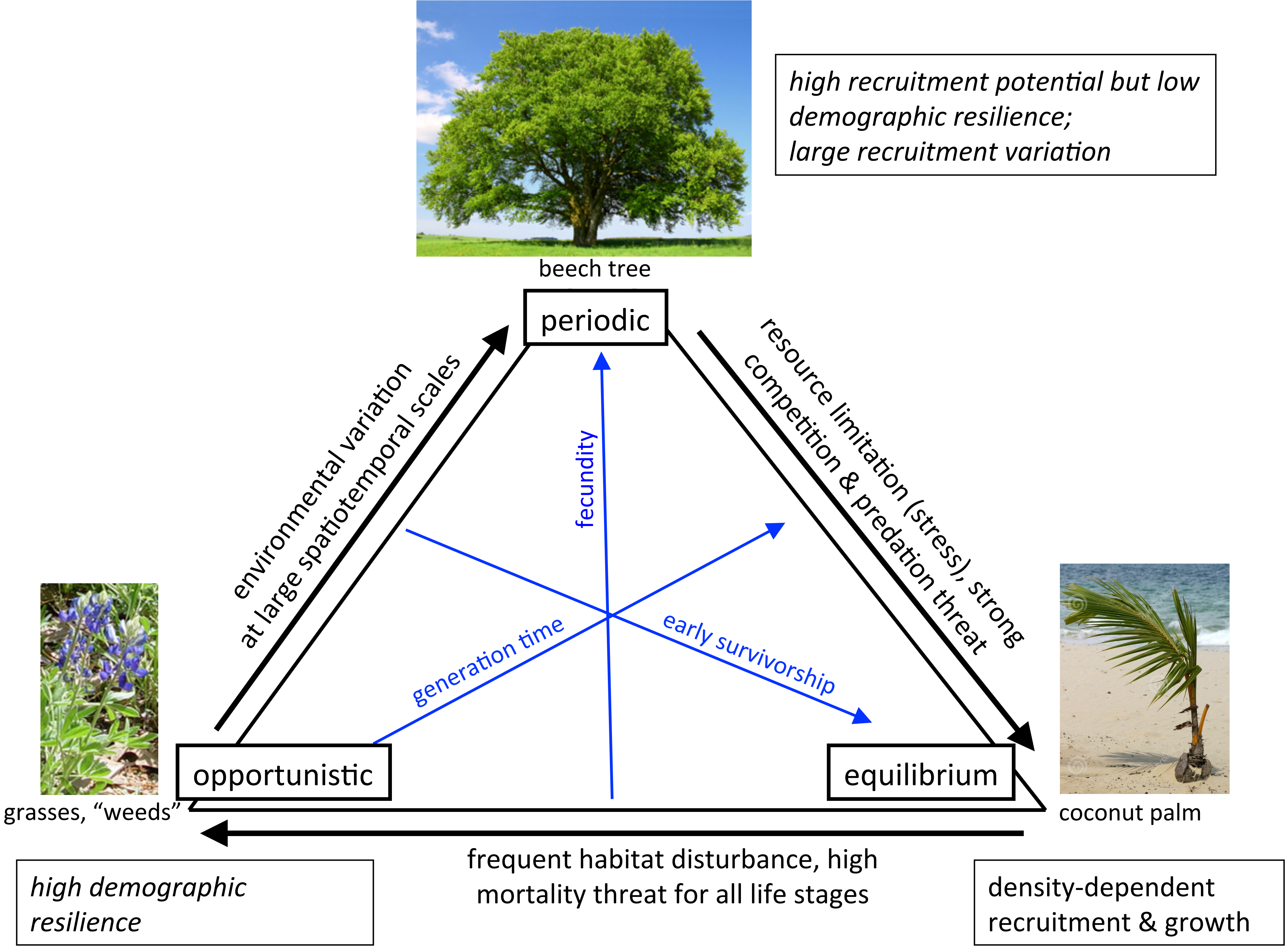
Theoretical Population Biology **58**, 211–237 (2000)
doi:10.1006/tpbi.2000.1486, available online at http://www.idealibrary.com on IDEAL®
TPB

General Theory of Competitive Coexistence in Spatially-Varying Environments

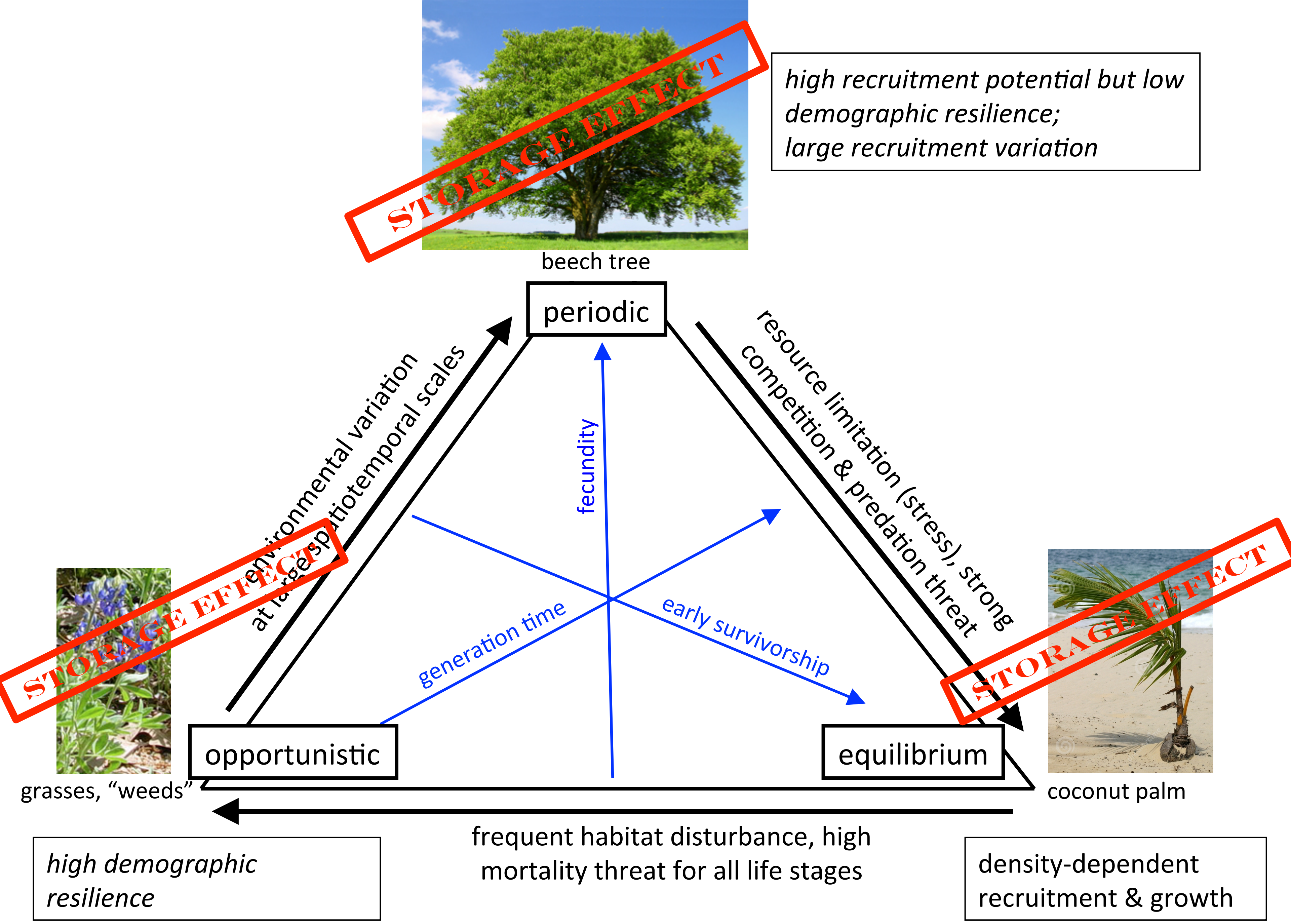
Peter Chesson
Section of Evolution and Ecology, University of California, Davis, California 95616



STORAGE EFFECT
high recruitment potential but low demographic resilience;
large recruitment variation;
often highly migratory
dog-eating catfish
periodic
environmental variation at large spatiotemporal scales
resource limitation, community saturation
fecundity
generation time
early survivorship
opportunistic
equilibrium
rasbora
STORAGE EFFECT
giant snakehead
higher habitat disturbance, predation & harvest
high demographic resilience;
may be migratory over shorter distances
relatively sedentary;
density-dependent recruitment & growth



high recruitment potential but low demographic resilience; large recruitment variation
beech tree
periodic
environmental variation at large spatiotemporal scales
resource limitation (stress), strong competition & predation threat
fecundity
generation time
early survivorship
opportunistic
equilibrium
grasses, "weeds"
coconut palm
frequent habitat disturbance, high mortality threat for all life stages
high demographic resilience
density-dependent recruitment & growth



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density-dependent recruitment & growth

Miyazono, S., J.N. Aycock, L.E. Miranda, and T.E. Tietjen. 2010. Assemblage patterns of fish functional groups relative to habitat connectivity and conditions in floodplain lakes. Ecology of Freshwater Fish 19:578-585.

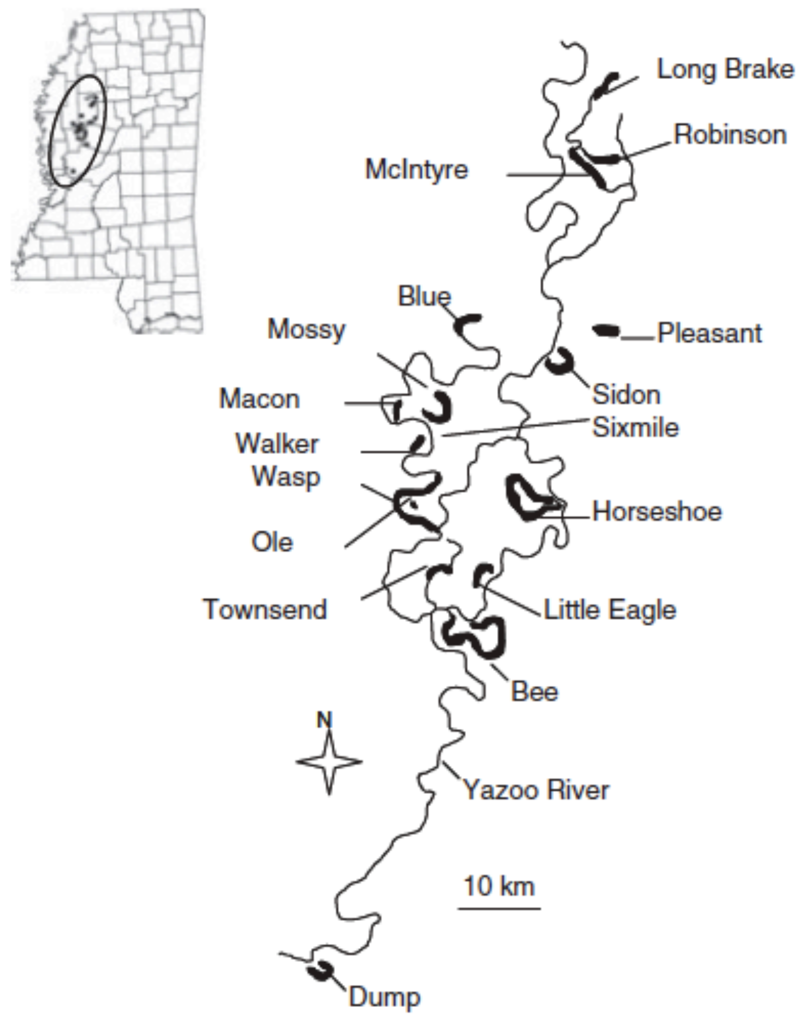


Fig. 1. Map of the spatial distribution of the 17 lakes in the Yazoo River Basin in Mississippi included in this study.

(Miyazono, S., et al. 2010. Ecology of Freshwater Fish 19:578-585)

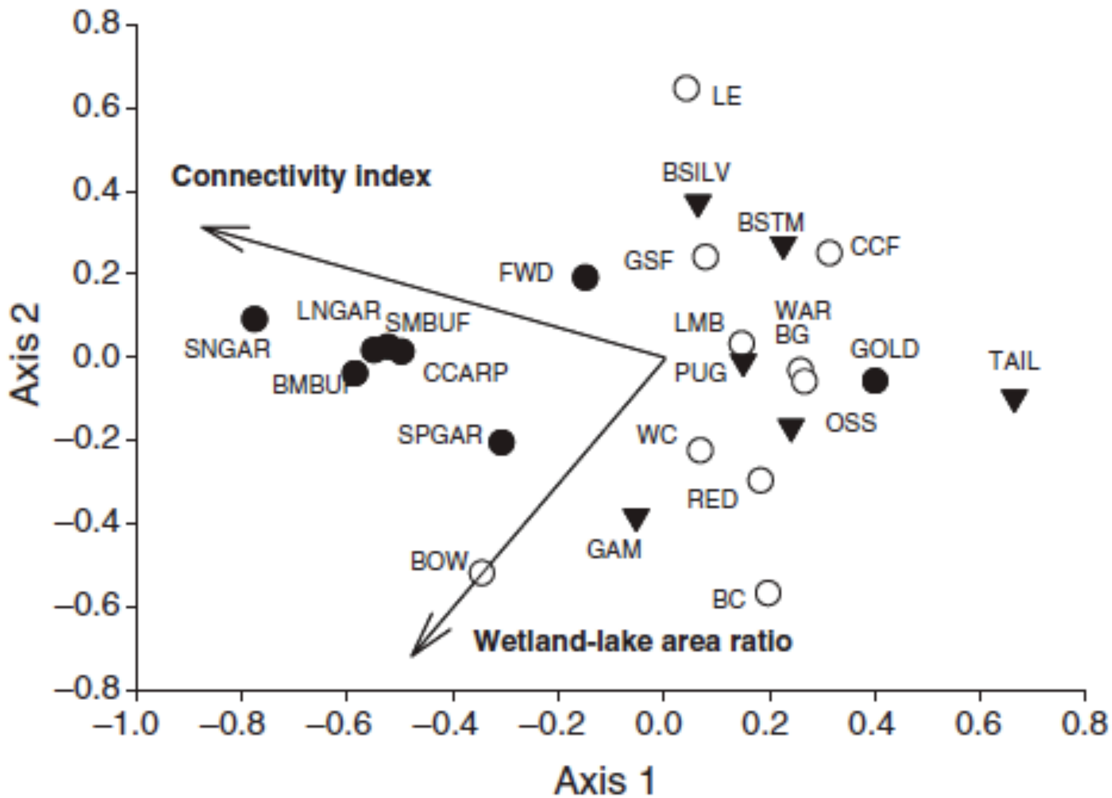
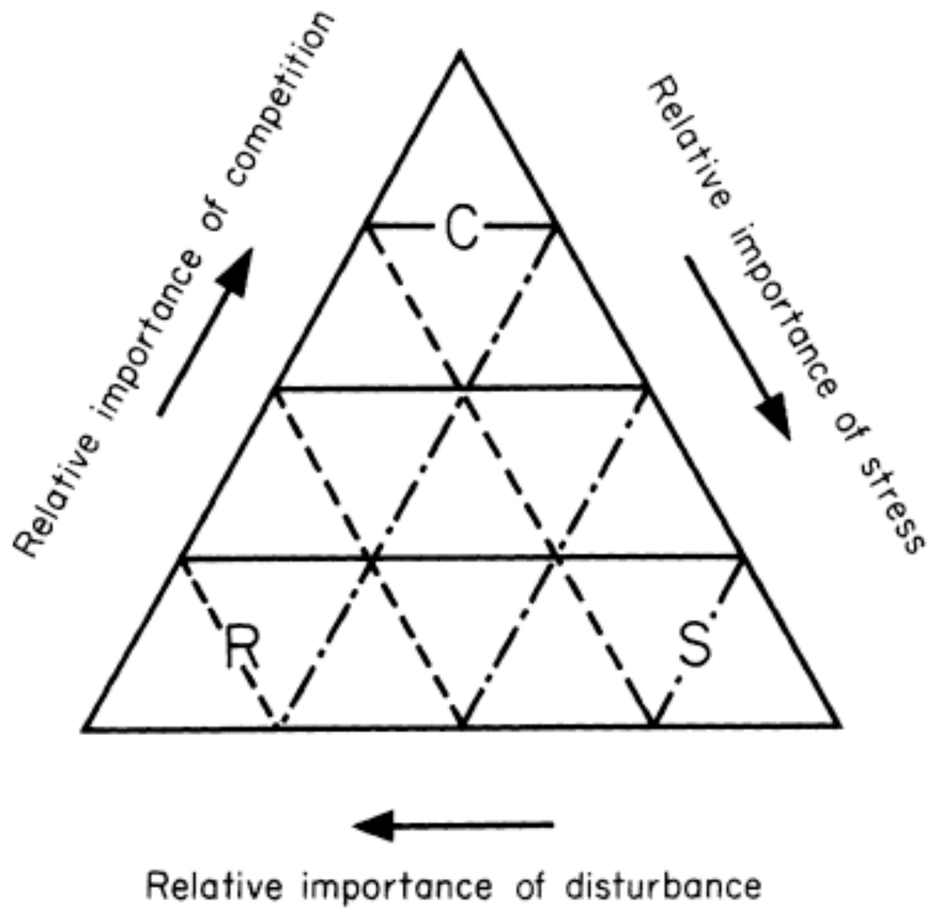


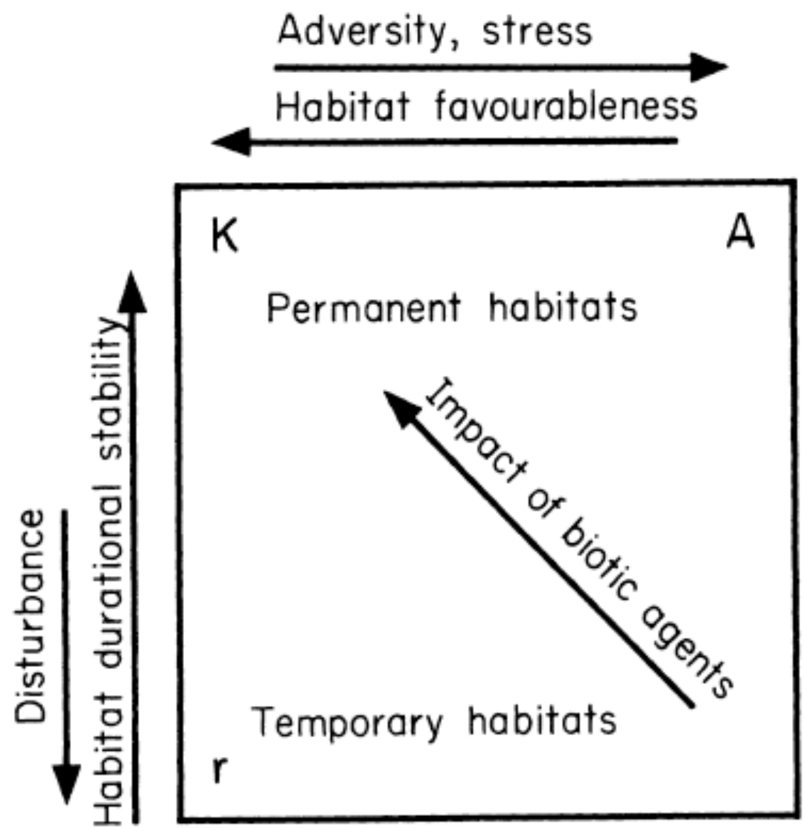
Fig. 2. Ordination plot (axis 1 and axis 2) of the species scores computed by the canonical correspondence analysis for the fish assemblages in the 17 lakes. Symbols represent periodic strategists (solid circles), equilibrium strategists (empty circles) and opportunistic strategists (solid triangles).

Grime, J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169-1194.

- ruderals
- stress-tolerant
- competitive



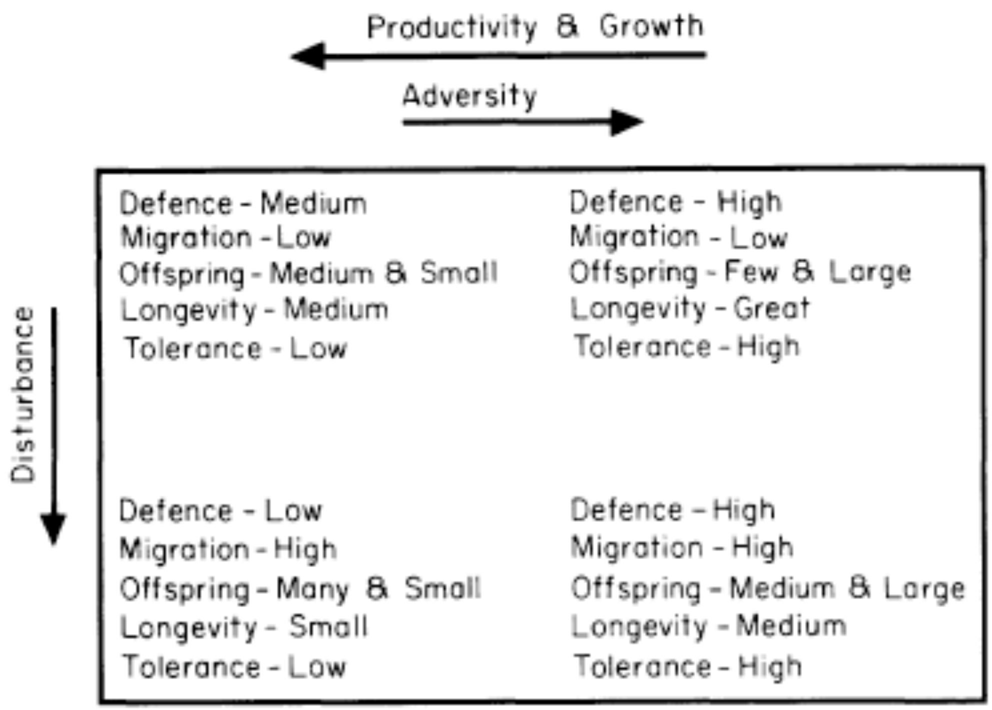
Southwood, T.R.E. 1988. Tactics, strategies and templets. Oikos 52:3-18.



Southwood – Greenslade

$$r_c = \ln\left(\sum_t l_t m_t\right) / T_c$$

Southwood, T.R.E. 1988. Tactics, strategies and templets. Oikos 52:3-18.



Templets - Common predictions
(Offspring, number & size)

The patch-dynamics concept of metacommunities

Assumptions:

- Tradeoff between colonizing ability and competitiveness
  (r strategists vs. K strategists)

- **Intermediate disturbance yields highest diversity**
  (too high, and diversity is reduced)
  (too low, and competitive dominants exclude r strategists)

Origins of the intermediate disturbance hypothesis

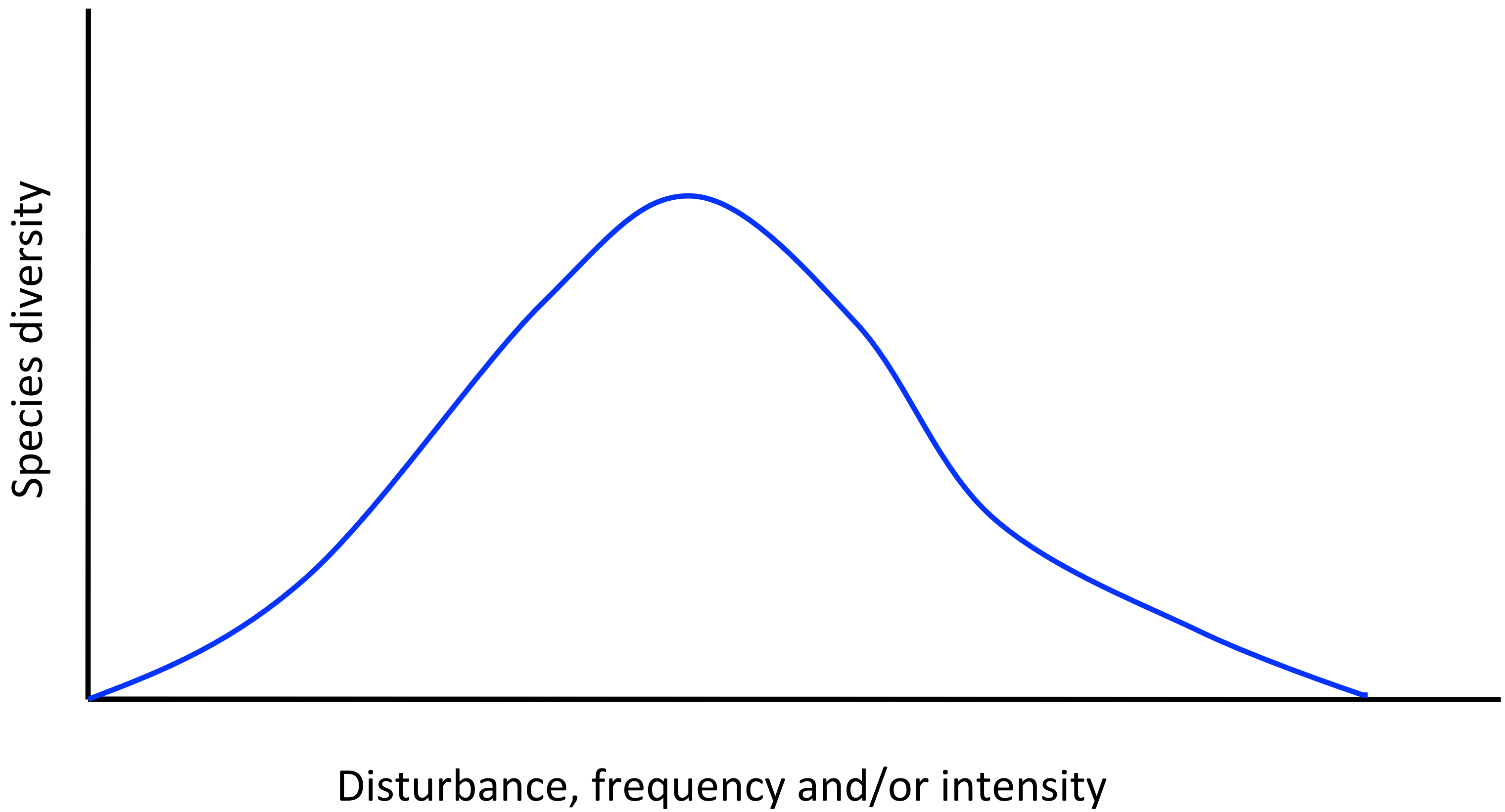
Grime JP (1973) Competition exclusion in herbaceous vegetation. *Nature* 242:344–347.

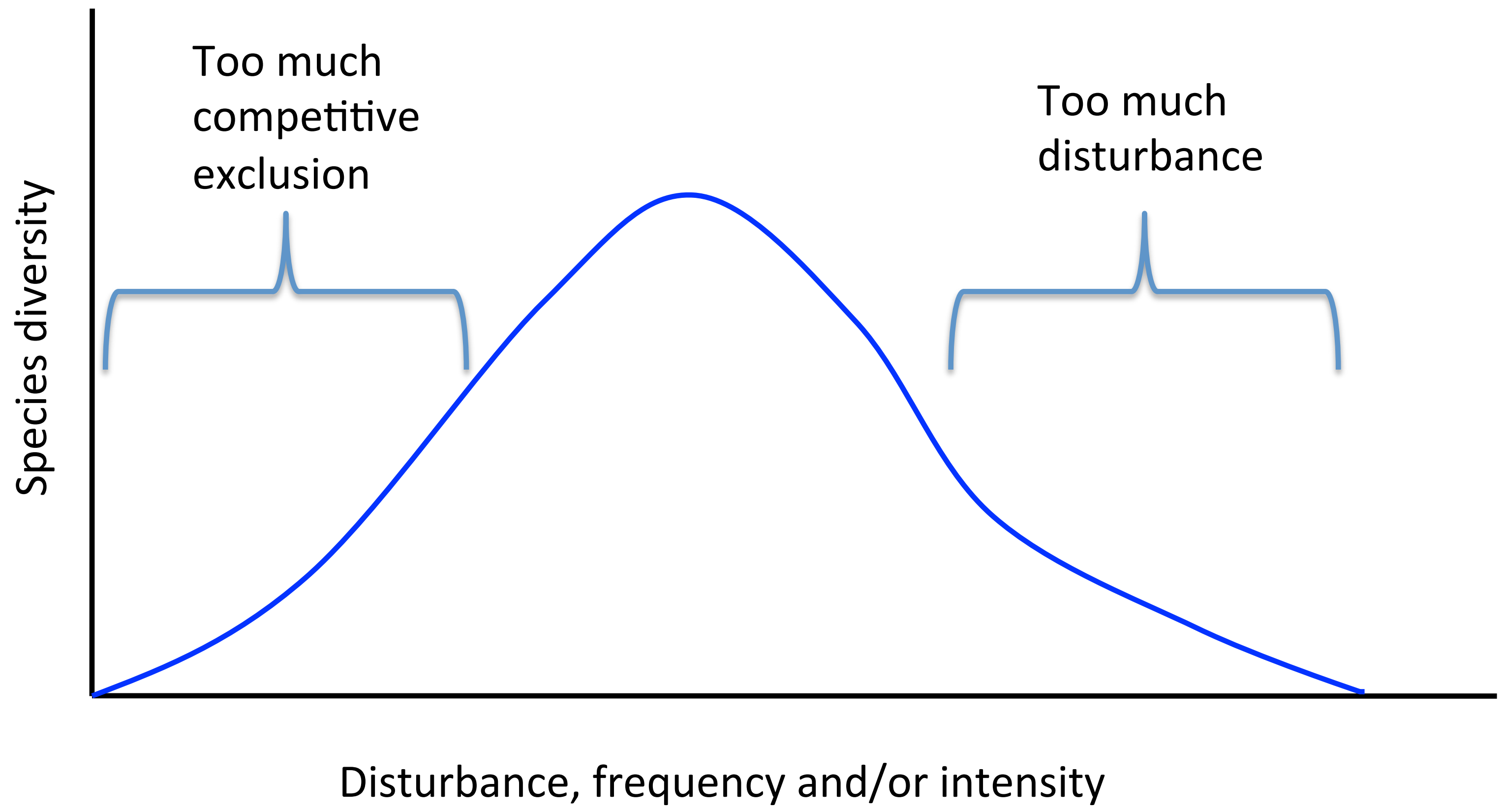
Horn, H.S. (1975) Markovian properties of forest succession. In Cody, M.L. and Diamond, J.M. *Ecology and Evolution of Communities*. Belknap Press, Massachusetts, USA. Pp. 196-211.

Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.

Huston M (1979) A general hypothesis of species diversity. *Am Nat* 113:81–101.

Paine R, Levin S (1981) Intertidal landscapes: Disturbance and the dynamics of pattern. *Ecol Monogr* 5:145–178.


Species diversity
Disturbance, frequency and/or intensity


Too much competitive exclusion
Too much disturbance
Species diversity
Disturbance, frequency and/or intensity

Intermediate disturbance hypothesis, continued:

Menge, B.A.; Sutherland, J.P. (1976). Species diversity gradients: synthesis of the roles of predation, competition and temporal heterogeneity. *American Naturalist* 110 (973): 351–369.

Sousa, W.P. (1979). Disturbance in Marine Intertidal Boulder Fields: The Nonequilibrium Maintenance of Species Diversity. *Ecology* 60 (6): 1225–1239.

Denslow, J.S. (1985). The disturbance-mediated co-existence of species. In Pickett, S.T.A. and White, P.S.. *Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Florida, USA.*

Collins, S.L.; Barber, S.C. (1986). Effects of disturbance on diversity in mixed-grass prairie. *Plant Ecology* 64 (2-3): 87–94.

Petraitis P, Latham R, Niesanbaum R. (1989) The maintenance of species diversity by disturbance. *Quarterly Review of Biology* 64:393-418.

Intermediate disturbance hypothesis, continued:

Collins, S.L.; Glenn, S.M.; Gibson, D.J. (1995). Experimental Analysis of Intermediate Disturbance and Initial Floristic Composition: Decoupling Cause and Effect. *Ecology* 76(2): 486-492.

Wootton JT (1998) Effects of disturbance on species diversity: A multitrophic perspective. *Am Nat* 152:803-825.

Mackey R, Currie D (2001) The diversity-disturbance relationship: Is it generally strong and peaked? *Ecology* 82:3479-3492.

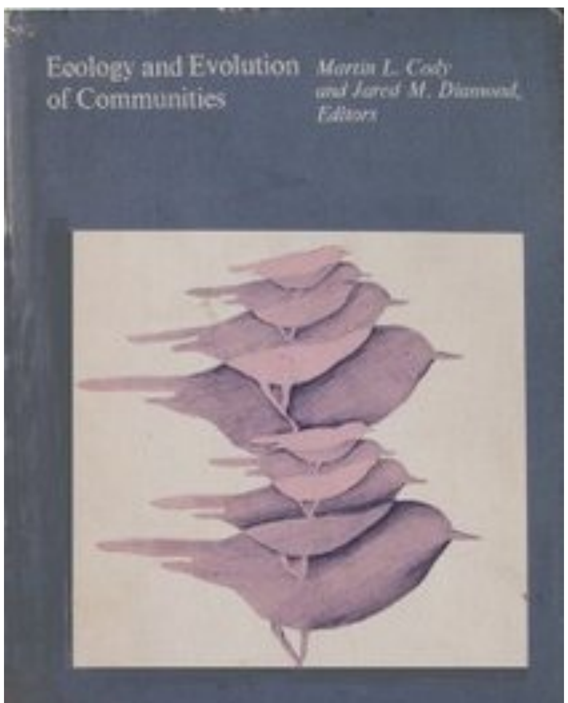
Roxburgh, S.H., Shea, K., Wilson, J.B. (2004) The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. *Ecology* 85(2): 359–371.

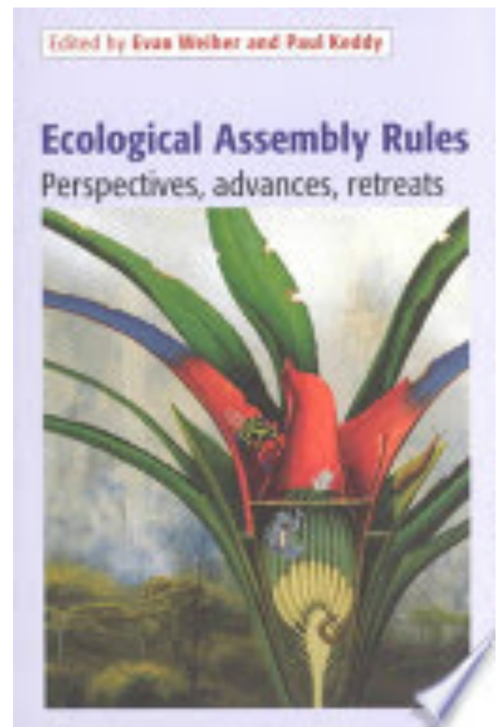
Cadotte MW, et al. (2006) On testing the competition-colonization trade-off in a multispecies assemblage. *Am Nat* 168:704-709.

Cadotte MW (2007) Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology* 88:823-829.

Assembly of Biotic Communities

Diamond, J.M. 1975. Assembly of species communities. Pp. 342-444 in: Ecology and Evolution of Communities (M.L. Cody and J.M. Diamond, eds.). Belknap Press, Cambridge, MA.





Presley, S.J., C.L. Higgins, and M.R. Willig. 2010. A comprehensive framework for the evaluation of metacommunity structure. *Oikos 119: 908-917.*

Clements - communities with coincident range boundaries and compositional unity.

vs.

Gleason – idiosyncratic species responses to the environment, with coexistence resulting from chance similarities in requirements or tolerances.

- Tradeoffs in competitive ability may yield distributions that are more evenly spaced along environmental gradients than expected by chance.
- Alternatively, strong competition may result in checkerboard patterns produced by pairs of species with mutually exclusive ranges (Diamond 1975).
- Communities may form nested subsets of increasingly more species-rich communities, with predictable patterns of species loss associated with variation in species-specific characteristics (e.g., dispersal ability, habitat specialization, tolerance to abiotic conditions).

(Presley, et al. 2010. *Oikos* 119: 908-917)

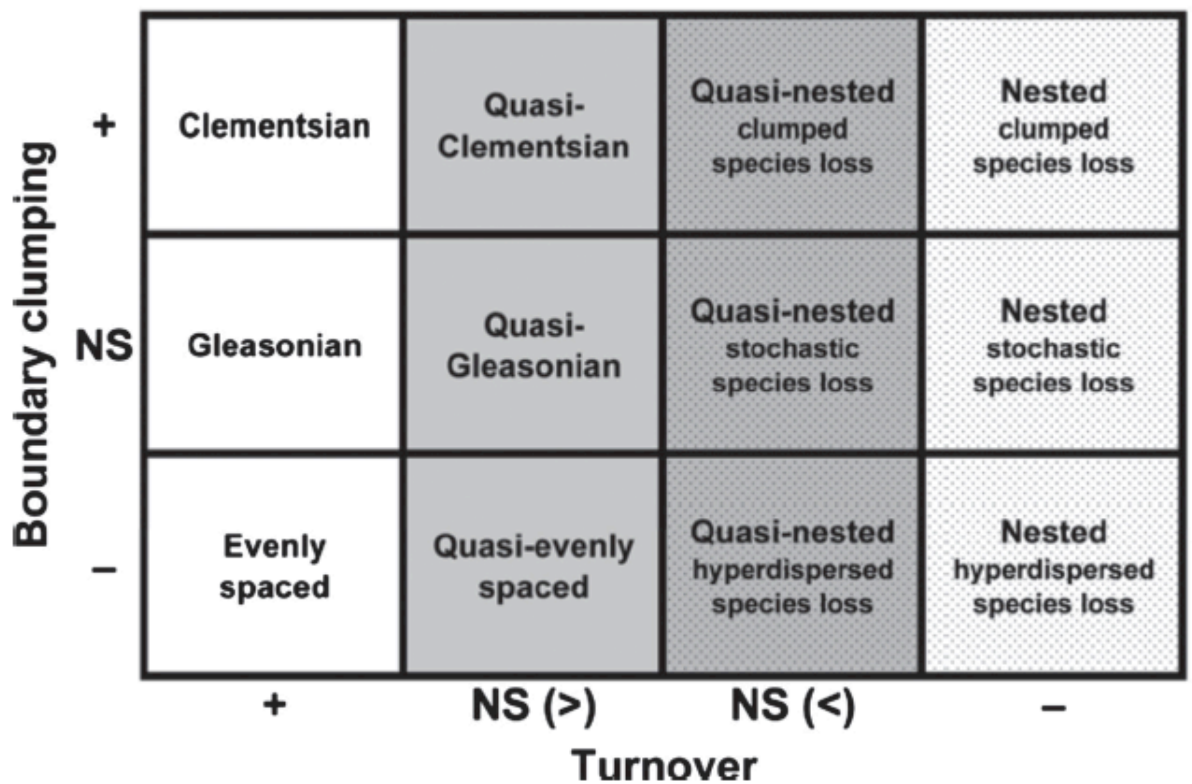


Figure 2. Twelve coherent metacommunity structures defined by range turnover and boundary clumping. Quasi-structures are shaded; nested structures that are distinguished by patterns of species loss are stippled. Significant positive results, +; significant negative results, –; non-significant clumping, NS, non-significant turnover but with more replacements than the average number in randomly generated metacommunities, NS (>); non-significant turnover but with fewer replacements than the average number in randomly generated metacommunities, NS (<).

Presley, S.J. et al. 2010. *Oikos* 119: 908-917.

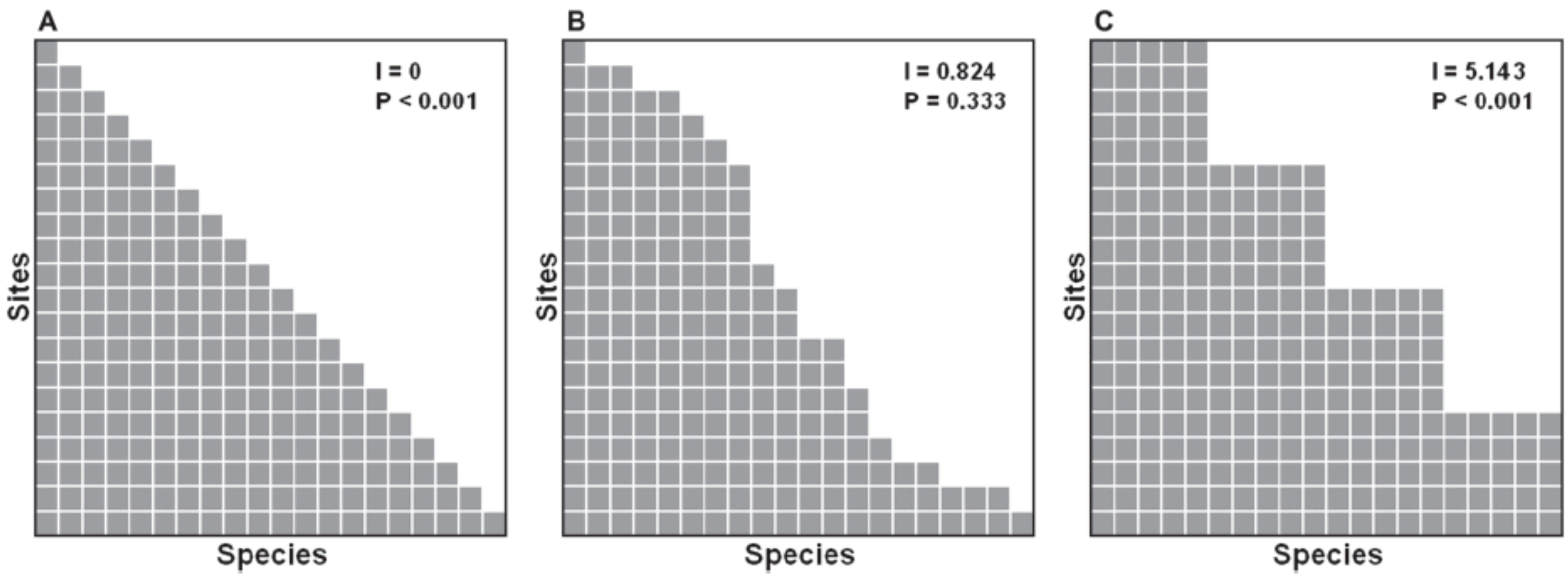


Figure 3. Three perfectly nested metacommunities that exhibit different patterns of species loss that can be distinguished via analysis of range boundary clumping. Shaded cells represent species presences. Species in metacommunity A exhibit hyperdispersed species loss (no clumping), species in metacommunity B exhibit stochastic species loss (one group of three and four groups of two clumped boundaries), and species in metacommunity C exhibit clumped species loss (five clumped boundaries in each of four groups). Morisita's index, I.

Ulrich, W. et al. 2009. A consumer 's guide to nestedness analysis. Oikos 118: 3-17.

Winemiller, K.O. and M.A. Leslie. 1992. Fish communities across a complex freshwater-marine ecotone. *Environmental Biology of Fishes* 34:29-50.

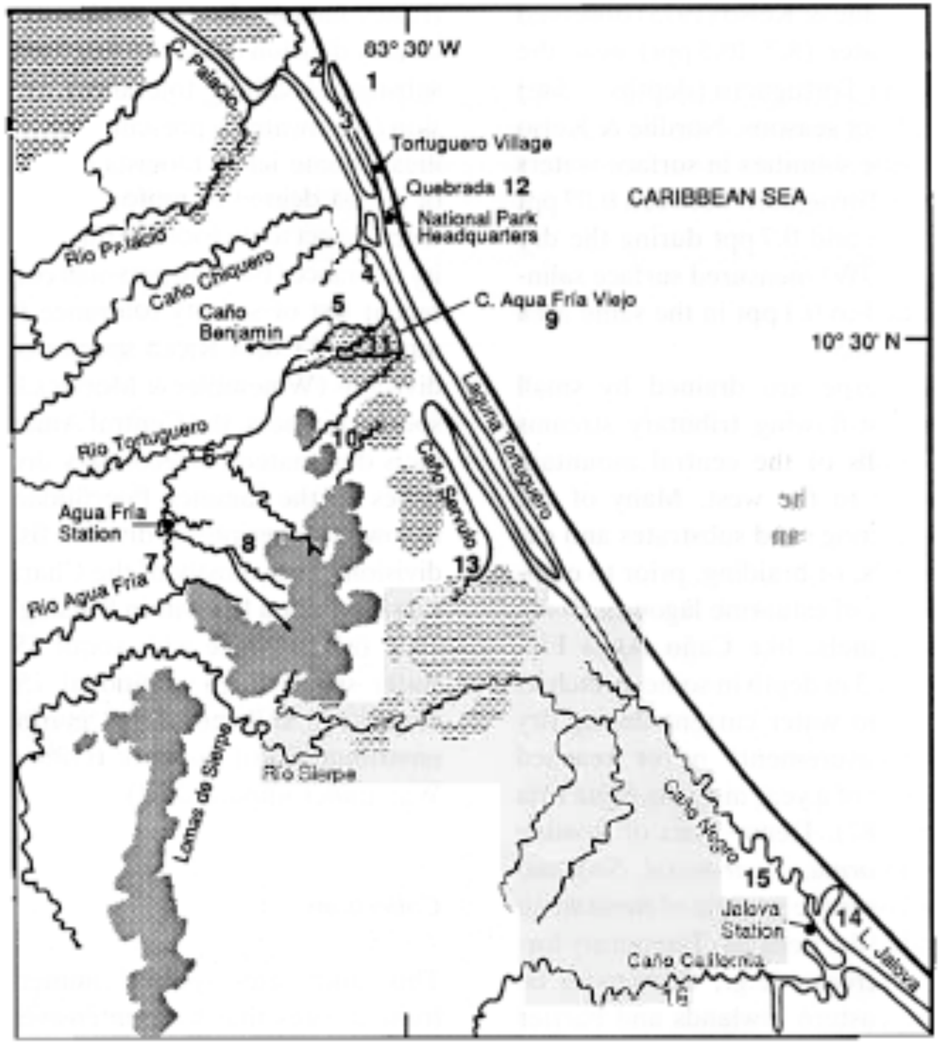


Fig. 1. Map of Tortuguero region. Locations of 16 study sites within the Río Tortuguero, Río Sierpe, and Caño California drainages are indicated by numbers. Dark shading represents Lomas de Sierpe, dashed regions represent low-lying, *Raphia* palm swamps.

Table 1. Common species characteristic of each of the four major faunal zones and ubiquitous species common in two or more adjacent zones (I) of the aquatic environmental gradient in Tortuguero National Park.

Creeks		Rivers		Lagoons		Ocean
Bryconamericus scleroparius						
Gymnotus cylindricus						
Rhamdia guatemalensis						
Rivulus isthmensis						
Priapichthys annectens						
Cichlasoma septemfasciatum						
	Astyanax fasciatus		*Astyanax fasciatus*			
	Alfaro cultratus					
	Phallichthys amates					
	Cichlasoma alfari					
	Cichlasoma nigrofasciatum					
	Gobiomorus dormitor		*Gobiomorus dormitor*			
	Eleotris amblyopsis		*Eleotris amblyopsis*			
	Eleotris pisonis					
		Atractosteus tropicus				
		Brycon guatemalensis				
		Roeboides guatemalensis				
		Brachyrhaphis parismina				
		Cichlasoma dovii				
		Cichlasoma nicaraguense				
		Cichlasoma rostratum				
			Belonesox belizanus			
			Poecilia gilli			
			Melaniris milleri			
			Strongylura timucu			
			Cichlasoma centrarchus			
			Cichlasoma citrinellum			
			Cichlasoma loisellei			
			Cichlasoma maculicauda			
			Herotilapia multispinosa			
			Pomadasys crocro			
			Lutjanus jocu			
			Centropomus pectinatus			
			Oostethus lineatus			
			Achirus lineatus			
			Citharichthys spilopterus			
			Trinectes paulistanus			
			Dormitator maculatus			
			Evorthodus lyricus			
			Gobionellus boleosoma			
			Gobionellus fasciatus			
			Gobiosoma spes			
				Anchoa lamprotaenia		
				Anchoviella elongata		
				Myrophis punctatus		
				Hyporhamphus roberti		
				Centropomus parallelus		
				Diapterus plumieri		
				Diapterus rhombeus		
				Eucinostomus melanopterus		
				Bairdella ronchus		
				Micropogonias furnieri		
				Microdesmus carri		
				Bathygobius soporator		
				Sphoeroides testudineus		
					Megalops atlanticus	
					Mugil curema	
					Caranx hippos	
					Caranx latus	
					Oligoplites palometa	
					Centropomus undecimalis	
						Harengula jaguana
						Odontognathus compressus
						Opisthonema oglinum
						Pellona harroweri
						Coleotropis blackburni
						Polydactylus virginicus
						Conodon nobilis
						Pomadasys corvinaeformis
						Larimus breviceps
						Ophioscion panamensis
						Stellifer colonensis

Diamond, J.M. 1975. Assembly of species communities. Pp. 342-444 in: Ecology and Evolution of Communities (M.L. Cody and J.M. Diamond, eds.). Belknap Press, Cambridge, MA.

The checkerboard test

a	a b	b	a b	a	b
a	b	a b		a	a
a	b	a	a b	a b	a
	b	a	b	b	b

Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81(9):2606-2621.

TABLE 1. Summary of four co-occurrence indices.

	Index			
	CHECKER	*C* score	*V* ratio	COMBO
Description	Number of species pairs forming perfect checkerboard distributions	Checkerboard score	Variance ratio	Number of unique species combinations
Calculation	Scan matrix rows for species pairs forming checkerboards	$\Sigma(S_i - Q)(S_k - Q)/((R)(R - 1)/2)$	σ^2(column sums)/ Σ row σ^2	Scan matrix columns for unique species combinations
Source	Diamond (1975)	Stone and Roberts (1990)	Robson (1972); Schluter (1984)	Pielou and Pielou (1968)
Theoretical range	0 to $R(R - 1)/2$	0 to $\Sigma S_i S_k/((R)(R - 1)/2)$	0 to ∞	1 to 2^R
Pattern expected in a competitively structured community	Observed > simulated	Observed > simulated	Observed < simulated	Observed < simulated
Comments	Most readily testable prediction of Diamond's (1975) assembly rules	Measures species segregation, but does not require perfect checkerboard distributions	Measures pattern in marginal totals of matrix	May reflect "forbidden species combinations" (Diamond 1975)

Notes: S_i = total for row *i*; *R* = number of rows (=species) in the matrix; *Q* = number of sites in which both members of a species pair are present.

Gotelli, N.J. 2000. Null model analysis of species co-occurrence patterns. *Ecology* 81(9):2606-2621.

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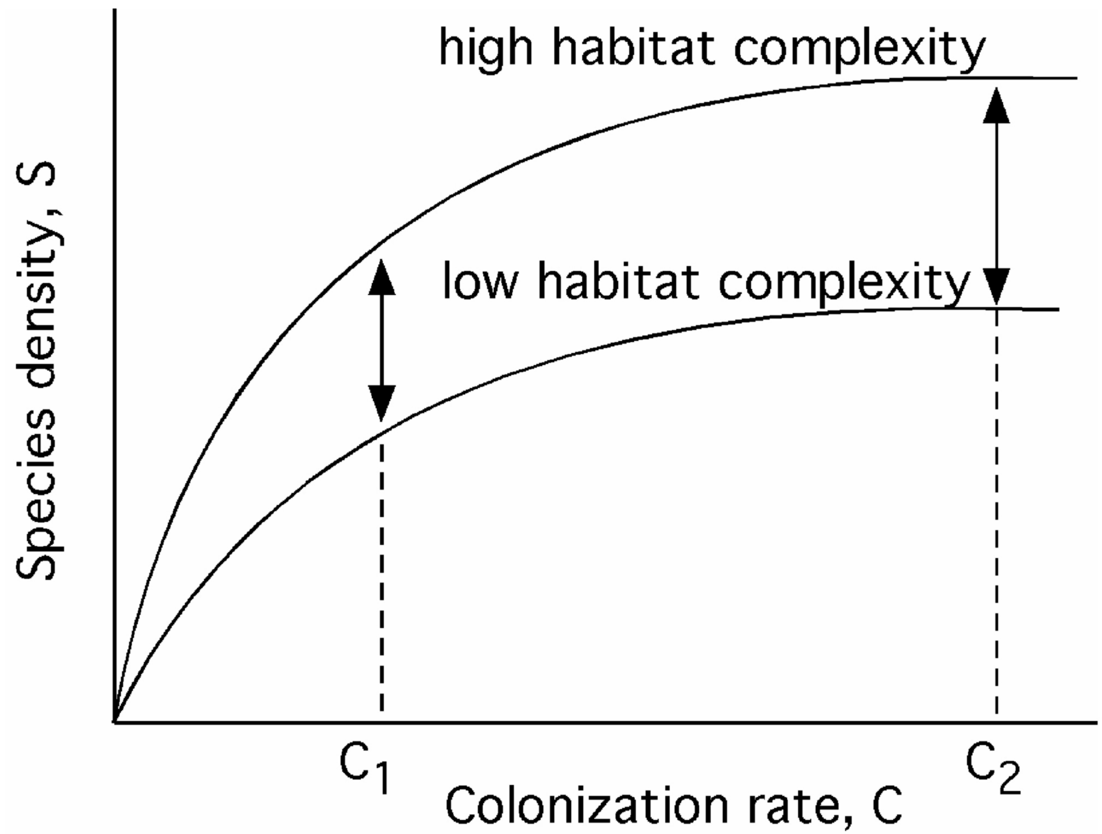
Cinaruco River, Venezuela

A great diversity of fishes occurs in littoral-zone habitats with high structural complexity.

As water level drops, these habitat patches are repeatedly colonized then abandoned.

Arrington, D.A., K.O. Winemiller, and C.A. Layman. 2005. Community assembly at the patch scale in a species rich tropical river. *Oecologia* 144:157-167.

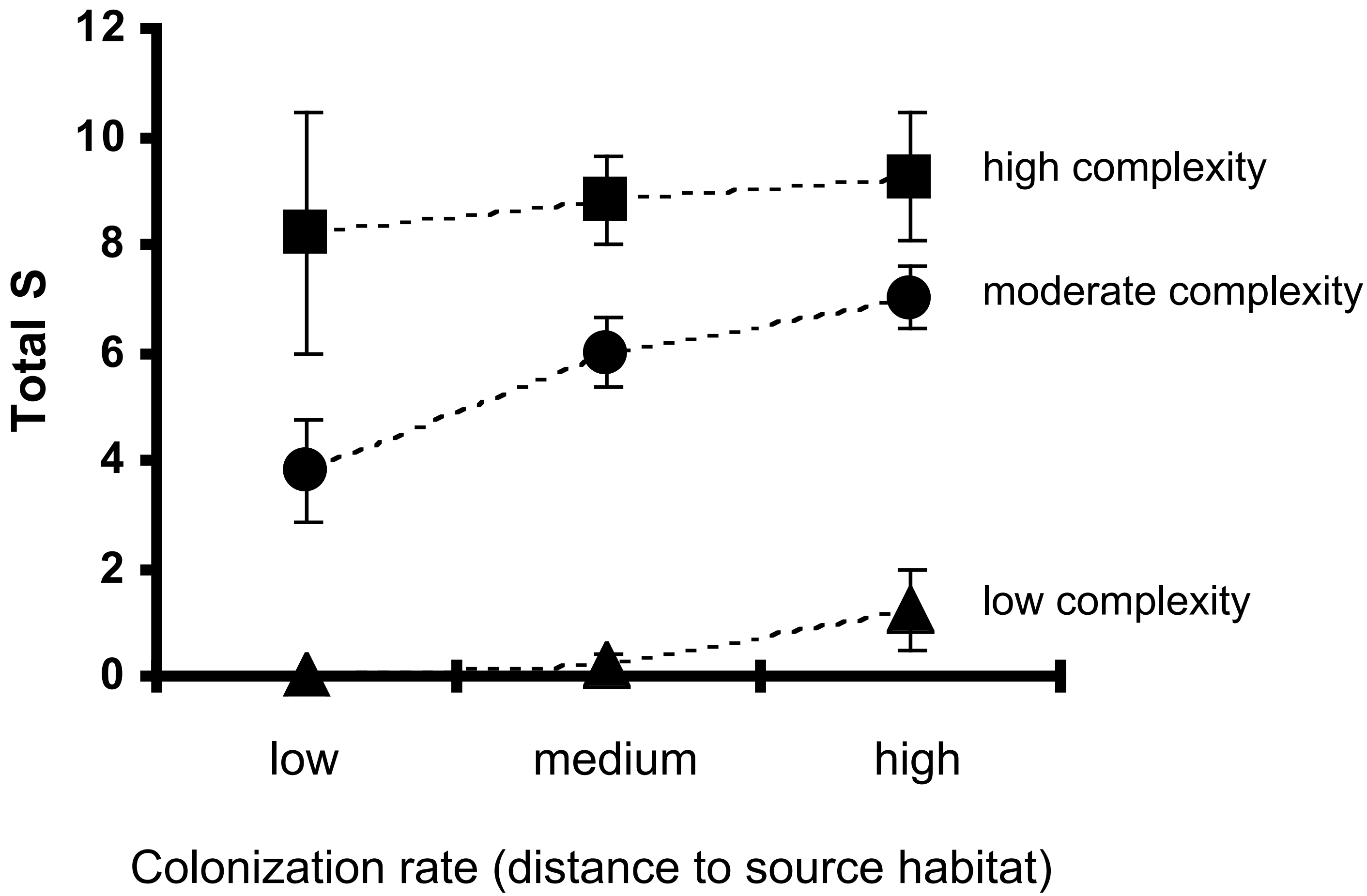
Niche vs. Neutral ?



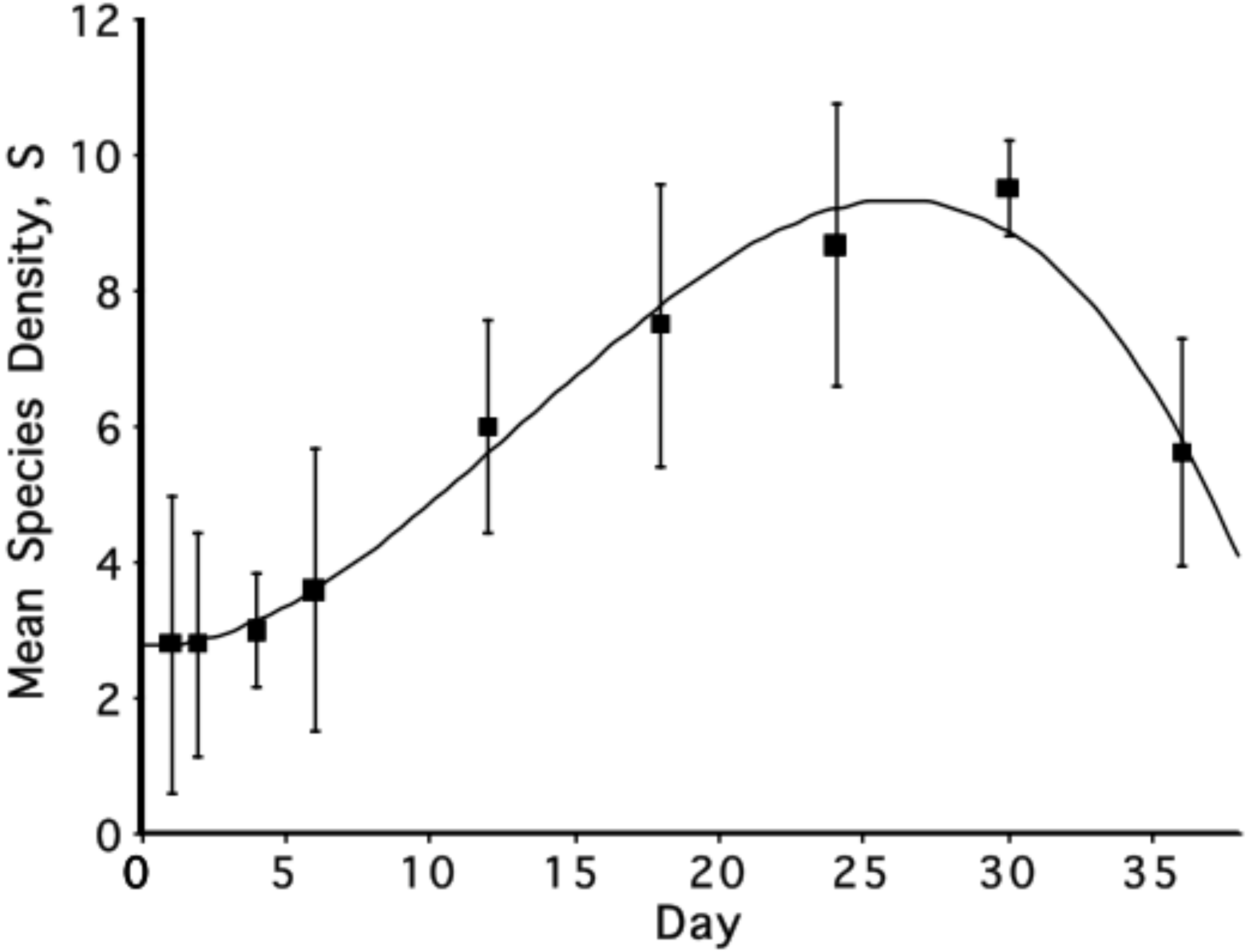
We manipulated –

- *patch structural complexity while keeping patch size constant*
- *colonization rate (distance to source habitat)*

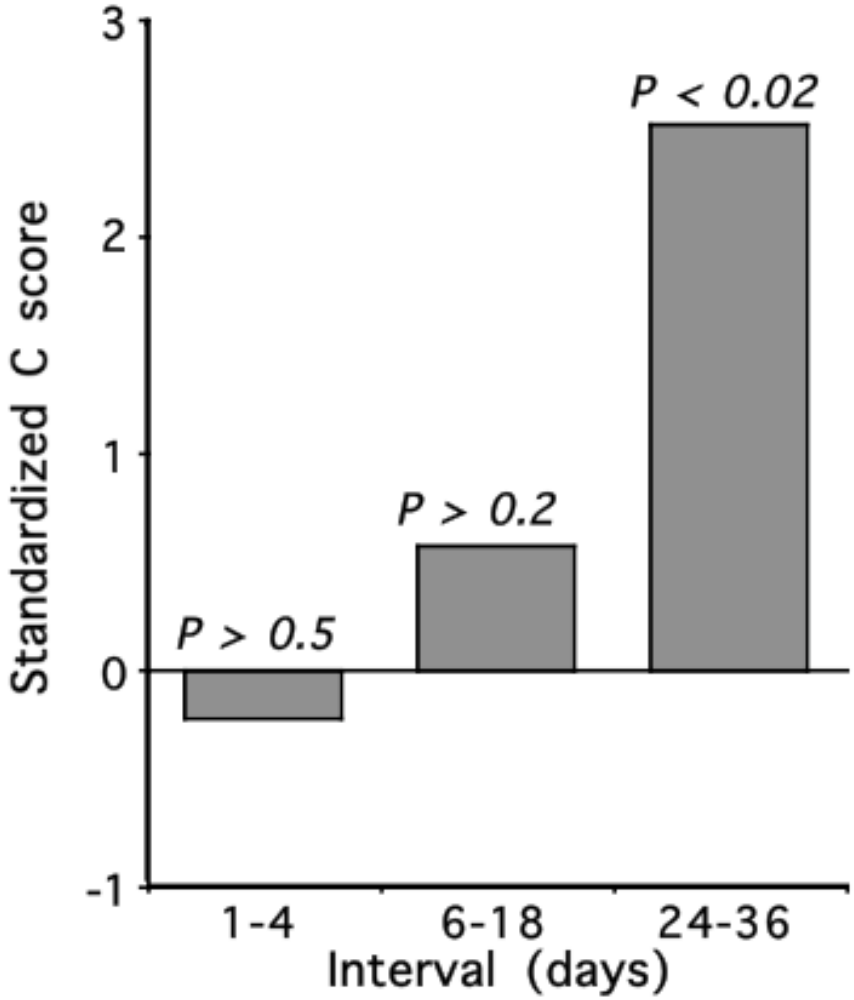
Results from experiment varying habitat complexity & colonization rate



Results from experiment varying the amount of time elapsed for colonization



Degree of non-random community organization increases over time



Gotelli, N.J. & D.J. McCabe. 2002. Species co-occurrence: a meta-analysis of J.M. Diamond's assembly rules model. *Ecology* 83:2091-2096.

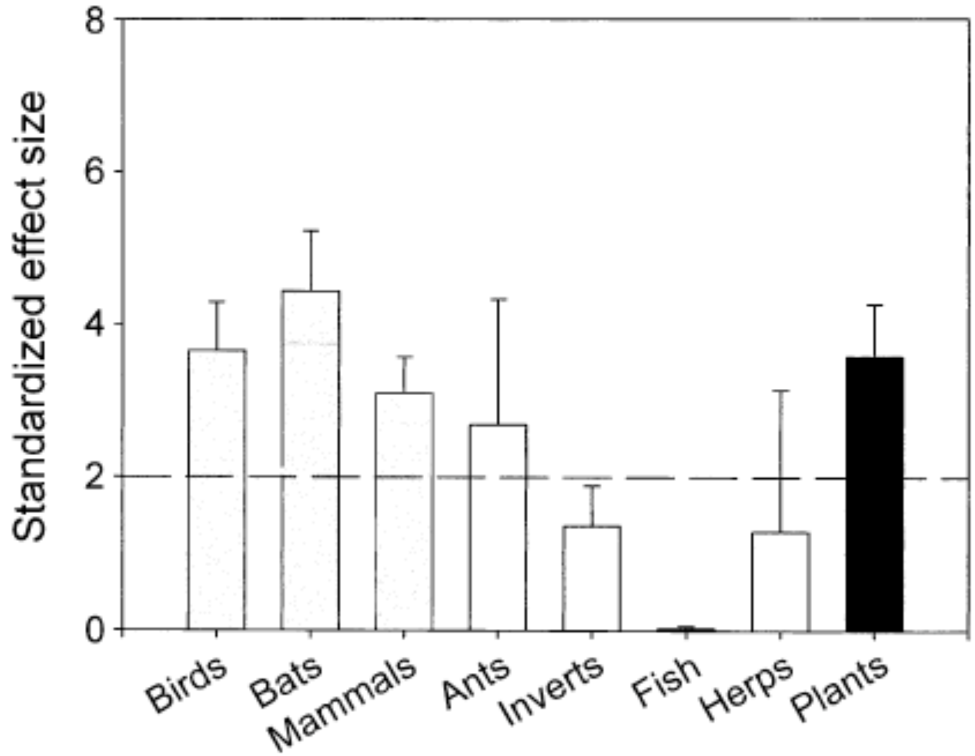
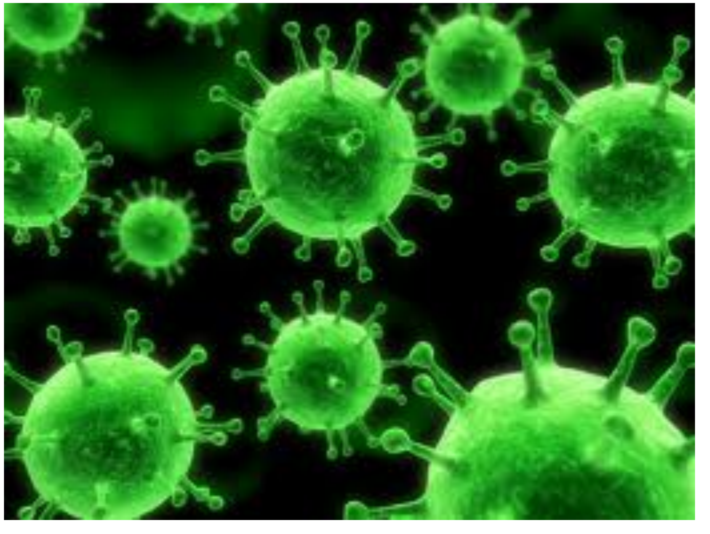


FIG. 2. Effect sizes for the *C* score of different taxonomic groups (means ± 1 SE; $F_{7,87} = 2.20$, $P = 0.041$). The dashed line indicates a standardized effect size of 2.0, which is the approximate 5% significance level. Matrices for homeotherms (gray bars) were significantly more structured than matrices for poikilotherms (open bars; linear contrast $F_{1,87} = 7.70$, $P = 0.009$). Sample sizes were: birds, $N = 25$; bats, $N = 3$; mammals, $N = 16$; ants, $N = 3$; invertebrates, $N = 18$; fish, $N = 3$; herps (reptiles and amphibians), $N = 15$; plants, $N = 13$.

Koenig, J.E., A. Spor, N. Scalfone, A.D. Fricker, J. Strombaugh, R. Knight, L.T. Angenent, and R.E. Ley. 2011. Succession of microbial consortia in the developing infant gut microbe. *Proceedings of the National Academy of Sciences, USA,* 108, Supplement 1:4578-4585.



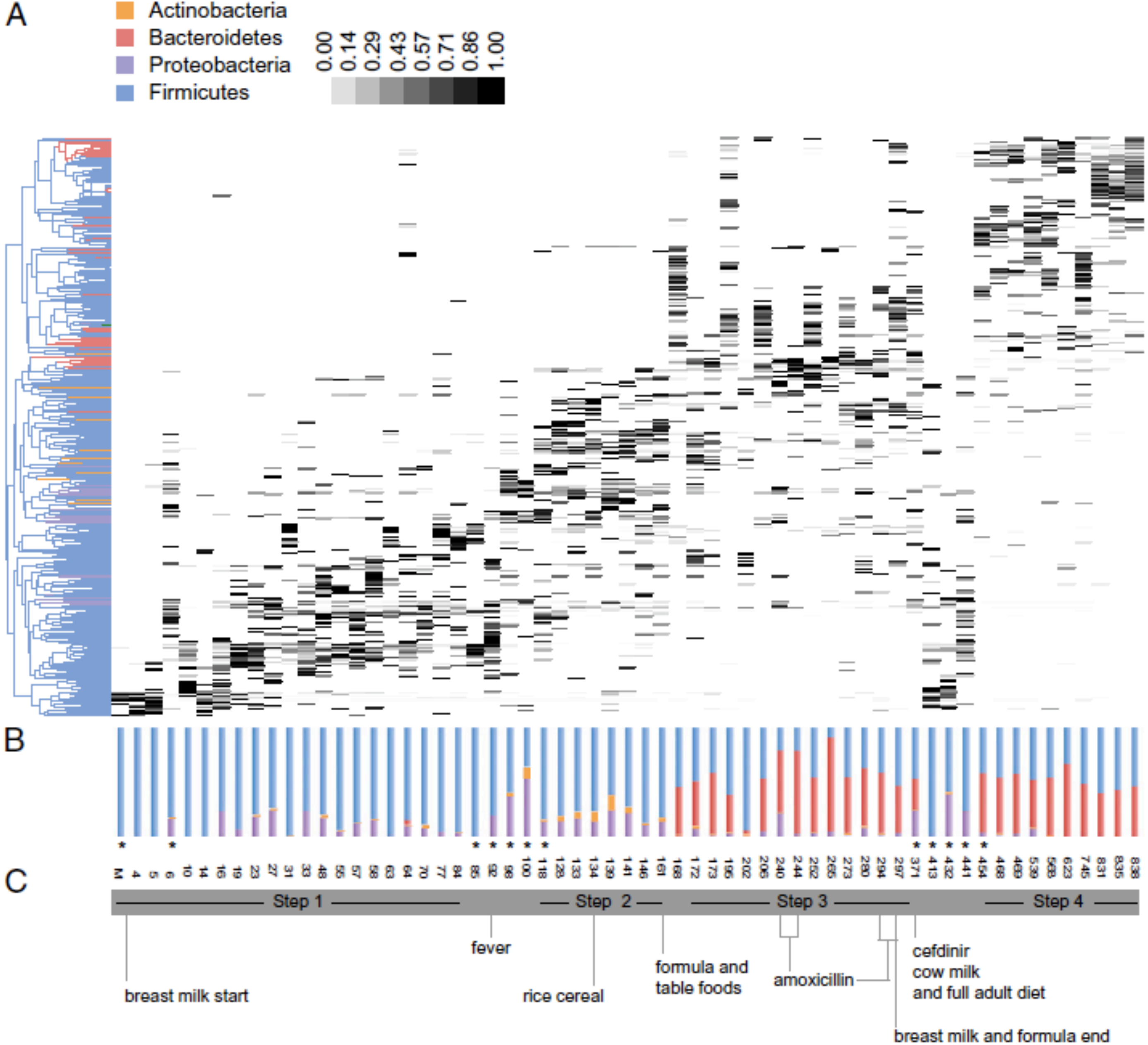


Fig. 3. OTU-based community structure and composition in the gut microbiota. (*A*) Each vertical lane corresponds to a sample day, and the gray-scale shaded rectangles represent the abundance of the different OTUs. The dendogram on the left shows how the OTUs are clustered according to cooccurrence, and branches are colored to indicate the taxonomical assignment of the OTUs at the phylum level. Samples selected for metagenomic analyses are indicated with asterixes. (*B*) Relative abundances of the bacterial phyla in each samples. (*C*) Significant events pertaining to changes in the infant's diet are indicated. Steps characterized by specific bacterial consortia supported by linear discriminate analysis are shown.

Koenig, et al. 2011. *PNAS* 108, Suppl. 1, 4578-4585

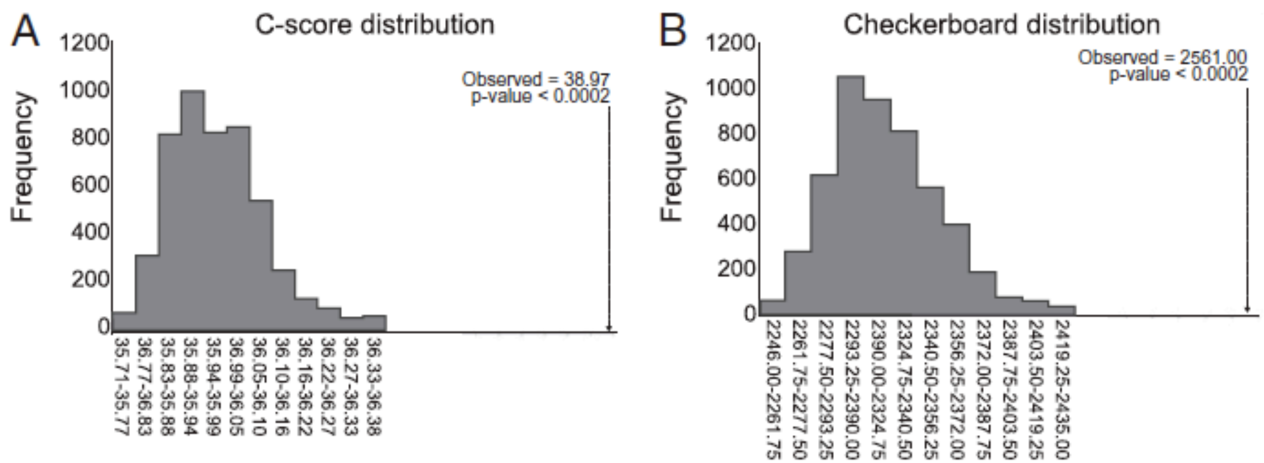


Fig. 4. Community assembly is nonrandom. (*A*) C-score distributions for observed and randomized OTU occurrence in each sample. (*B*) Checkerboard indices for observed and randomized OTU occurrence. Values for the observed distributions are indicated with arrows.

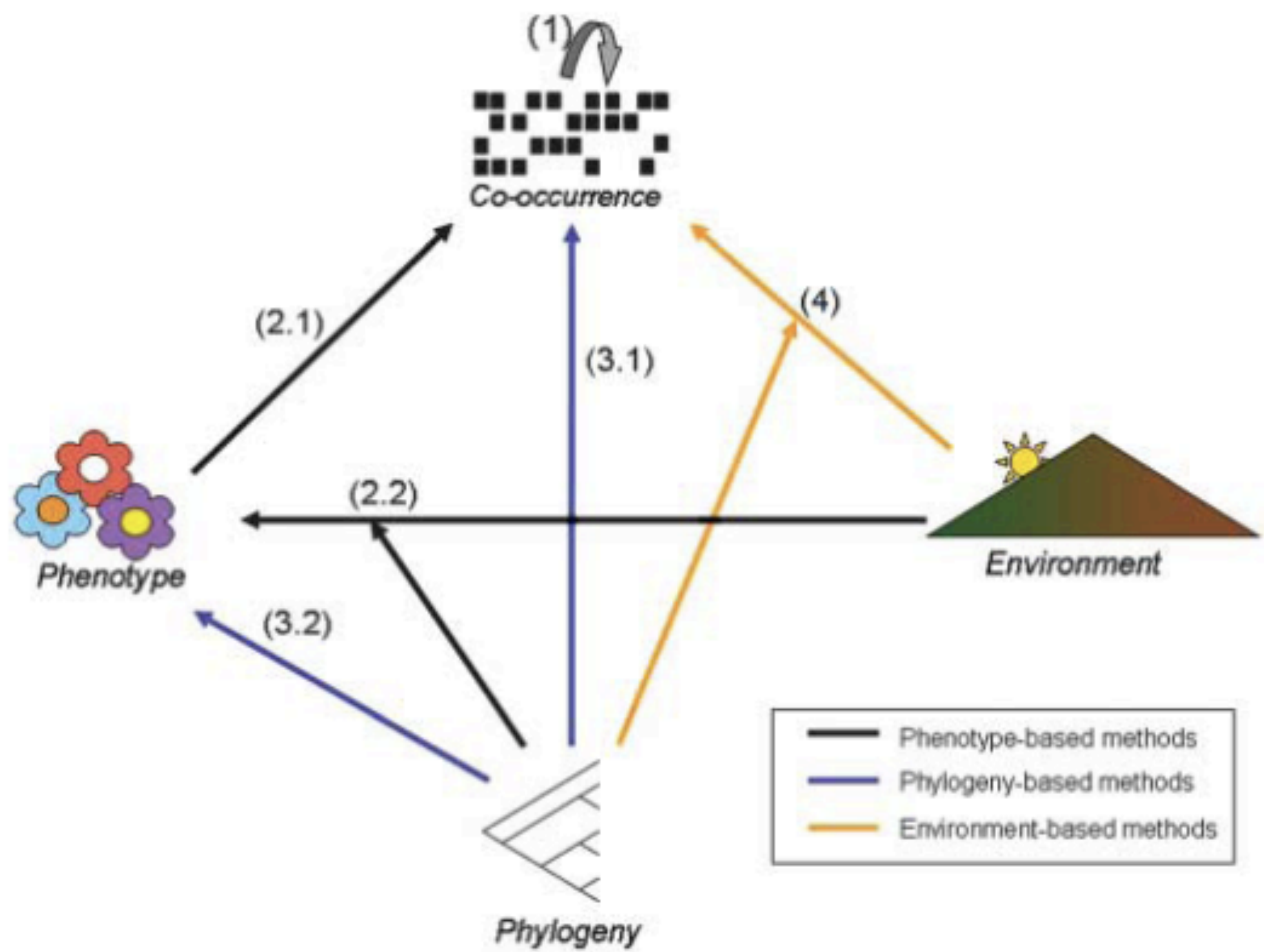


Figure 1. Methods for analyzing community structure can be represented in a simple framework in which the relationships (arrows) between the four key concepts (phylogeny, phenotype, environment, and co-occurrence) are integrated. Bracketed numbers refer to (1) the co-occurrence pattern

Pausas, J.G. & Verdú, M. 2010. The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *BioScience* 60:614-625

Table 1. Available software for community structure analysis.

Software name	**Availability (Web address)**	**Use**
EcoSim	*www.garyentsminger.com/ecosim, http://cran.r-project.org/web/packages/picante*	1 in figure 1
TraitHull	*www.pricklysoft.org/software/traithull.html*	2.1 in figure 1
Ape	*ape.mpl.ird.fr, cran.r-project.org/web/packages/ape*	2.2 in figure 1, box 3
PhySig (MatLab scripts)	*www.biology.ucr.edu/people/faculty/Garland/PHYSIG.html, http://cran.r-project.org/web/packages/picante*	3.2 in figure 1
BayesTraits	*www.evolution.reading.ac.uk/BayesTraits.html*	3.2 in figure 1
PDAP	*www.biology.ucr.edu/people/faculty/Garland/PDAP.html*	3.2 in figure 1
Phylocom	*www.phylodiversity.net/phylocom, http://cran.r-project.org/web/packages/picante*	3.1 and 3.2 in figure 1, box 3
MatLab scripts	Supplementary material in Helmus and colleagues (2007b), *http://cran.r-project.org/web/packages/picante*	3.1 in figure 1, box 2
SpaCoDi	*www.ulb.ac.be/sciences/bioancel/ohardy/, http://cran.r-project.org/web/packages/picante*	3.1 in figure 1, box 2
EcoPhyl	*www.cbs.umn.edu/cavender/*	3.1 in figure 1, box 2
MatLab scripts	As supplementary material in Helmus and colleagues (2007a)	4 in figure 1
Geiger	*cran.r-project.org/web/packages/geiger*	Box 3

Distribution of traits in communities

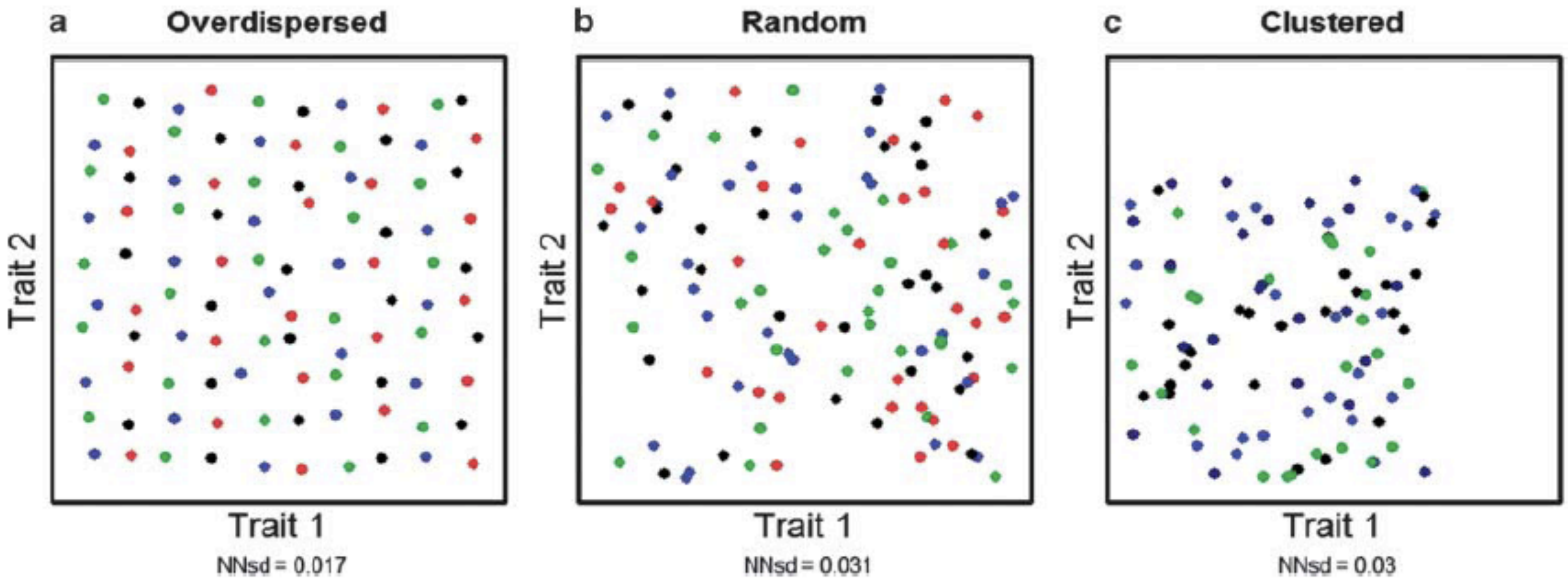


Figure 2. Graphical example of (a) phenotypically overdispersed, (b) random, and (c) clustered communities. Each point represents a species in the morphospace determined by three noncorrelated traits, two quantitative traits (x- and y-axes), and a qualitative trait (symbol color). Overdispersed communities have the lowest standard deviation of the nearest-neighbor distance (NNsd), whereas clustered communities have a reduced range of trait values (i.e., reduced trait space occupied the species, plot c).

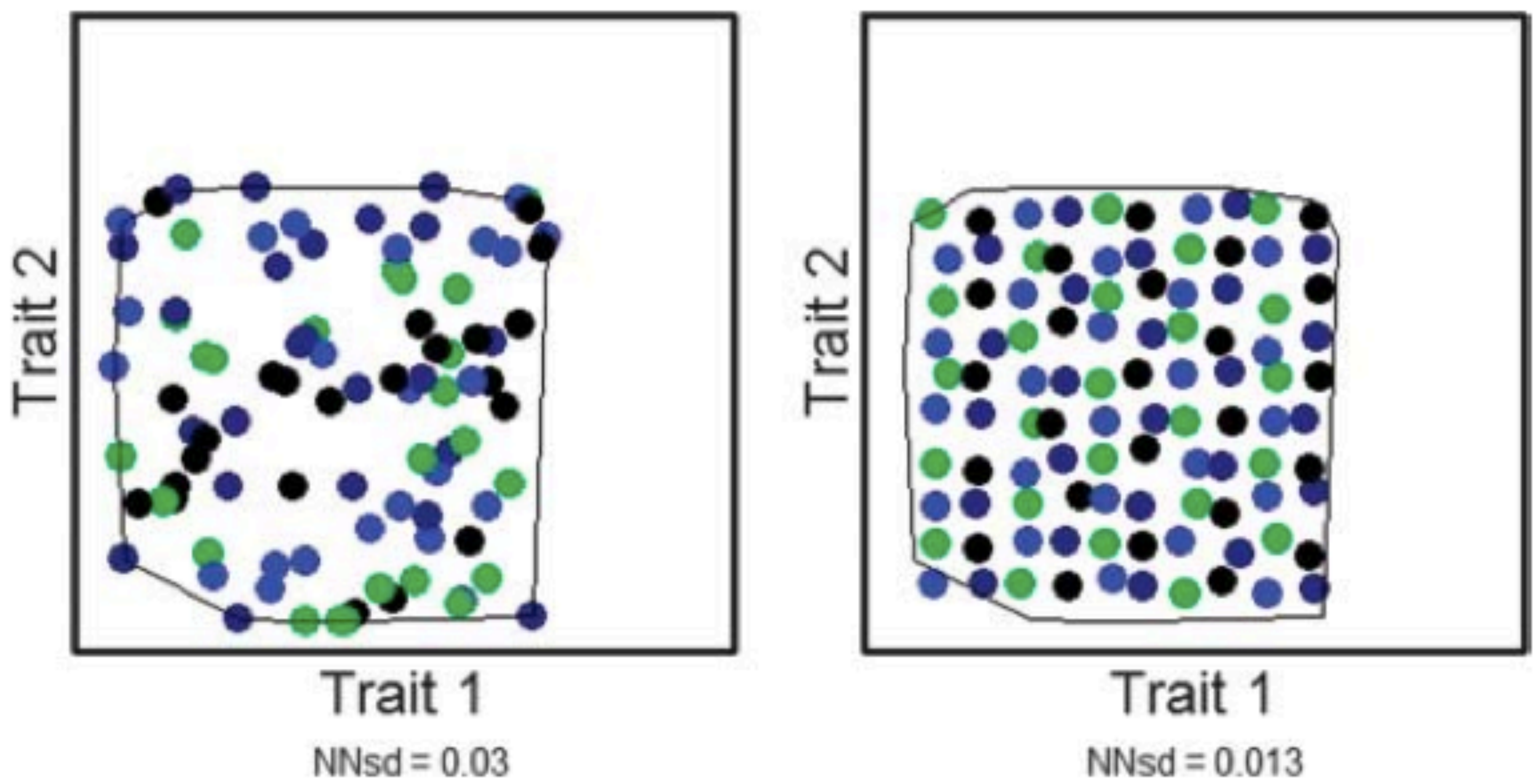


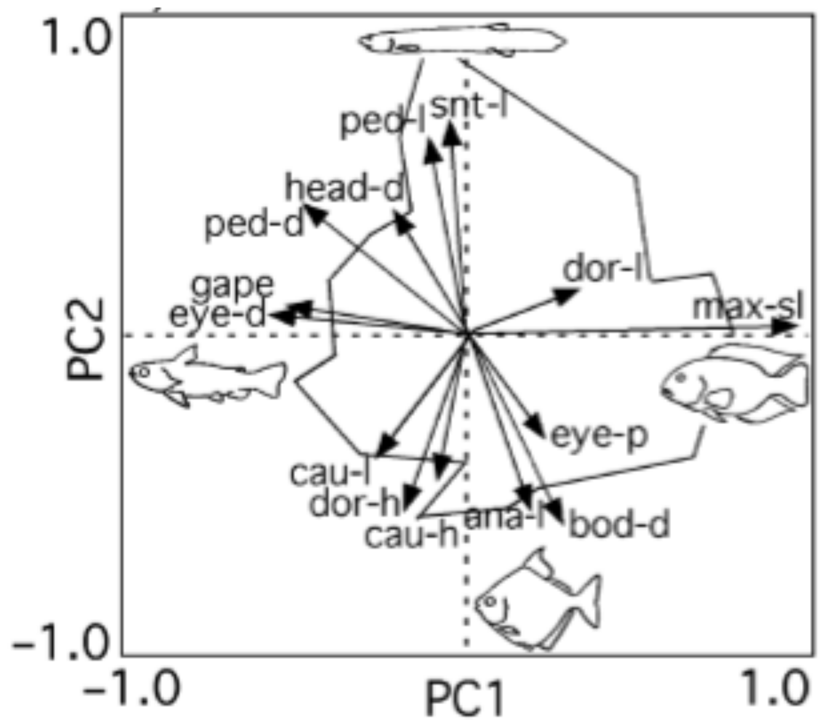
Figure 4. The distribution of trait values within the reduced morphospace by habitat filtering (from figure 2c) may be random (left) and overdispersed (right; with lower standard deviation of the nearest-neighbor distance, NNsd). In the former case only one assembly process (filtering) is acting, whereas in the latter both filtering and limiting similarity are acting. The polygon indicates the convex hull.

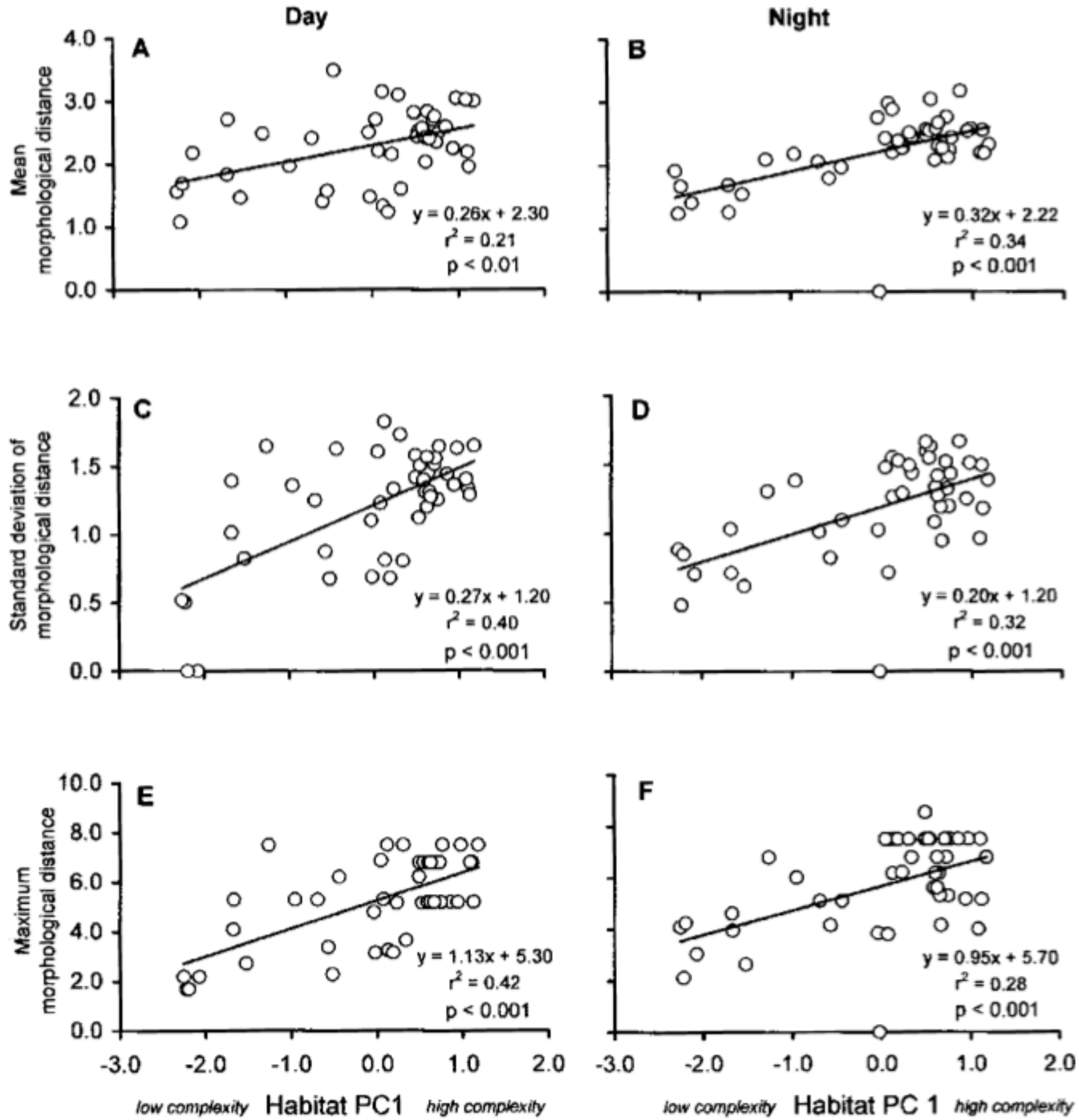
Oecologia (2005) 142: 284–295
DOI 10.1007/s00442-004-1723-z

COMMUNITY ECOLOGY

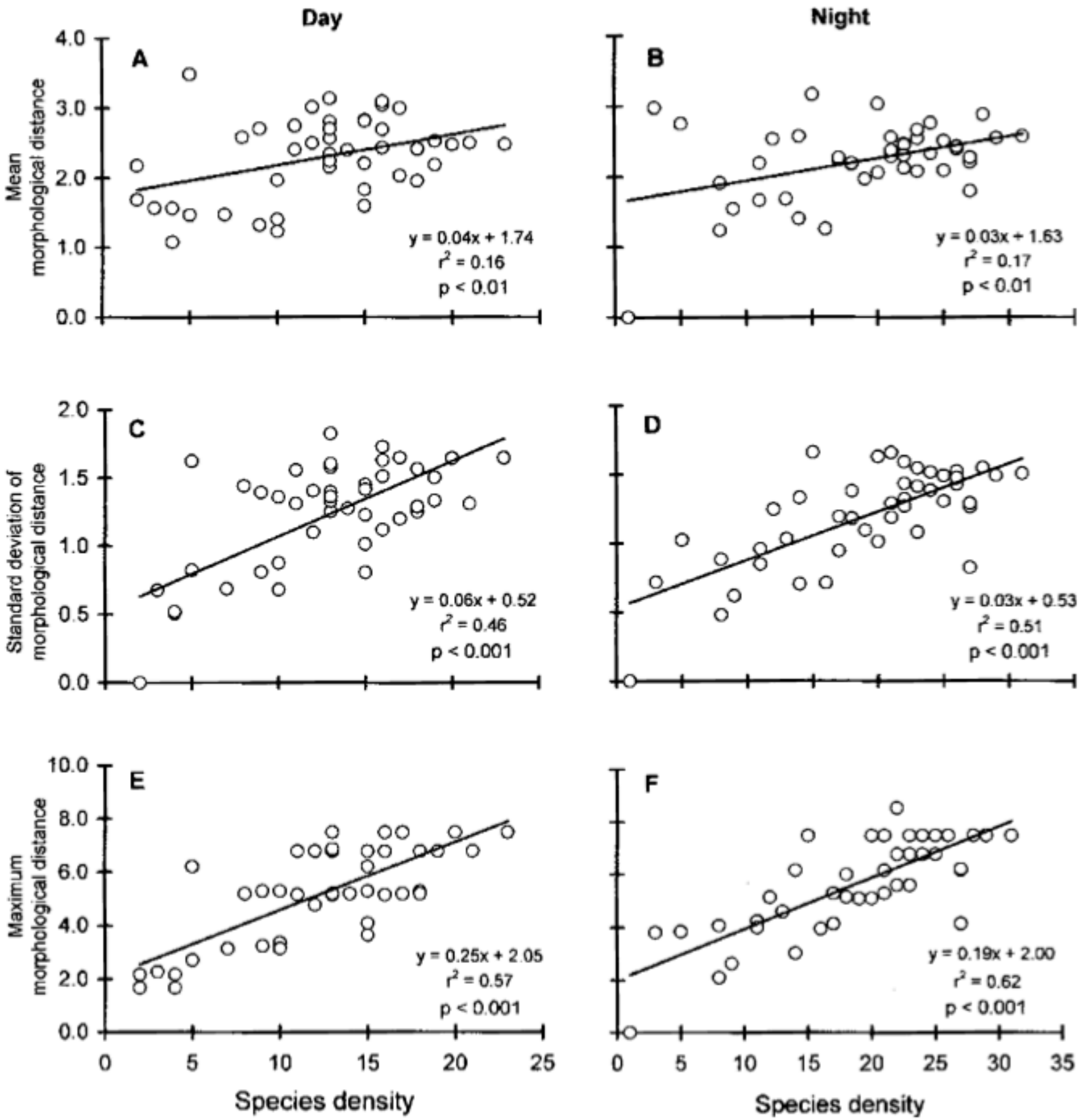
S. C. Willis · K. O. Winemiller · H. Lopez-Fernandez

Habitat structural complexity and morphological diversity of fish assemblages in a Neotropical floodplain river

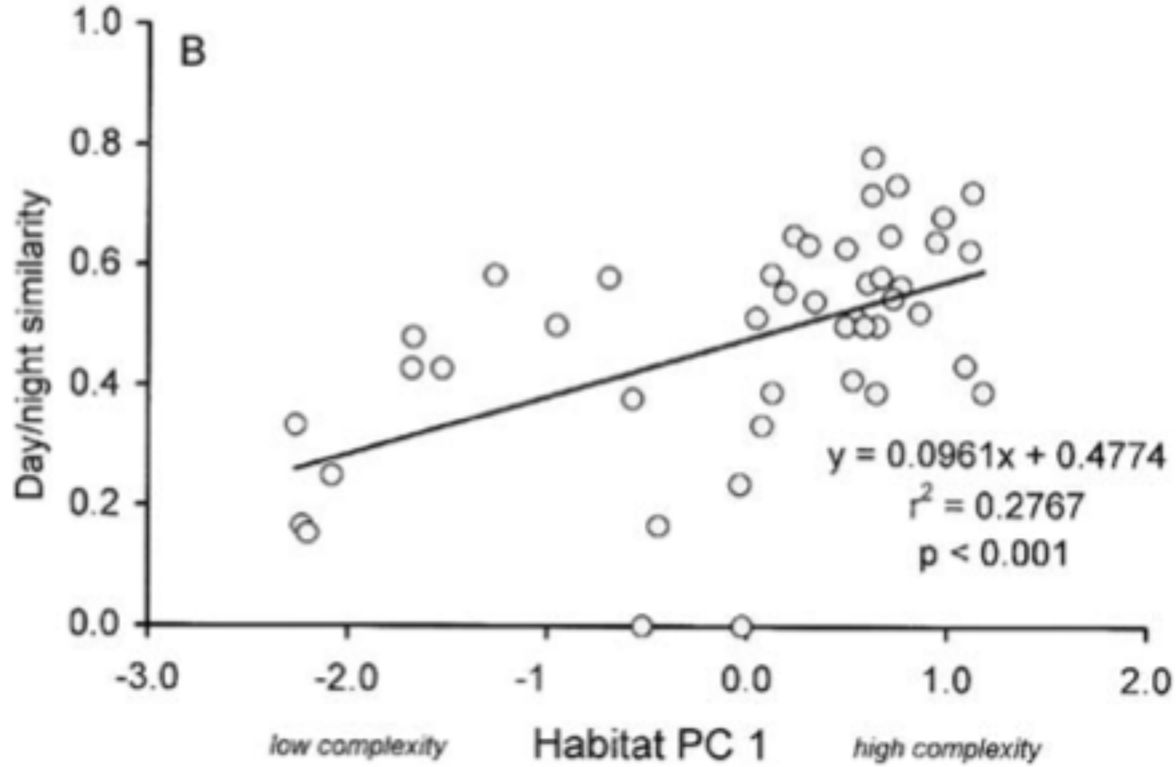




Day
Night
A
B
C
D
E
F
Mean morphological distance
Standard deviation of morphological distance
Maximum morphological distance
y = 0.26x + 2.30
r^2 = 0.21
p < 0.01
y = 0.32x + 2.22
r^2 = 0.34
p < 0.001
y = 0.27x + 1.20
r^2 = 0.40
p < 0.001
y = 0.20x + 1.20
r^2 = 0.32
p < 0.001
y = 1.13x + 5.30
r^2 = 0.42
p < 0.001
y = 0.95x + 5.70
r^2 = 0.28
p < 0.001
low complexity
Habitat PC1
high complexity
low complexity
Habitat PC 1
high complexity



Day
Night
A
B
C
D
E
F
Mean morphological distance
Standard deviation of morphological distance
Maximum morphological distance
y = 0.04x + 1.74
r^2 = 0.16
p < 0.01
y = 0.03x + 1.63
r^2 = 0.17
p < 0.01
y = 0.06x + 0.52
r^2 = 0.46
p < 0.001
y = 0.03x + 0.53
r^2 = 0.51
p < 0.001
y = 0.25x + 2.05
r^2 = 0.57
p < 0.001
y = 0.19x + 2.00
r^2 = 0.62
p < 0.001
Species density
Species density



B
1.0
0.8
0.6
0.4
0.2
0.0
Day/night similarity
y = 0.0961x + 0.4774
r2 = 0.2767
p < 0.001
-3.0
-2.0
-1
0.0
1.0
2.0
low complexity
Habitat PC 1
high complexity

(Patrick & Swan, 2011)

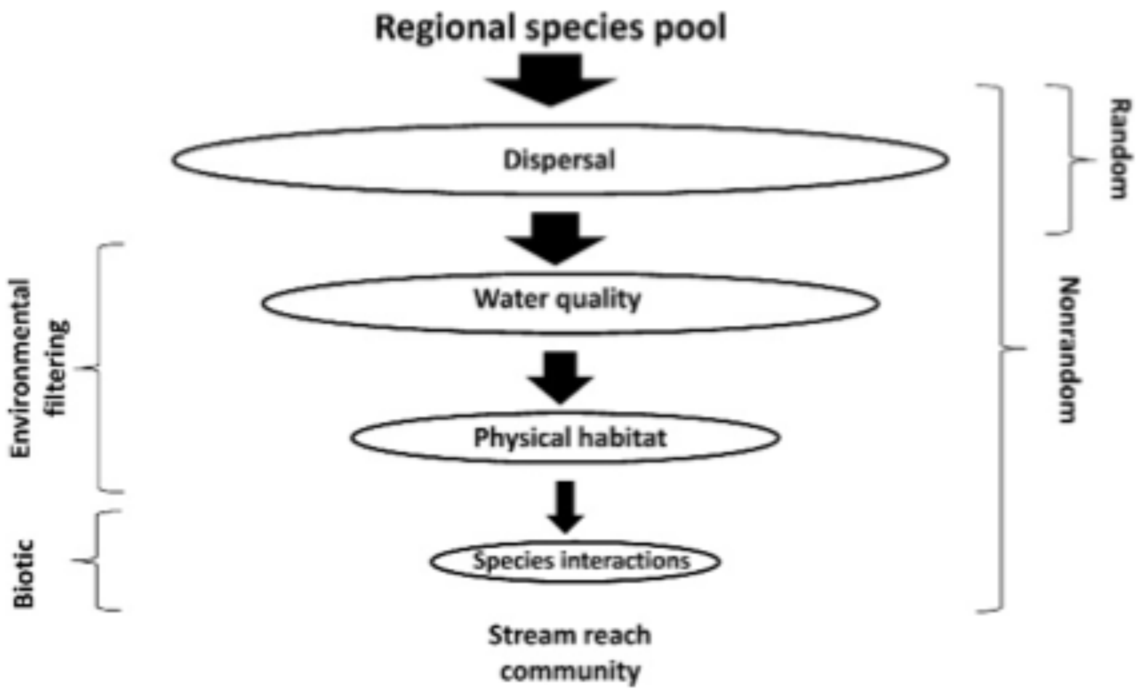


FIG. 1. Hierarchical-filtering model of community assembly. Potential colonists from the regional species pool must pass through a series of filters (dispersal, water quality [water character], physical habitat, interspecific interactions) before they become part of the equilibrium community in an individual stream reach (modified from Poff 1997).

Ecological Monographs, 84(1), 2014, pp. 91–107

Intercontinental comparison of fish ecomorphology: null model tests of community assembly at the patch scale in rivers

Carmen G. Montaña,[1,3] Kirk O. Winemiller,[1] and Andrew Sutton[2]

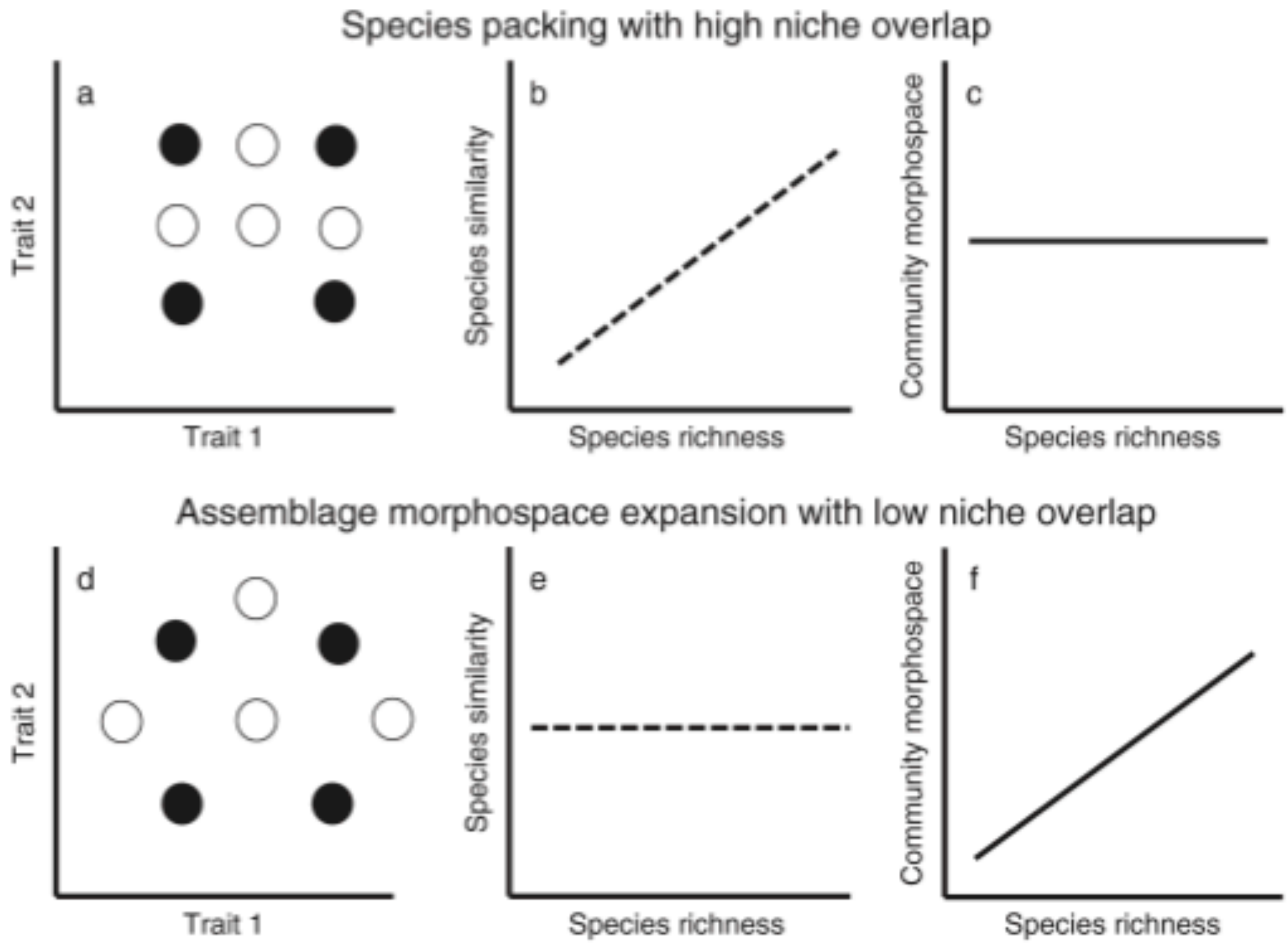
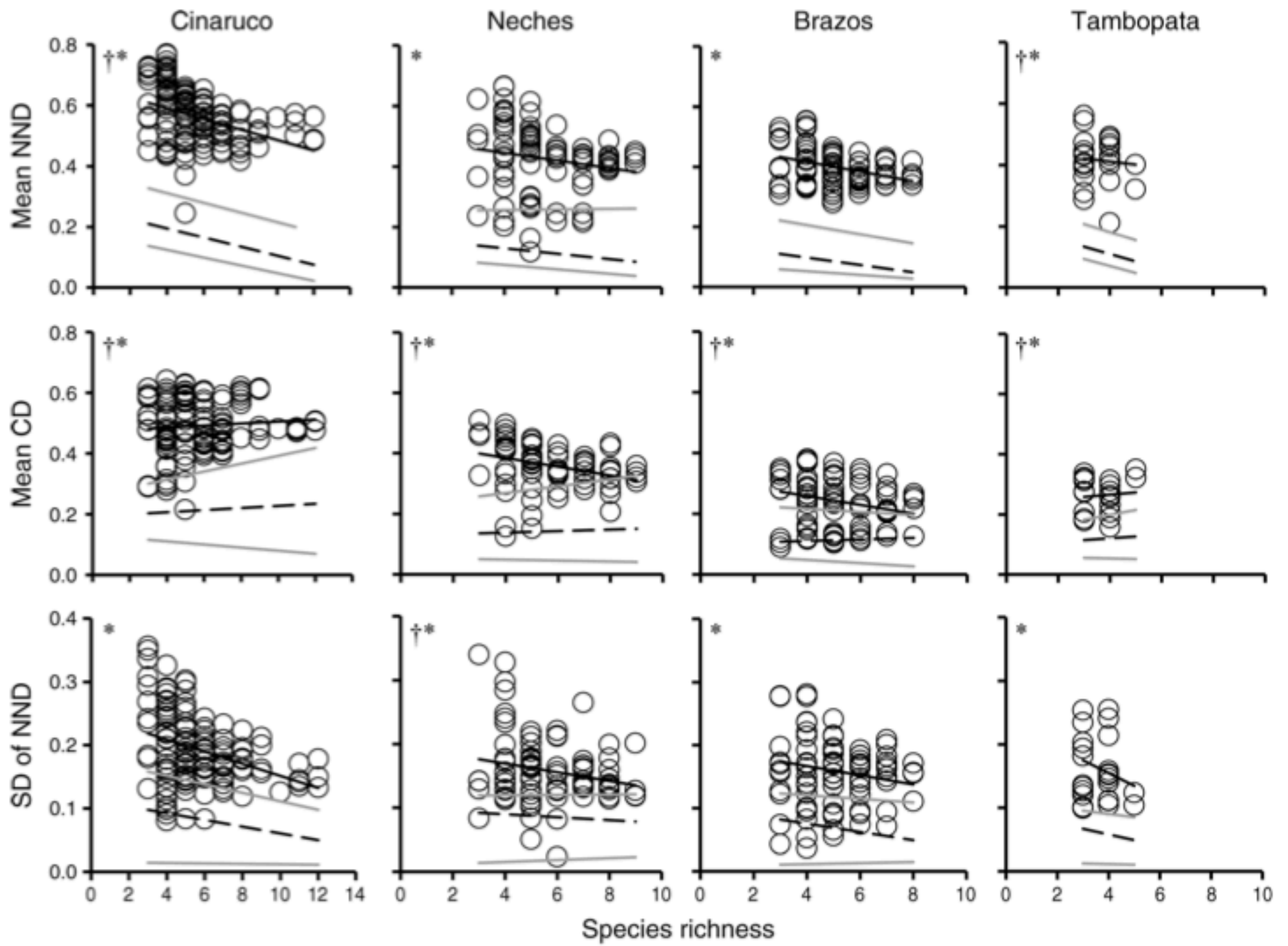


FIG. 1. Theoretical models of species distribution in morphological space and the relationships with species richness, showing original species in morphological space (solid circles), new species added (open circles), niche volume (solid lines), and species dissimilarities (dashed lines). (a–c) Under the niche compression model, average similarity among species increases as new species are added to the assemblage, with total morphological niche volume remaining relatively constant. (d–f) Under the niche expansion model, average differences among species remain relatively constant as new species are added, and assemblage morphological niche volume increases as species richness increases.

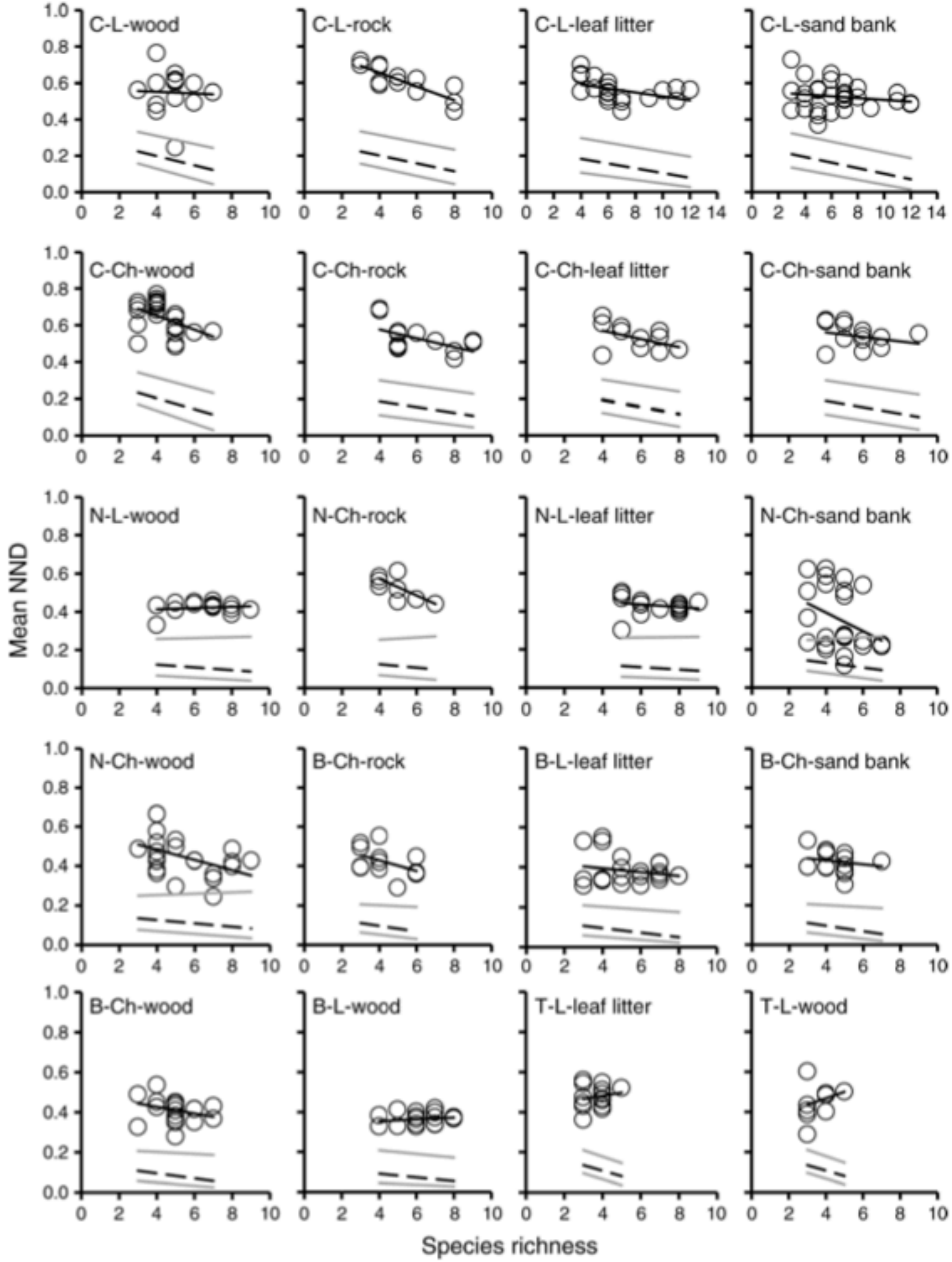


Cinaruco
Neches
Brazos
Tambopata
Mean NND
Mean CD
SD of NND
†*
*
Species richness

TABLE 3. Summary of nonrandom ecomorphological patterns of perciform assemblages within mesohabitats and macrohabitats of four rivers from temperate and tropical regions.

River and macrohabitat	Mesohabitat category	Nearest-neighbor distance		Size of morphospace		Greater evenness
		Packed	Overdispersed	No difference	Expansion	
Cinaruco						
Floodplain lake	wood		√		√	
Floodplain lake	leaf litter		√		√	
Floodplain lake	rocks		√		√	
Floodplain lake	sand bank		√		√	
Channel	wood		√		√	
Channel	leaf litter		√		√	
Channel	rocks		√		√	
Channel	sand bank		√		√	
Tambopata						
Floodplain lake	leaf litter		√	√		
Floodplain lake	wood		√		√	
Neches						
Floodplain lake	wood		√	√		
Channel	rocks		√	√		
Floodplain lake	leaf litter		√	√		
Channel	sand bank		√	√		
Channel	wood		√	√		
Brazos						
Channel	rocks		√	√		
Floodplain lake	leaf litter		√	√		
Channel	sand bank		√	√		
Channel	wood		√	√		
Floodplain lake	wood		√	√		
Number of cases		0	20	11	9	0

Note: A check mark (√) indicates support for the pattern.

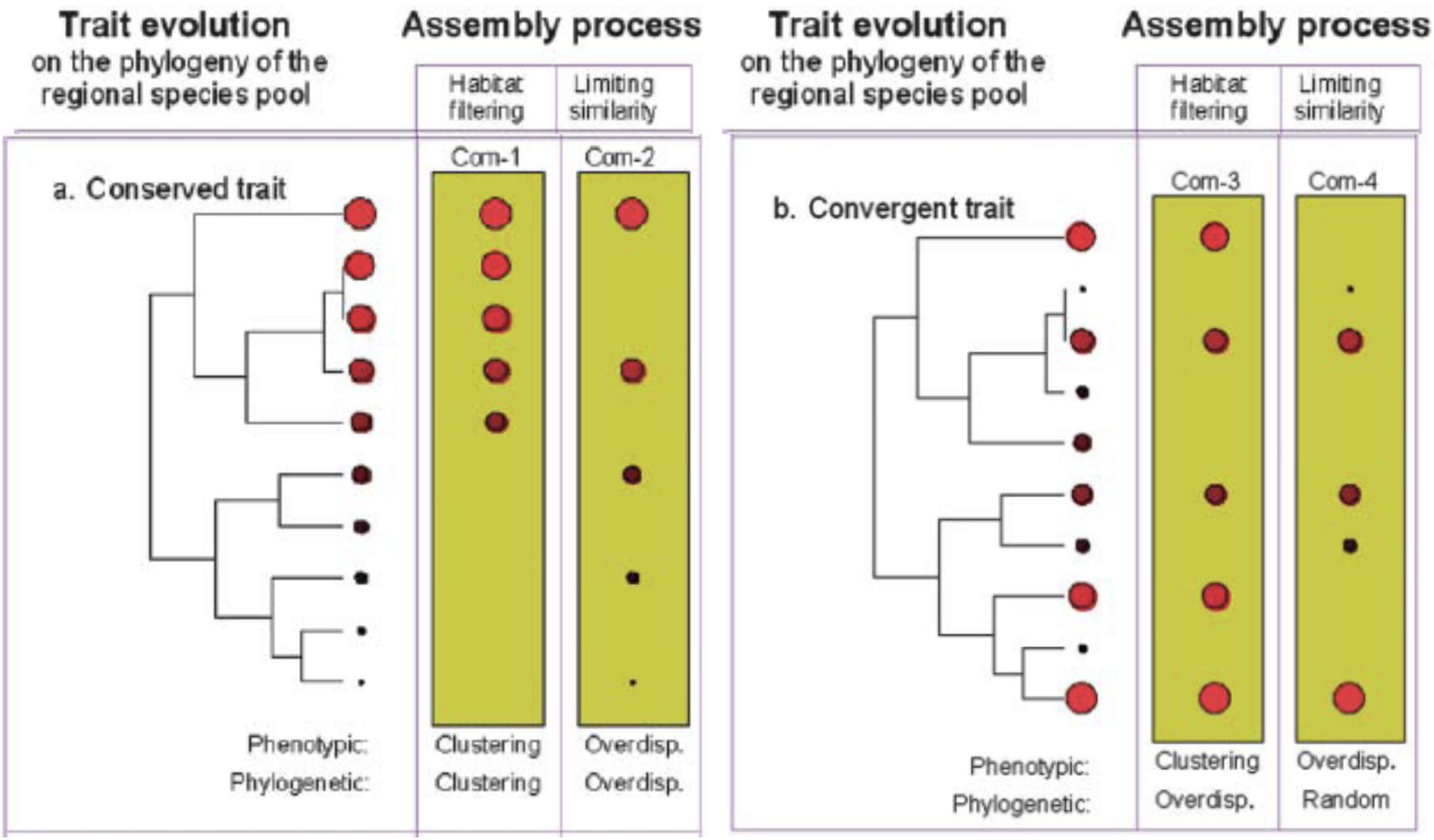


C-L-wood
C-L-rock
C-L-leaf litter
C-L-sand bank
C-Ch-wood
C-Ch-rock
C-Ch-leaf litter
C-Ch-sand bank
N-L-wood
N-Ch-rock
N-L-leaf litter
N-Ch-sand bank
N-Ch-wood
B-Ch-rock
B-L-leaf litter
B-Ch-sand bank
B-Ch-wood
B-L-wood
T-L-leaf litter
T-L-wood
Mean NND
Species richness

TABLE 4. Summary of support for alternative ecomorphological patterns in relation to species richness of perciform assemblages within mesohabitat patches in tropical and temperate rivers.

River and macrohabitat	Mesohabitat category	Nearest-neighbor distance		Size of morphospace		
		Packed	Overdispersed	No difference	Expansion	Greater evenness
Cinaruco						
Floodplain lake	wood			√		
Floodplain lake	leaf litter		√	√		
Floodplain lake	rocks	√		√		√
Floodplain lake	sand bank		√	√		√
Channel	wood			√		
Channel	leaf litter		√	√		
Channel	rocks	√			√	√
Channel	sand bank			√		
Tambopata						
Floodplain lake	leaf litter			√		
Floodplain lake	wood			√		
Neches						
Floodplain lake	wood			√		
Channel	rocks	√		√		√
Floodplain lake	leaf litter			√		
Channel	sand bank		√	√		√
Channel	wood			√		√
Brazos						
Channel	rocks	√		√		√
Floodplain lake	leaf litter		√	√		
Channel	sand bank		√	√		
Channel	wood	√		√		
Floodplain lake	wood		√	√		√
Number of cases		5	7	19	1	8

Notes: When the regression for mean nearest-neighbor distance (NND) had a statistically lower slope than expected at random, species packing with high niche overlap is supported (average similarity increases with species richness); if the regression slope has a significantly higher slope than expected at random, then limiting similarity is supported. When the regression slope of mean distance to the assemblage centroid (CD) was significantly higher than expected at random, greater species richness was associated with expansion of assemblage morphospace. Increased evenness of species dispersion within ecomorphological space with increasing species richness was supported by a negative trend in standard deviation of NND with a regression slope lower than expected at random. A check mark (√) indicates support for the pattern.


Trait evolution
on the phylogeny of the regional species pool
Assembly process
Habitat filtering
Limiting similarity
Com-1
Com-2
a. Conserved trait
Phenotypic:
Phylogenetic:
Clustering
Clustering
Overdisp.
Overdisp.
Trait evolution
on the phylogeny of the regional species pool
Assembly process
Habitat filtering
Limiting similarity
Com-3
Com-4
b. Convergent trait
Phenotypic:
Phylogenetic:
Clustering
Overdisp.
Overdisp.
Random

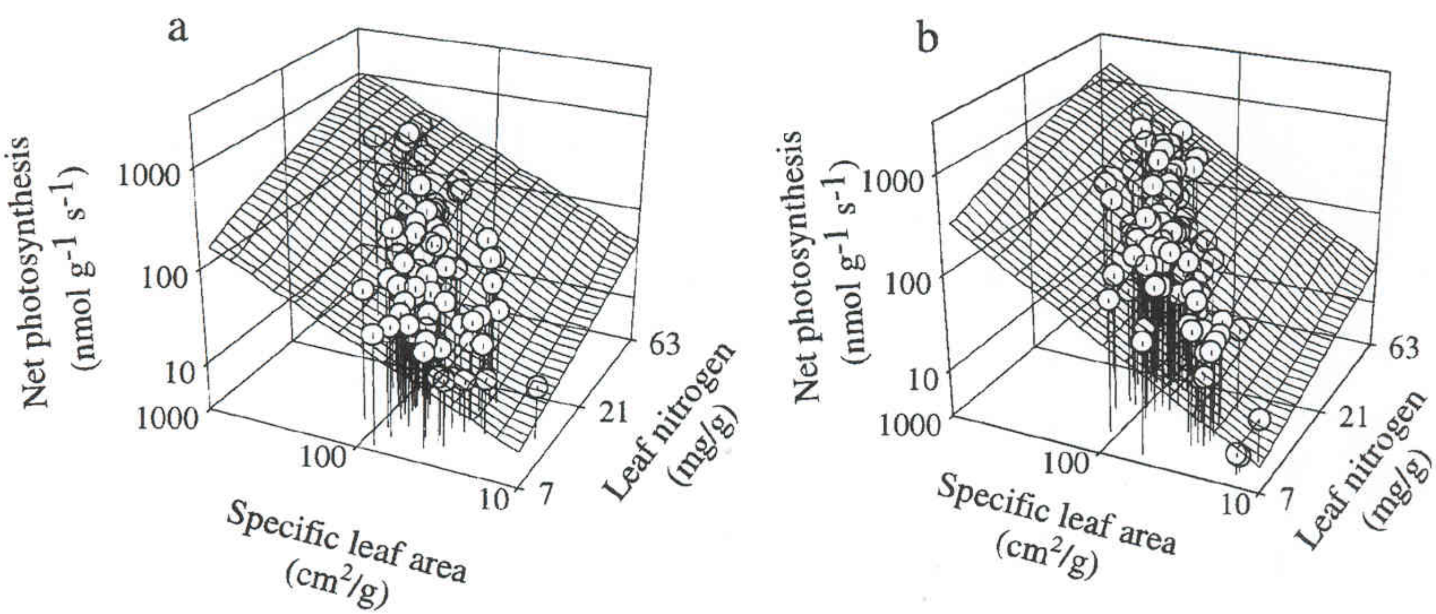
Assembly of Biotic Communities:

Convergence (Functional Similarity)

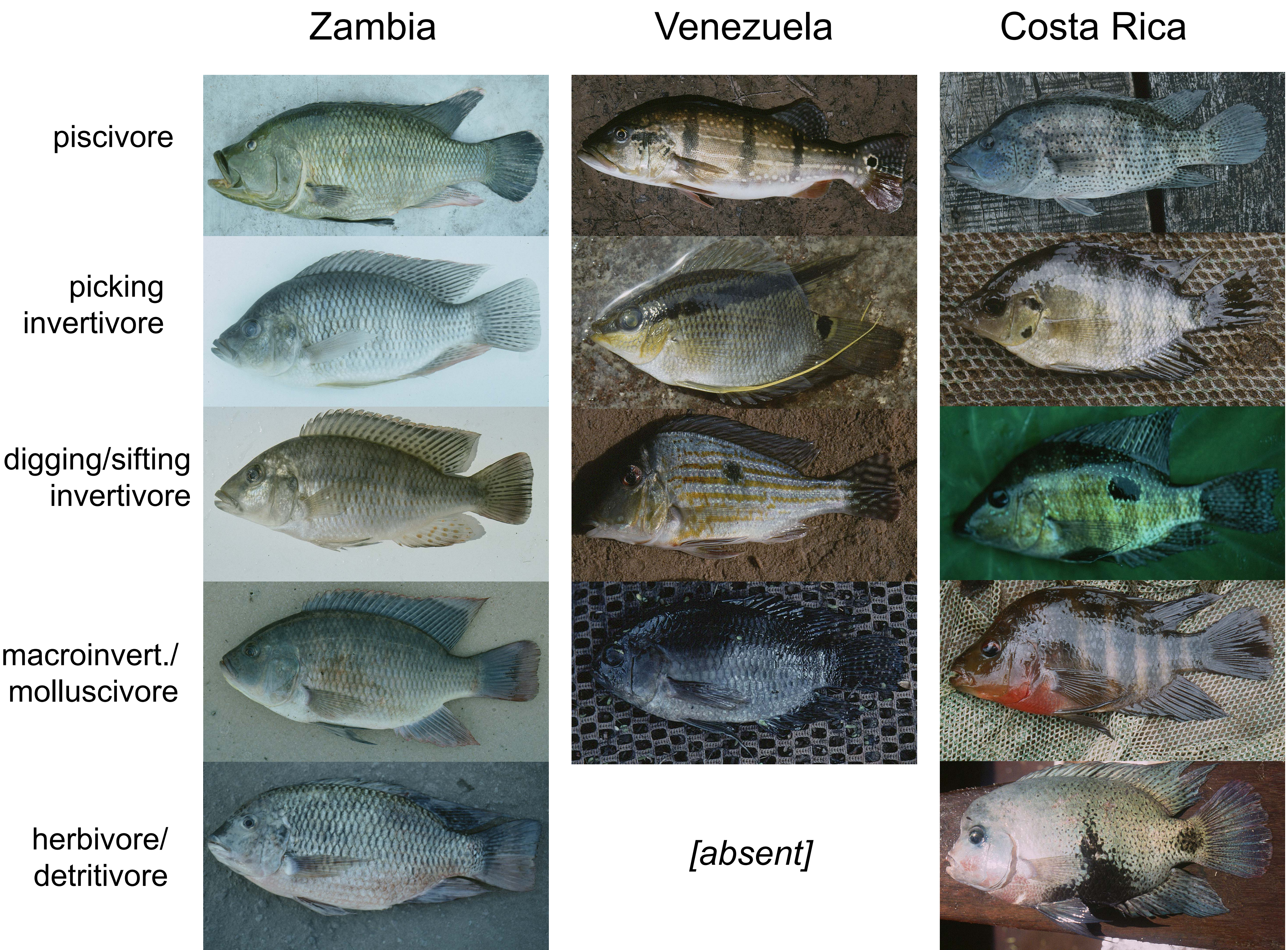
- Species
- Local Assemblages
- Regional Faunas

Reich, P.B., et al. 1997. From tropics to tundra: global convergence in plant functioning. *PNAS,USA* 94:13730-13734.

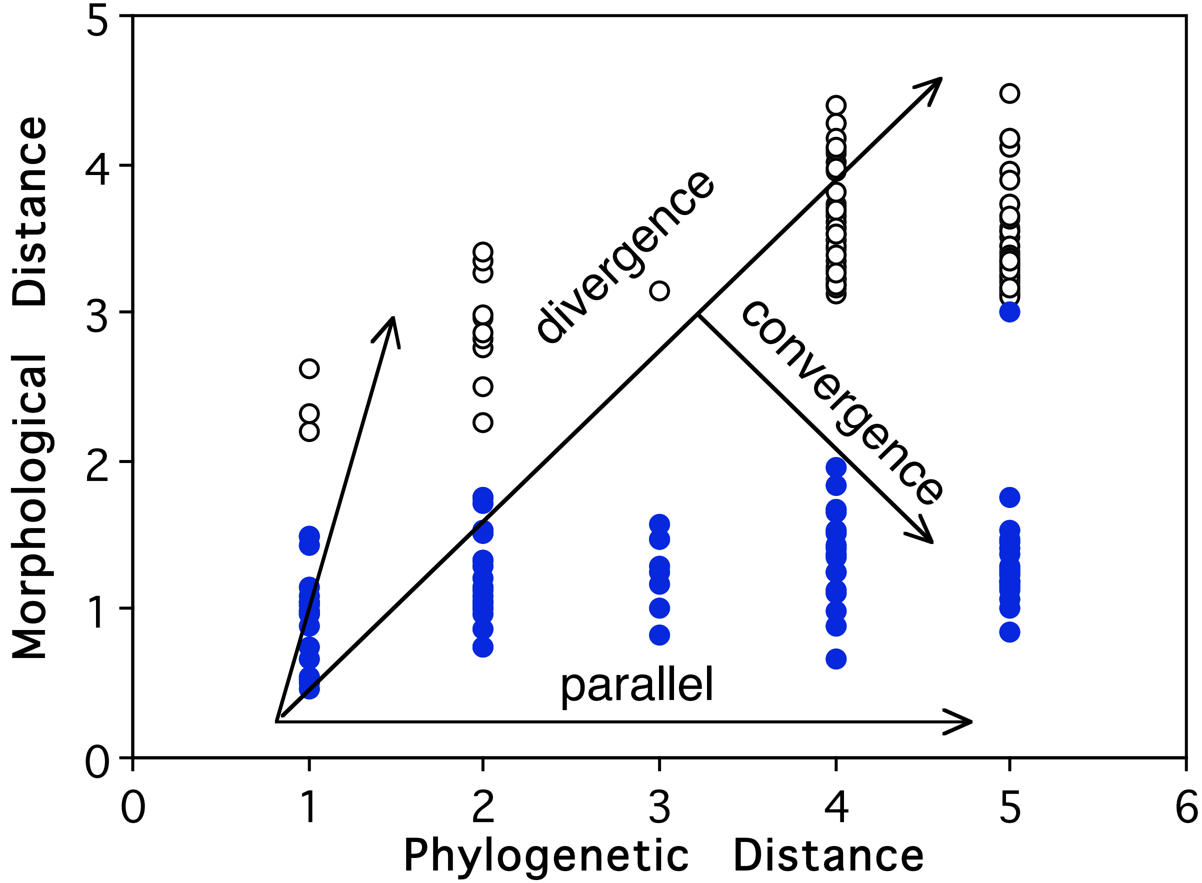
"Despite striking differences in climate, soils & evolutionary history among diverse biomes ranging from tropical & temperate forests to alpine tundra & desert, we found similar interspecific relationships among leaf structure & function & plant growth in all biomes."



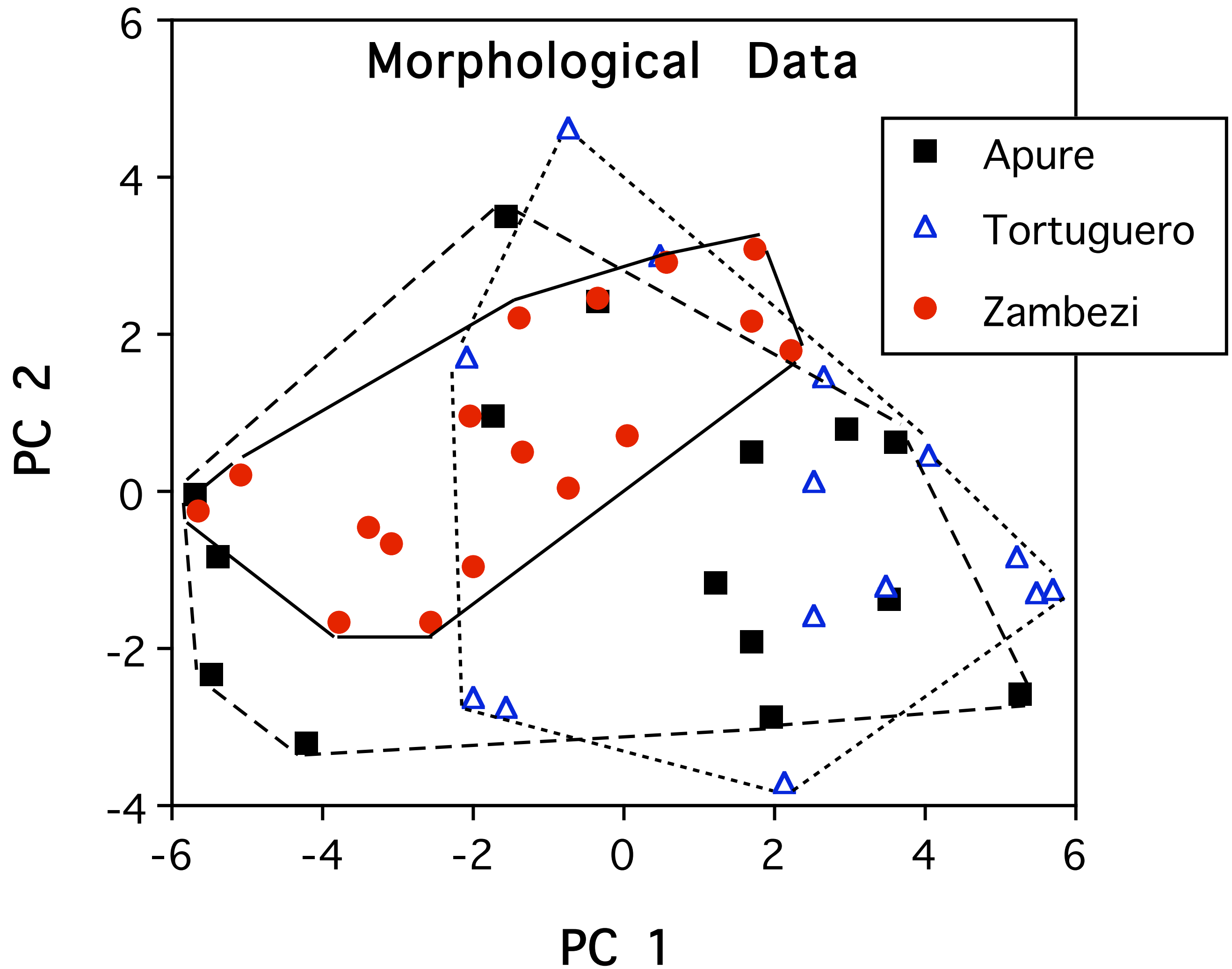
Convergent Cichlid Fishes



Cichlid fishes in fluviatile habitats show both ecomorphological divergence (adaptive radiations) & parallel and/or convergent evolution. (Winemiller et al. 1995, *Env. Biol. Fish.* 44:235-261).

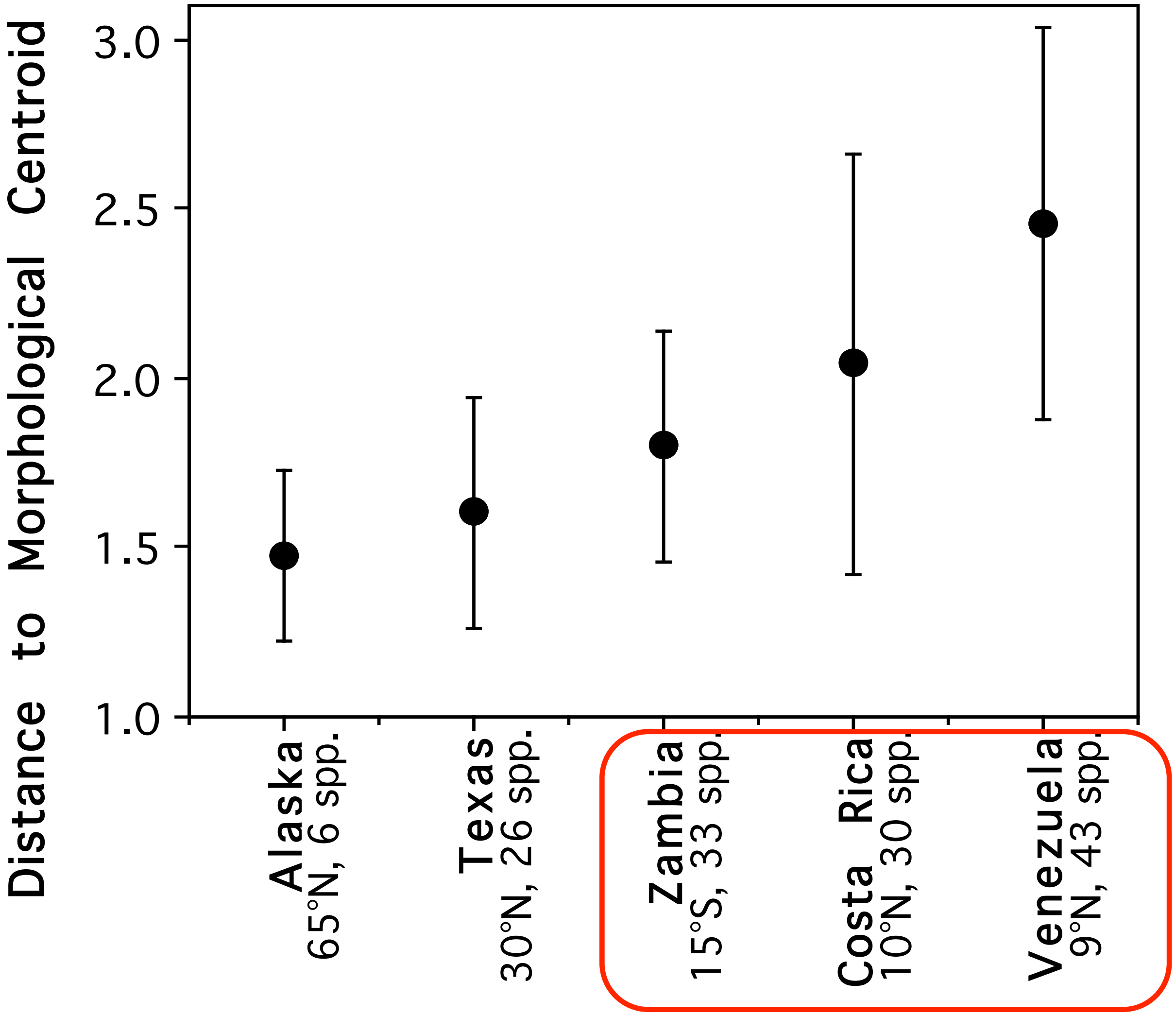


Eco-morpho space occupied by fluviatile cichlids in 3 regional assemblages overlaps broadly.



Yet, there is not 100% ecological equivalency between cichlids from comparable habitats in these 3 tropical regions.

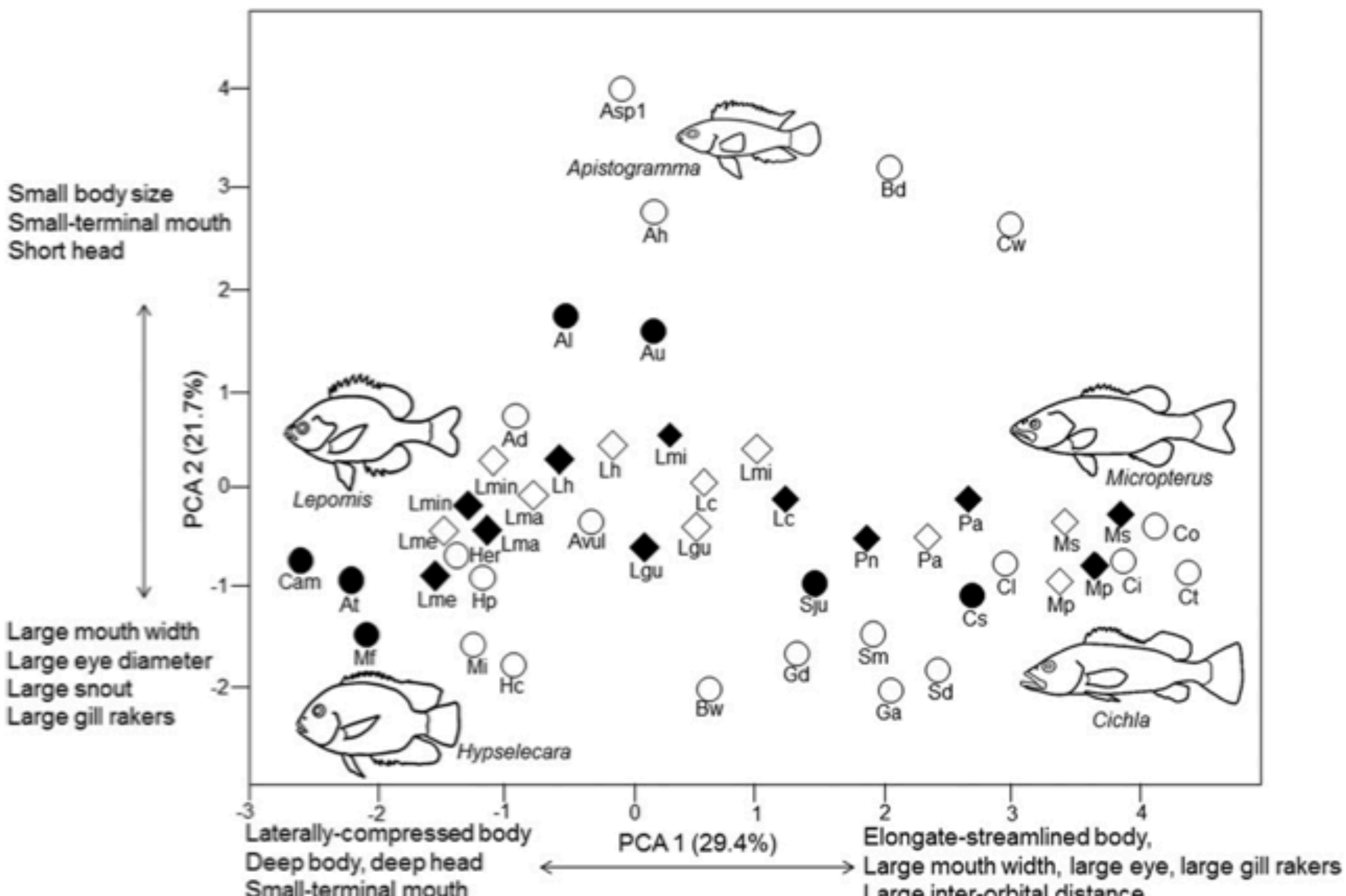
Ecomorphological diversity is greater in more species-rich tropical fish assemblages.

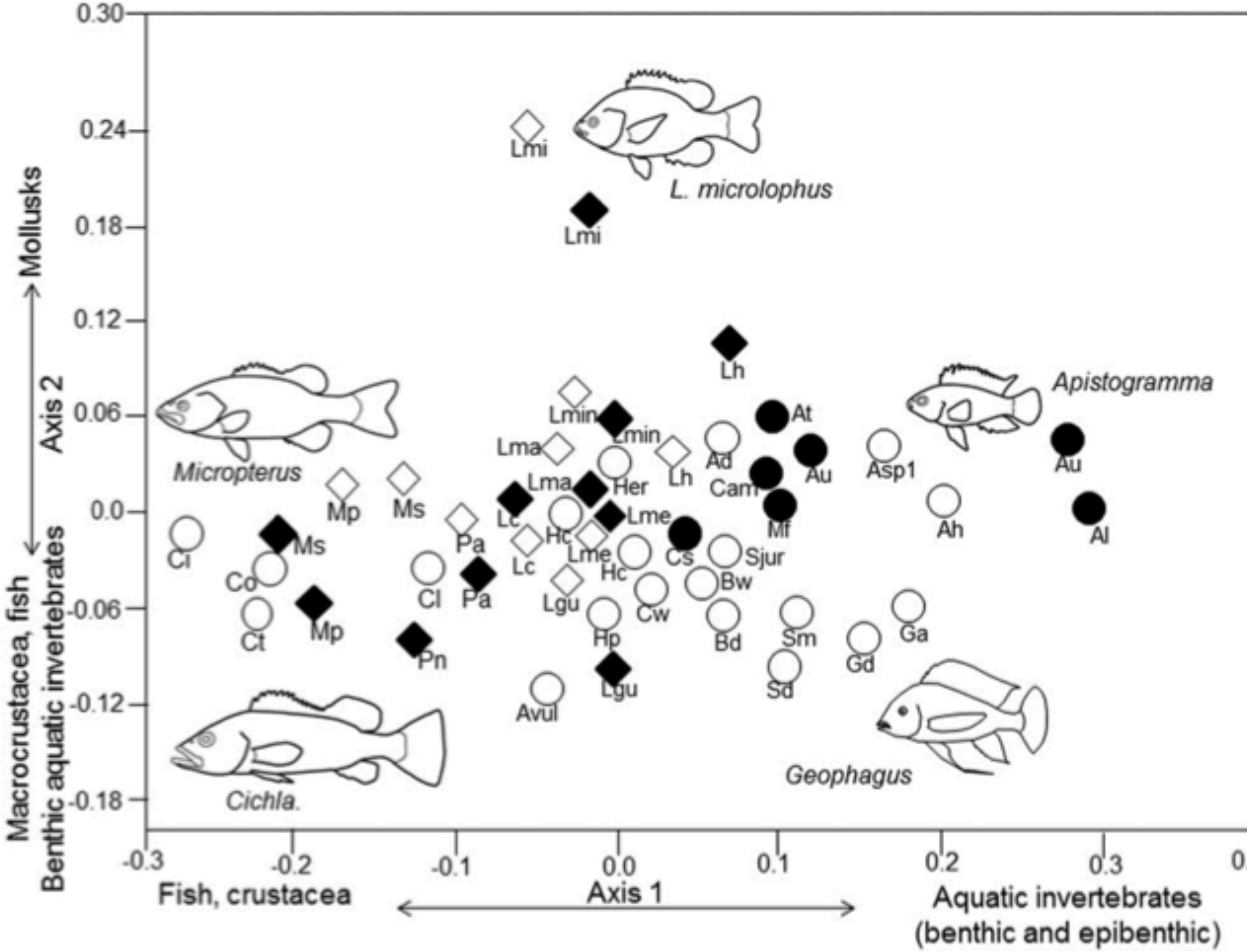


Biological Journal of the Linnean Society, 2013, **109**, 146–164. With 5 figures

Evolutionary convergence in Neotropical cichlids and Nearctic centrarchids: evidence from morphology, diet, and stable isotope analysis

CARMEN G. MONTAÑA* and KIRK O. WINEMILLER





Mollusks
Axis 2
Macrocrustacea, fish
Benthic aquatic invertebrates
Fish, crustacea
Axis 1
Aquatic invertebrates
(benthic and epibenthic)
L. microlophus
Micropterus
Cichla.
Apistogramma
Geophagus
0.30
0.24
0.18
0.12
0.06
0.0
-0.06
-0.12
-0.18
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
Lmi
Lmi
Lh
Lh
Lmin
Lmin
Lma
Lma
Lme
Lme
Lc
Lc
Lgu
Lgu
Mp
Mp
Ms
Ms
Pa
Pa
Pn
Ci
Co
Ct
Cl
Hc
Hc
Her
Hp
Avul
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Cs
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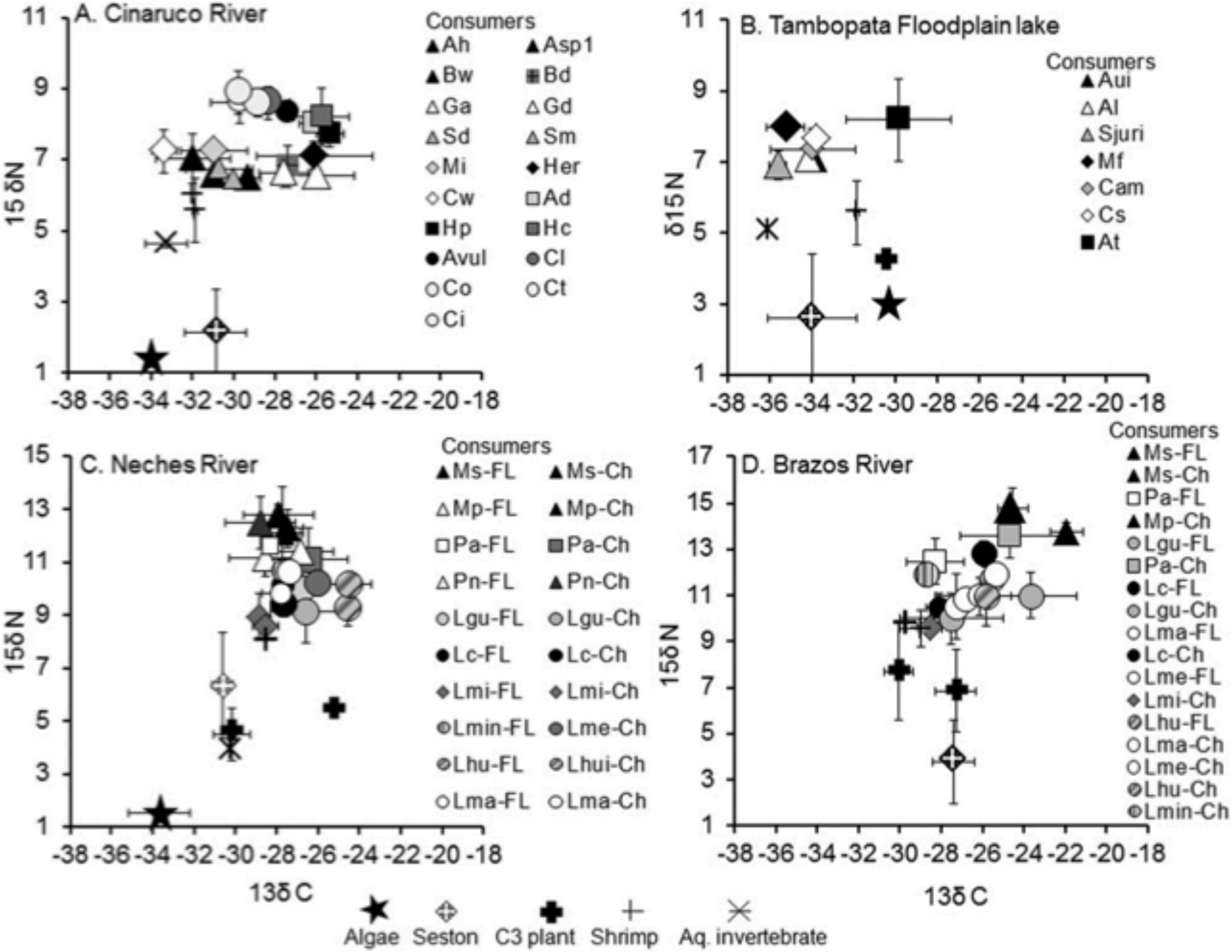
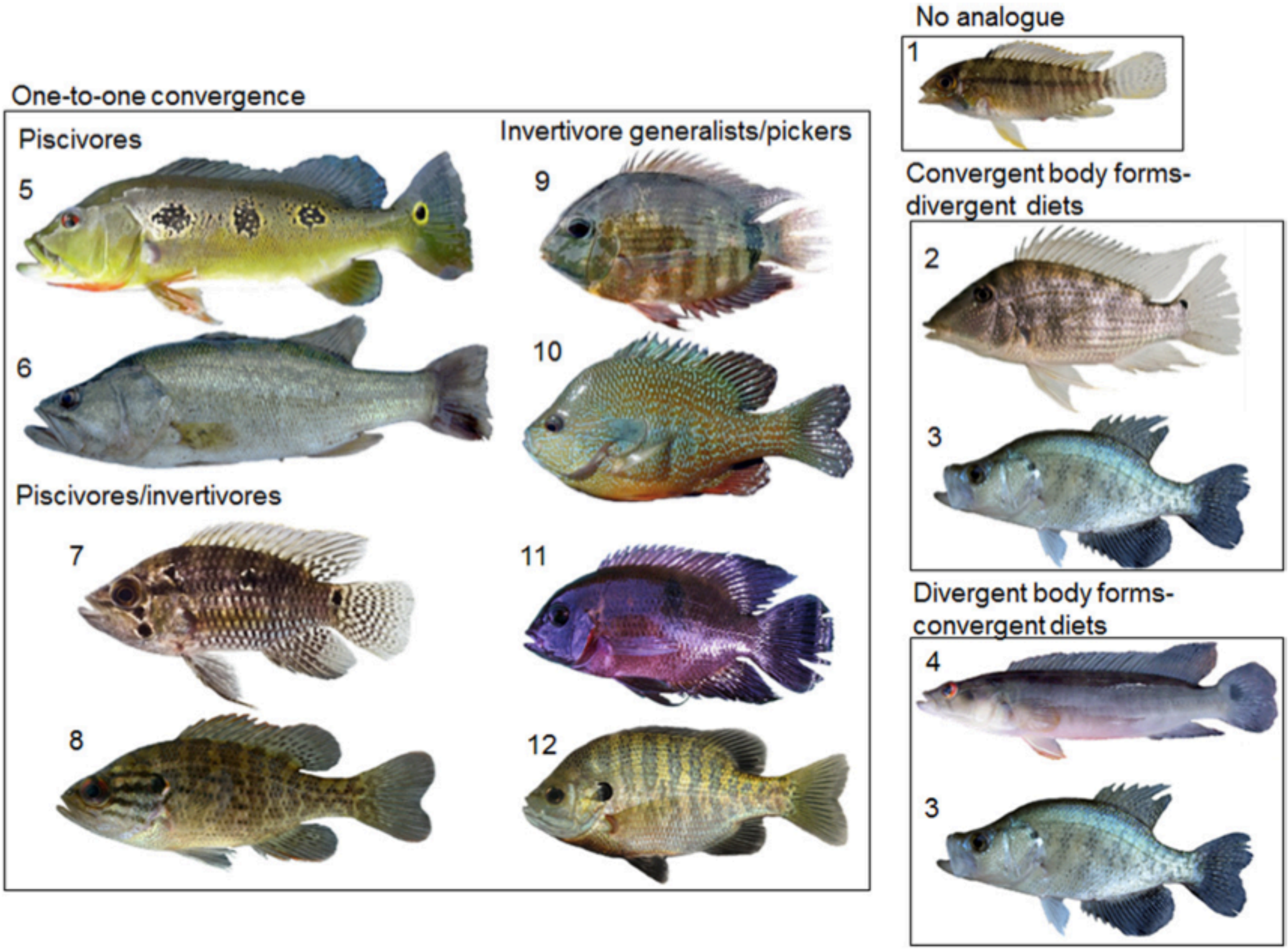
At
Au
Au
Mf
Asp1
Ah
Al
Sjur
Bw
Bd
Sm
Sd
Gd
Ga


A. Cinaruco River
15 δN
Consumers
Ah
Asp1
Bw
Bd
Ga
Gd
Sd
Sm
Mi
Her
Cw
Ad
Hp
Hc
Avul
Cl
Co
Ct
Ci
B. Tambopata Floodplain lake
δ15N
Consumers
Aui
Al
Sjuri
Mf
Cam
Cs
At
C. Neches River
15δN
Consumers
Ms-FL
Ms-Ch
Mp-FL
Mp-Ch
Pa-FL
Pa-Ch
Pn-FL
Pn-Ch
Lgu-FL
Lgu-Ch
Lc-FL
Lc-Ch
Lmi-FL
Lmi-Ch
Lmin-FL
Lme-Ch
Lhu-FL
Lhui-Ch
Lma-FL
Lma-Ch
13δ C
D. Brazos River
15δN
Consumers
Ms-FL
Ms-Ch
Pa-FL
Mp-Ch
Lgu-FL
Pa-Ch
Lc-FL
Lgu-Ch
Lma-FL
Lc-Ch
Lme-FL
Lmi-Ch
Lhu-FL
Lma-Ch
Lme-Ch
Lhu-Ch
Lmin-Ch
13δ C
Algae
Seston
C3 plant
Shrimp
Aq. invertebrate


No analogue
1
One-to-one convergence
Piscivores
5
6
Piscivores/invertivores
7
8
Invertivore generalists/pickers
9
10
11
12
Convergent body forms-
divergent diets
2
3
Divergent body forms-
convergent diets
4
3

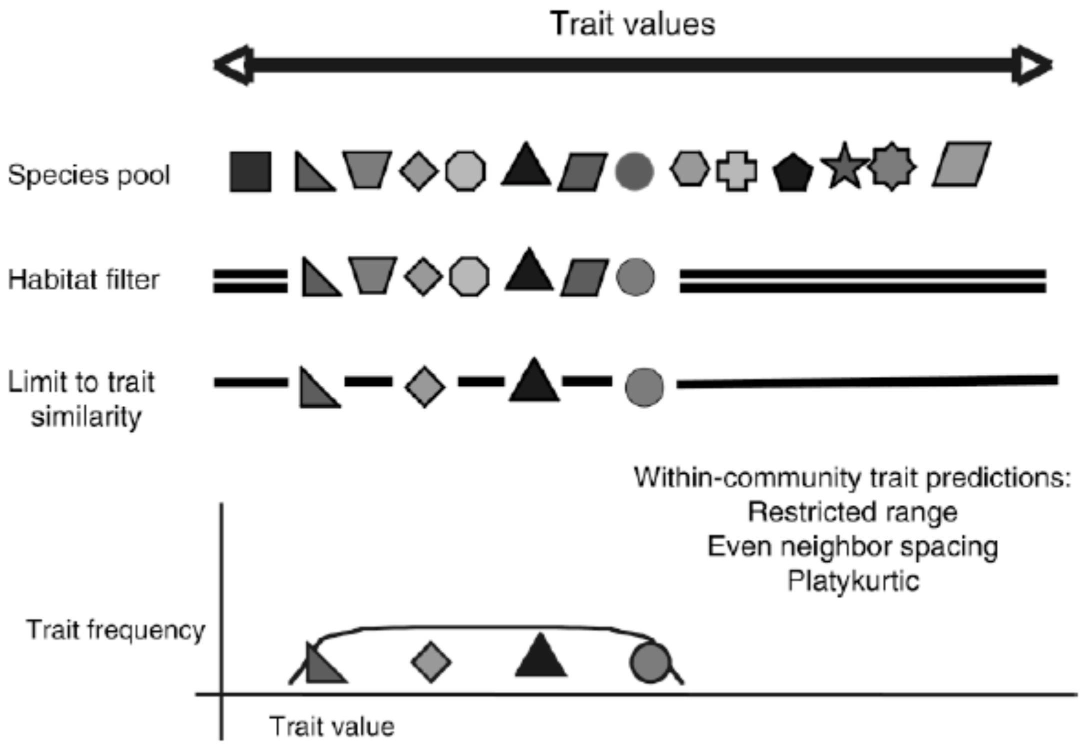


FIG. 1. A hypothesis for assembly effects on within-community trait distribution (following Diaz et al. [1998] and Weiher et al. [1998]). The strength of the habitat filter and limiting similarity is expected to depend on the identity of the trait in combination with the particular abiotic conditions at a site. Note that habitat filtering is hypothesized to affect the range of trait values; limiting similarity will affect the spacing and lead to a platykurtic (that is, flat-topped) distribution.

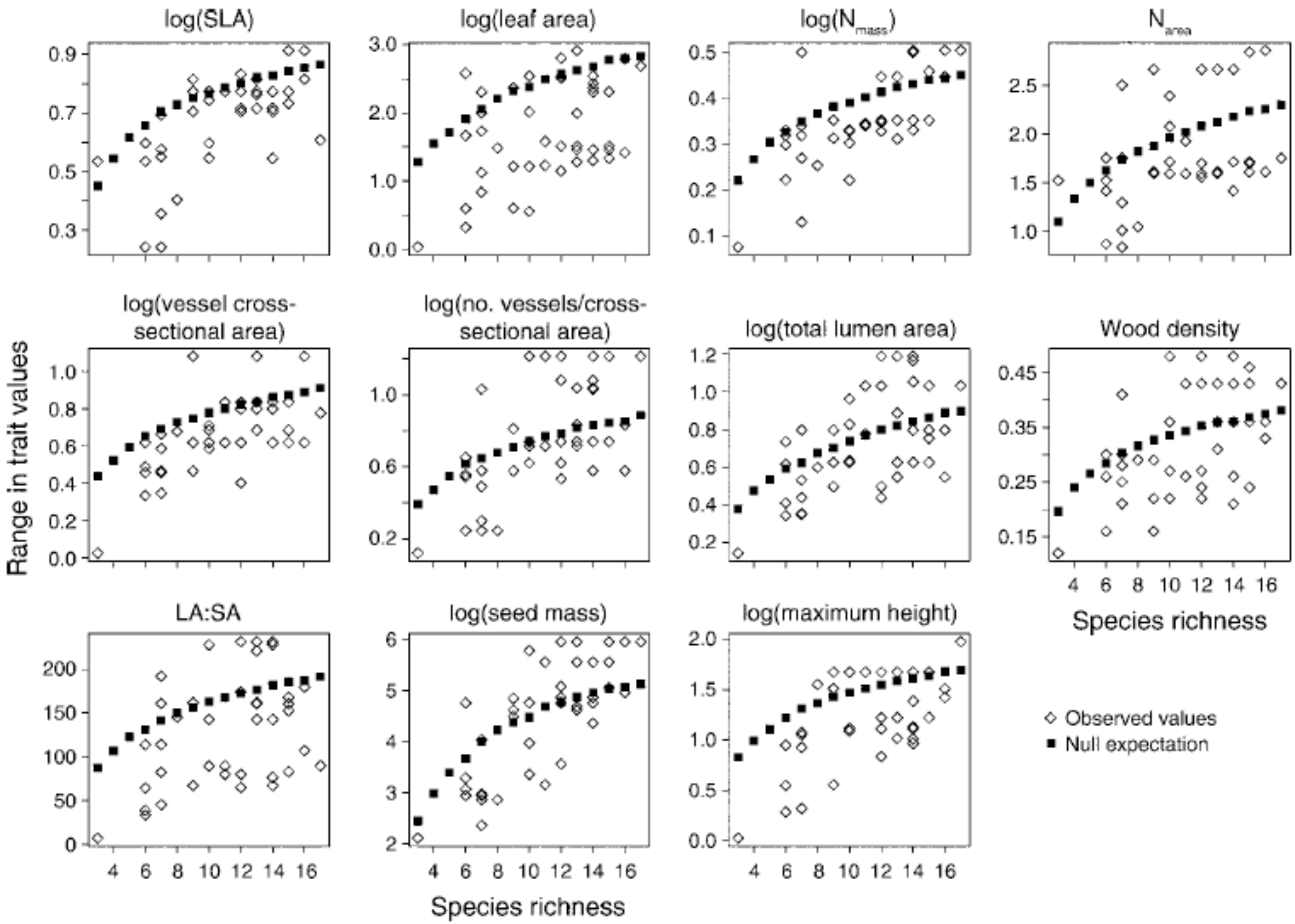
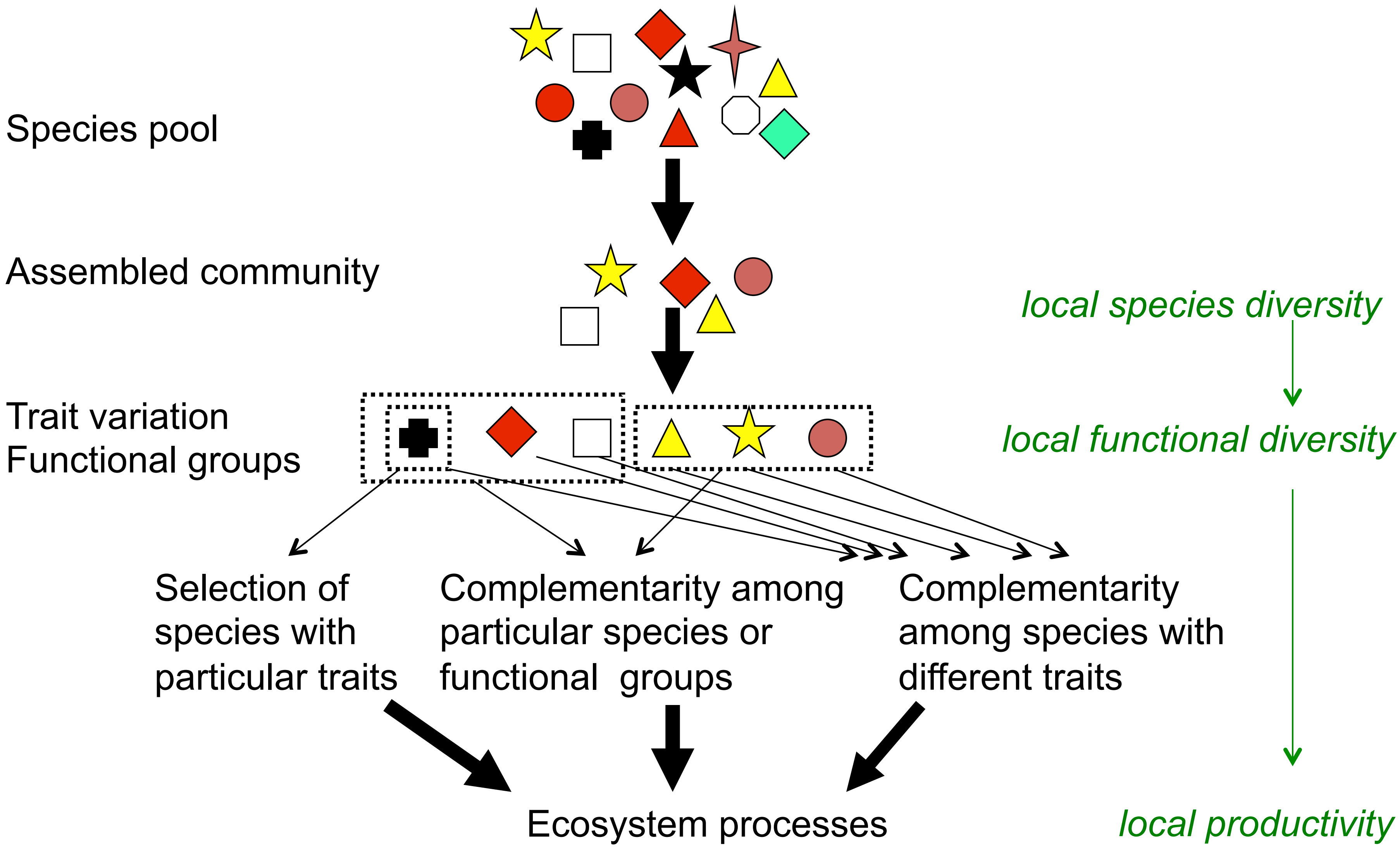
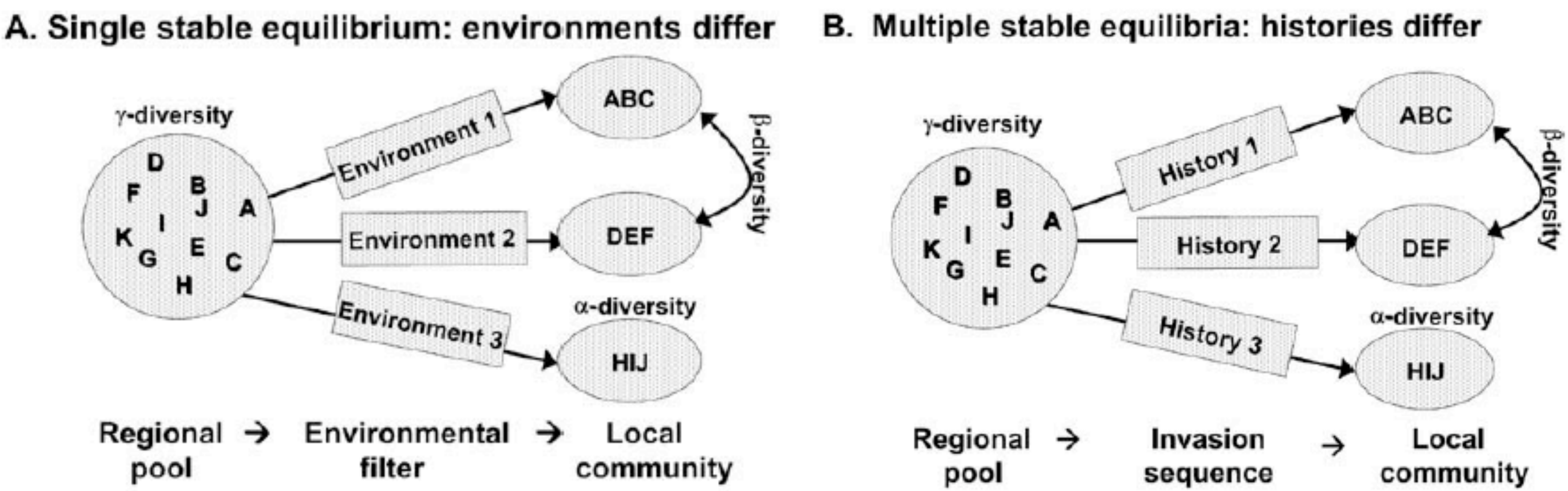


FIG. 4. The community-wide range of values for 11 leaf and stem traits at different levels of species richness. Open diamonds show the observed values for 44 plots; solid squares show the mean of 9999 null model trials at each of the corresponding levels of species richness. See Table 1 for a description of the traits; note that data have been log-transformed for all except N_{area}, wood density, and LA:SA.

M. Loreau, et al. 2002. Perspectives & challenges. p. 237-242 in *Biodiversity and Ecosystem Functioning*, M. Loreau et al., eds., Oxford University Press.



Chase, J.M. 2003. Community assembly: when should history matter? *Oecologia* 136:489-498.



(Chase, J.M. 2003. *Oecologia* 136:489-498)

Regional factors

- Size of regional species pool
- Rate of dispersal within region

Local factors

- Primary production
- Rate of disturbance

He tested the influence of factors by comparing macroscopic animals in ponds in the Midwestern U.S.

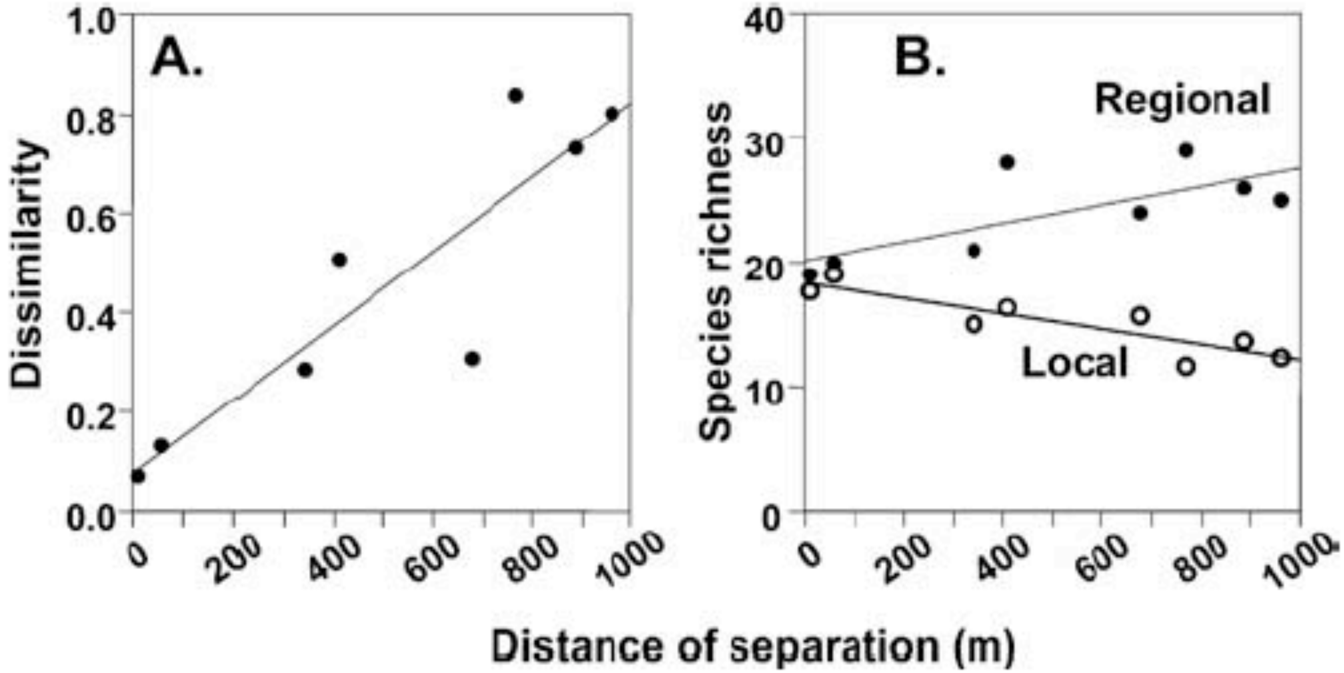
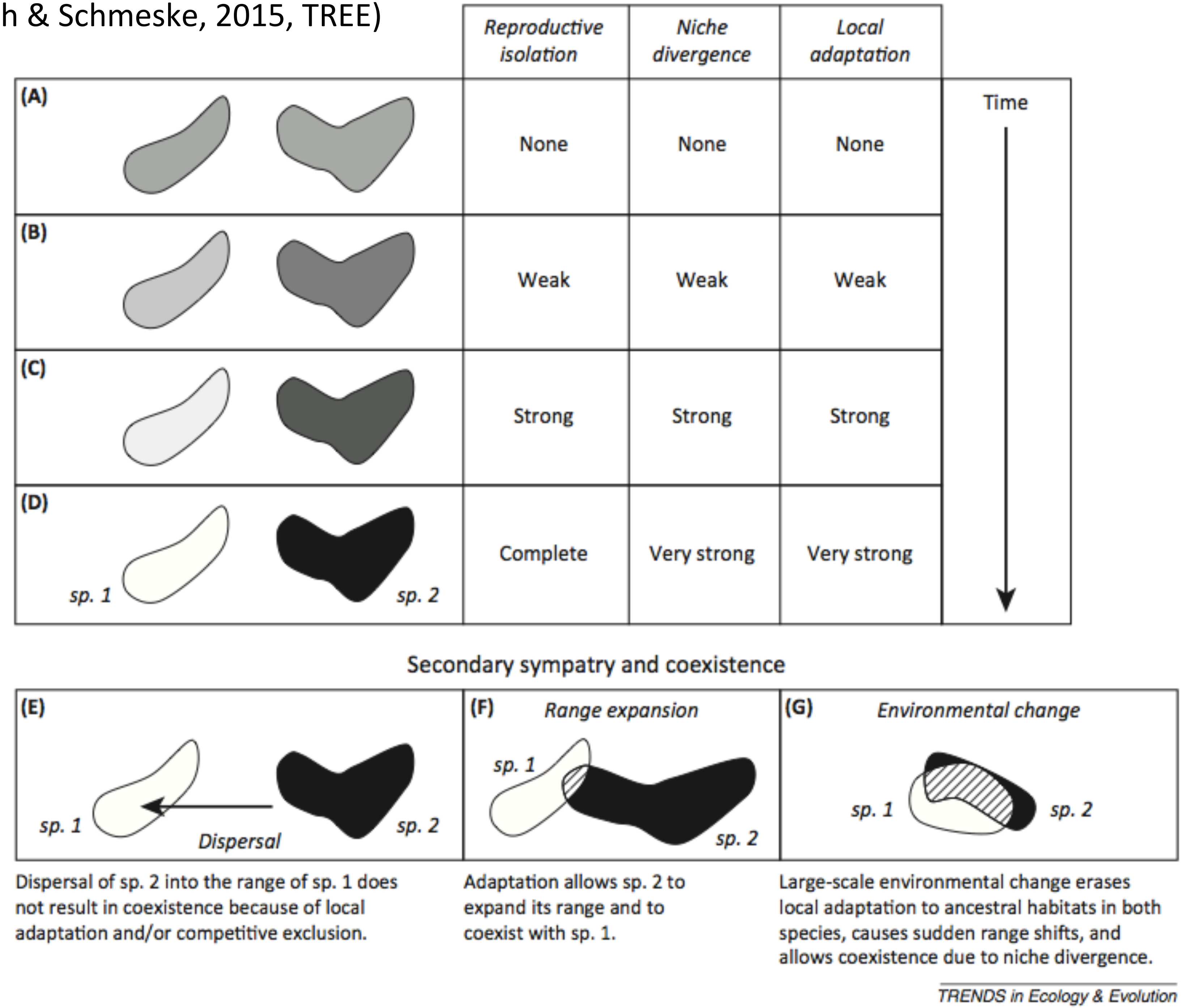
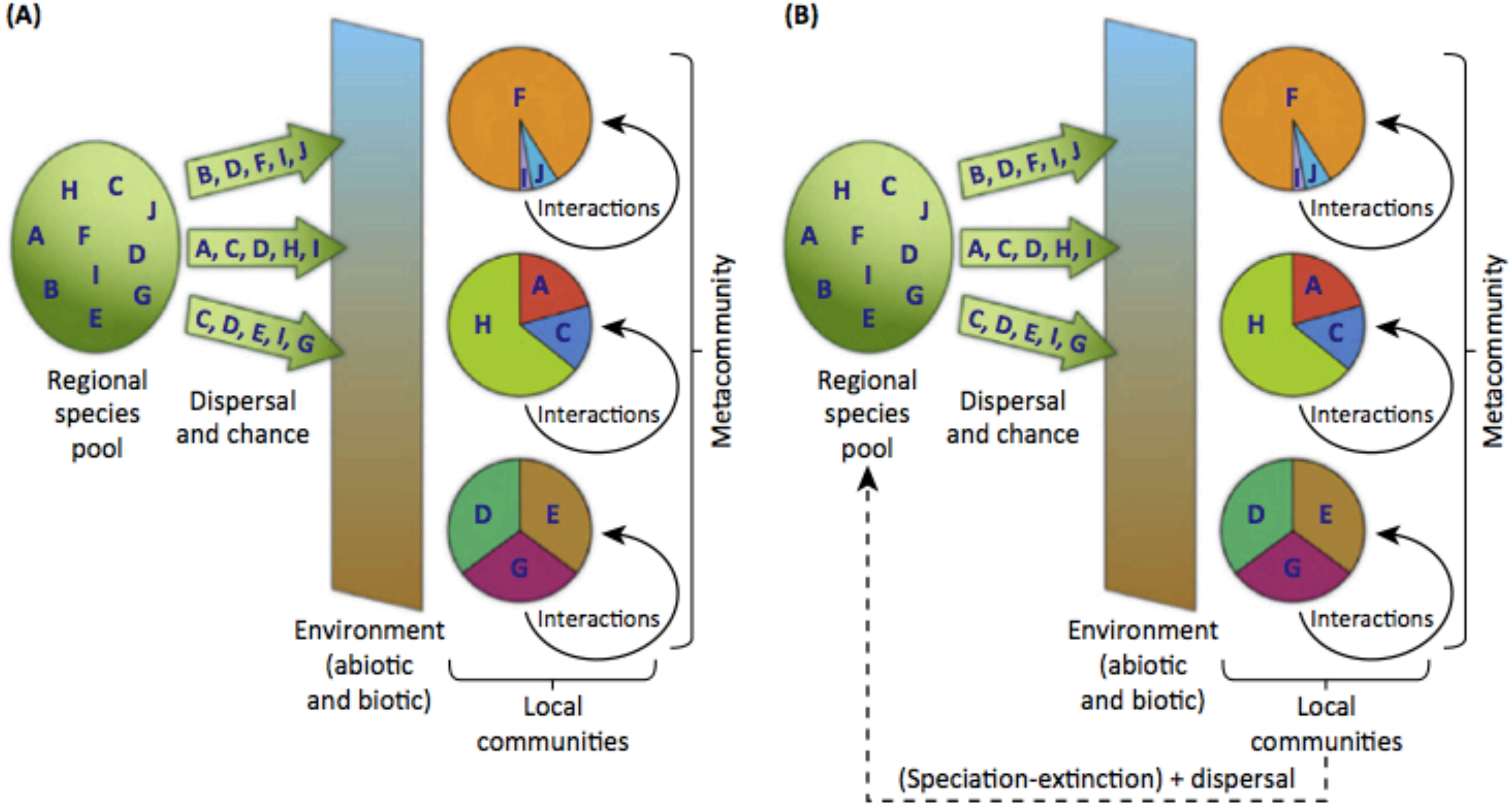


Fig. 2. A The relationship between average interpond distance and regional dissimilarity. The slope of the relationship is significantly positive (regression: n=8, r^2=0.80, P<0.003). **B** The relationship between average interpond distance and average local and regional species richness. Average local richness is negatively related to interpond distance (regression: n=8, r^2=0.75, P<0.004), whereas regional richness is positively related to interpond distance (regression: n=8, r^2=0.45, P<0.04)

(Mittelbach & Schmeske, 2015, TREE)





TRENDS in Ecology & Evolution

Freshwater Biology (2012) **57**, 1060–1075 doi:10.1111/j.1365-2427.2012.02768.x

Functional diversity and trait–environment relationships of stream fish assemblages in a large tropical catchment

ALLISON A. PEASE*, ALFONSO A. GONZÁLEZ-DÍAZ†, ROCÍO RODILES-HERNÁNDEZ† AND KIRK O. WINEMILLER*

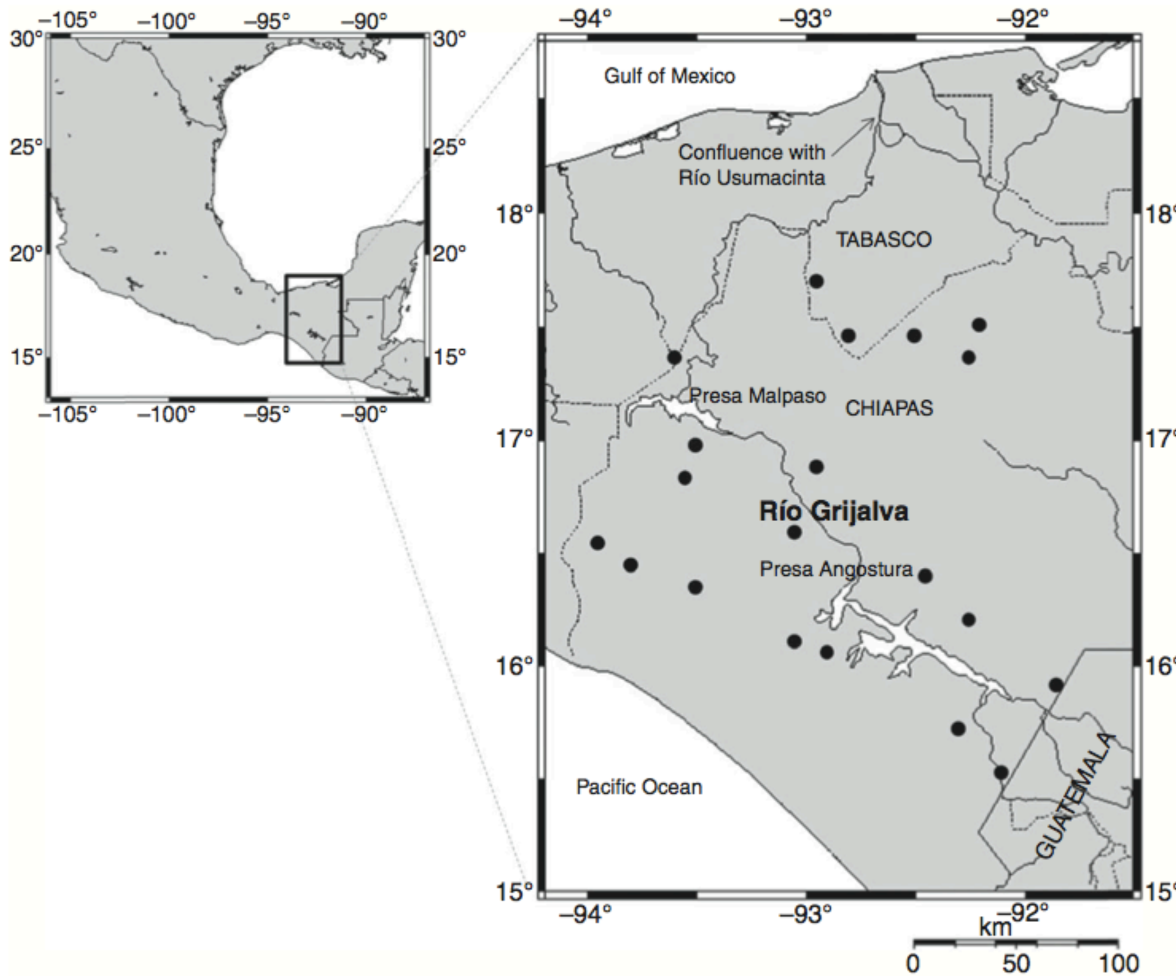


Fig. 1 Map of the study region, the Río Grijalva Basin, in Chiapas and Tabasco, Mexico. Solid dots indicate locations of surveyed stream reaches.

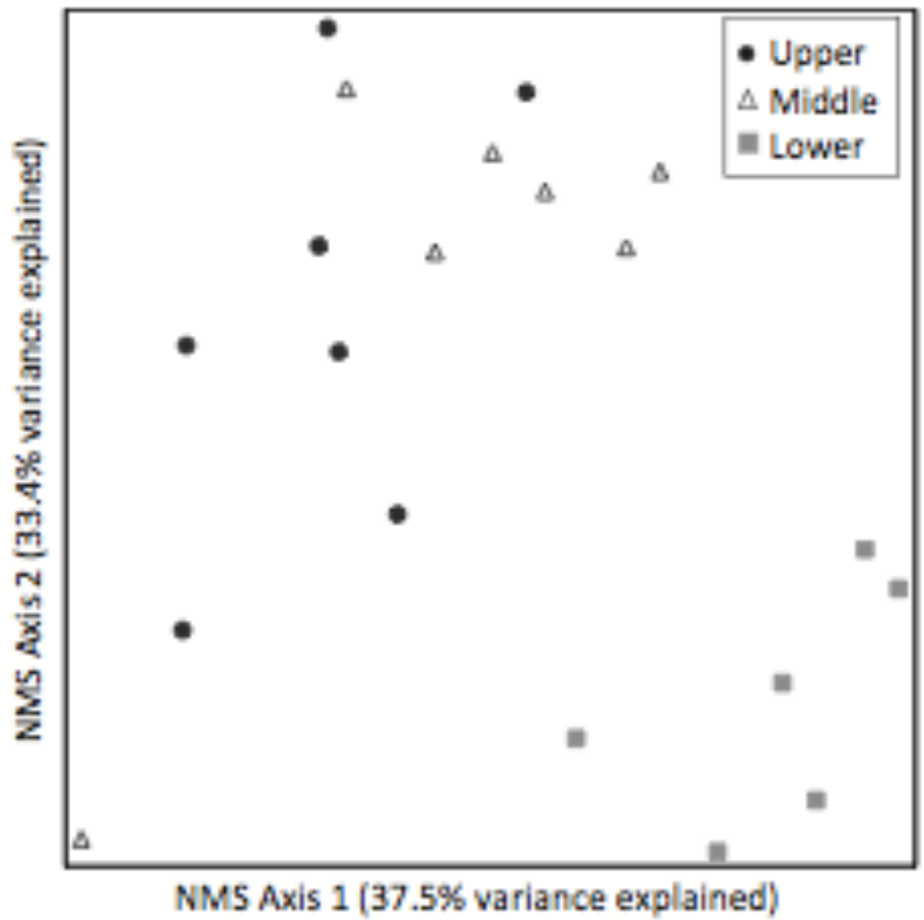
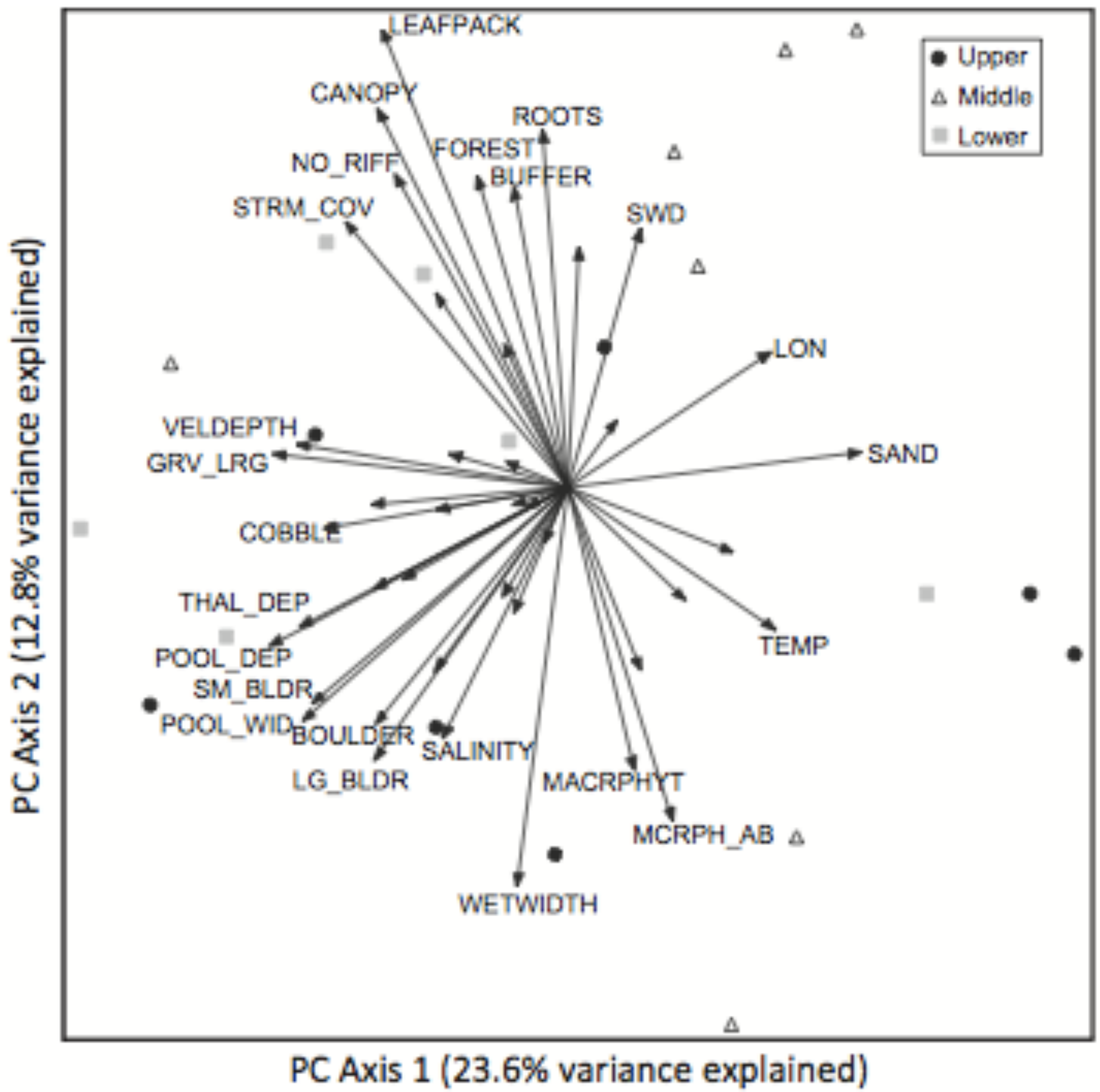
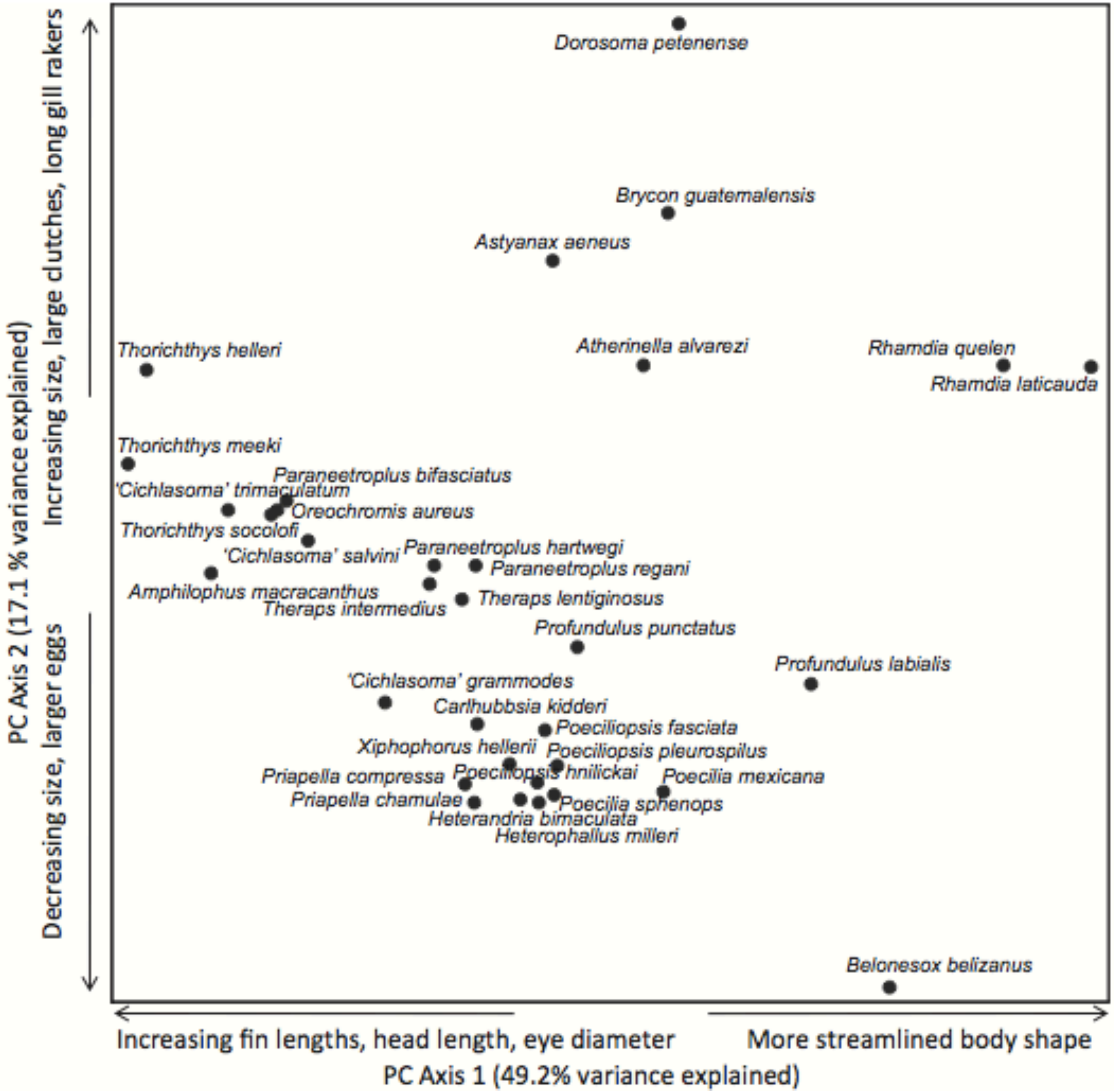


Fig. 2 NMS ordination of Río Grijalva stream reaches based on species composition of fish assemblages.


LEAFPACK
CANOPY
ROOTS
FOREST
NO_RIFF
BUFFER
STRM_COV
SWD
LON
SAND
VELDEPTH
GRV_LRG
COBBLE
THAL_DEP
POOL_DEP
SM_BLDR
POOL_WID
BOULDER
SALINITY
LG_BLDR
MACRPHYT
MCRPH_AB
TEMP
WETWIDTH
Upper
Middle
Lower
PC Axis 1 (23.6% variance explained)
PC Axis 2 (12.8% variance explained)


Dorosoma petenense
Brycon guatemalensis
Astyanax aeneus
Thorichthys helleri
Atherinella alvarezi
Rhamdia quelen
Rhamdia laticauda
Thorichthys meeki
Paraneetroplus bifasciatus
'Cichlasoma' trimaculatum
Oreochromis aureus
Thorichthys socolofi
Paraneetroplus hartwegi
'Cichlasoma' salvini
Paraneetroplus regani
Amphilophus macracanthus
Theraps lentiginosus
Theraps intermedius
Profundulus punctatus
Profundulus labialis
'Cichlasoma' grammodes
Carlhubbsia kidderi
Poeciliopsis fasciata
Xiphophorus hellerii
Poeciliopsis pleurospilus
Priapella compressa
Poeciliopsis hnilickai
Poecilia mexicana
Priapella chamulae
Poecilia sphenops
Heterandria bimaculata
Heterophallus milleri
Belonesox belizanus
Increasing size, large clutches, long gill rakers
Decreasing size, larger eggs
PC Axis 2 (17.1 % variance explained)
Increasing fin lengths, head length, eye diameter
More streamlined body shape
PC Axis 1 (49.2% variance explained)

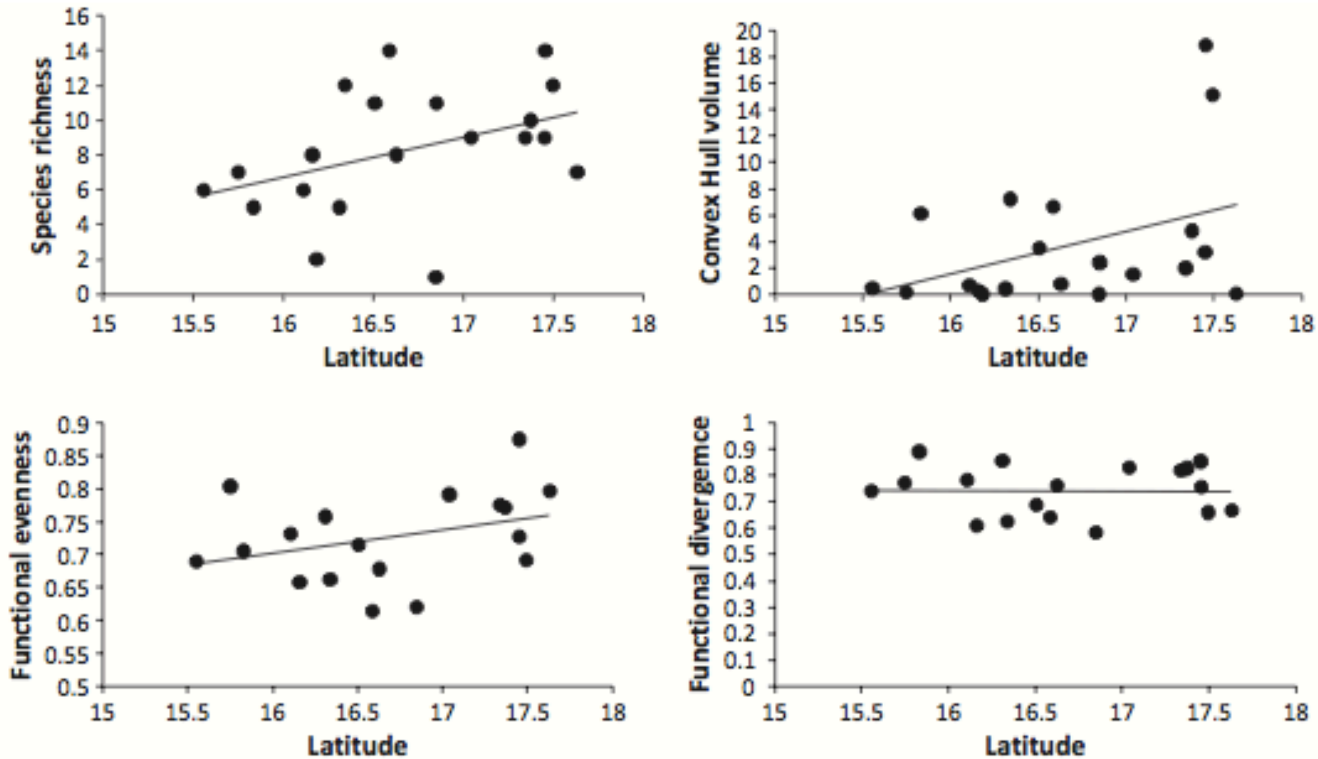


Fig. 6 Regression of species richness and three indices of functional diversity on latitude for the Río Grijalva Basin. Latitude corresponds to a great extent with the fluvial gradient of the Río Grijalva, which flows from south to north.

Moquet, N. and M. Loreau. 2003. Community patterns in source-sink metacommunities. American Naturalist 162:544-557.

P_{ik} is the proportion of sites occupied by species i in community k

a is the proportion of dispersal between communities (represents the fraction of local reproductive output that emigrates; a assumed equal for all species)

V_k is the number of vacant niches available

S is the number of species in local communities

N is the number of local communities

c_{ik} is the reproductive parameter

m_{ik} is the mortality rate

I_{jk} is the immigration function

θ is the probability that a migrant will find a new patch

v_k is the probability that a migrant will find a new community (dispersal success)

r_{ik} is the local basic reproductive rate of species i (the ratio of potential reproductive & mortality rates)

$$\frac{dP_{ik}}{dt} = [\theta I_{ik} + (1-a)c_{ik}P_{ik}]V_k - m_{ik}P_{ik},$$

where

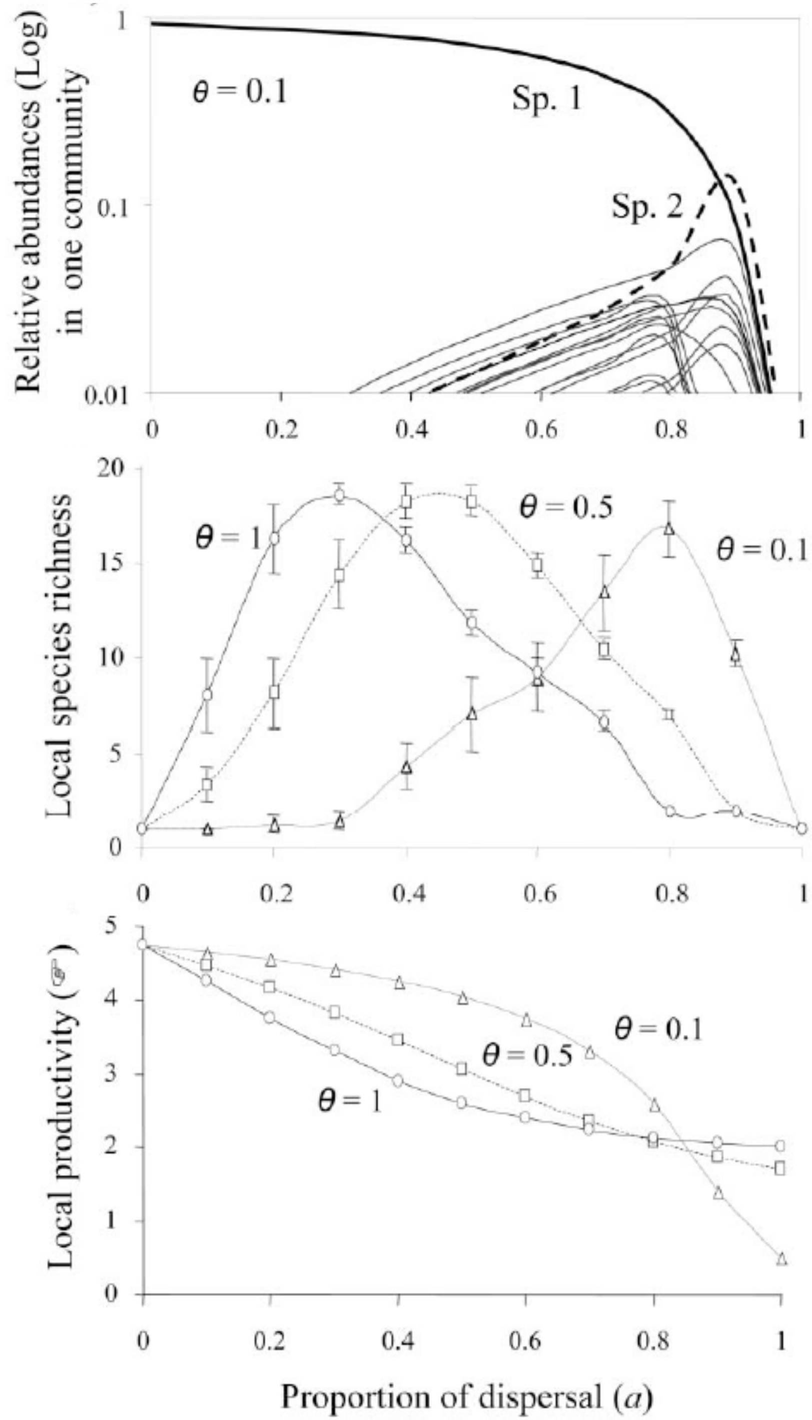
$$I_{ik} = \frac{a}{N-1}\sum_{l\neq k}^{N} c_{il}P_{il}$$

and

$$V_k = 1 - \sum_{j=1}^{S} P_{jk}.$$

$$r_{ik} = \frac{c_{ik}}{m_{ik}}.$$

θ is the probability that a migrant will find a new patch



Community productivity was therefore correlated with both the number of sites occupied per species and their local reproductive rates.

The importance of niches for the maintenance of species diversity

NATURE|Vol 461|10 September 2009

Jonathan M. Levine[1] & Janneke HilleRisLambers[2]

“Our theoretical approach predicts that without niche differences, species differ by several orders of magnitude in their per capita growth rates, which is sufficient for rapid competitive exclusion.”

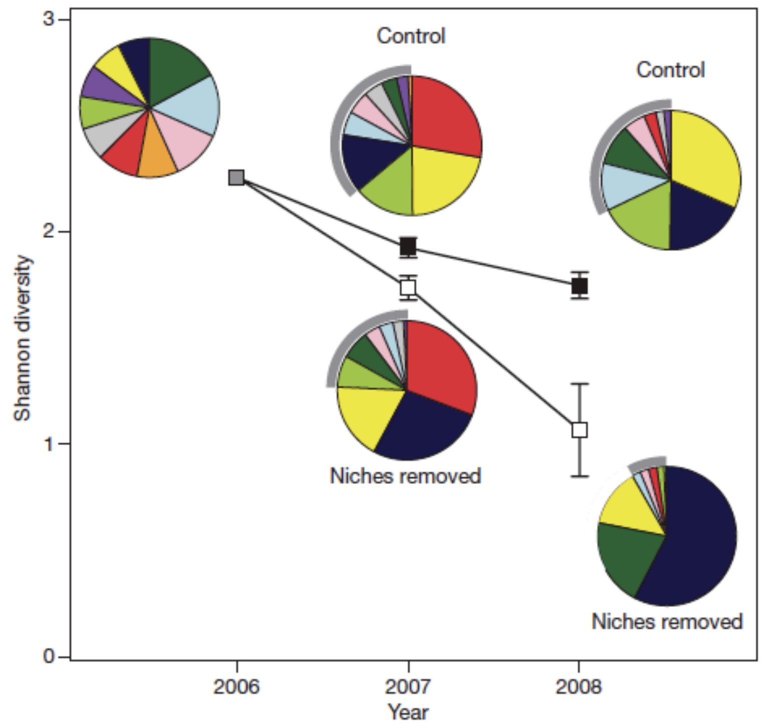


Figure 3 | Niche differences stabilize community dynamics. Two generations (2006–2007, 2007–2008) of change in the diversity and composition of communities stabilized by niche differences, versus those in which the demographic influence of niche differences was removed ($n = 10$). Pie charts show the average proportion of total community seed mass constituted by each focal species in each treatment and year. The grey arcs show the collective abundances of the seven rarest species. Species' relative abundances are not perfectly equal in the initial communities (2006) owing to differences in seed viability. Colours correspond to genus as in Fig. 2a and points show mean ± s.e.

Metacommunity concepts and **invasive species**

A great challenge of community ecology is to determine what makes certain species invasive and certain communities invasible.

Shea, K. & Chesson, P.L. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17, 170–176.

Melbourne, et al. 2007. Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters*, 10:77-94.

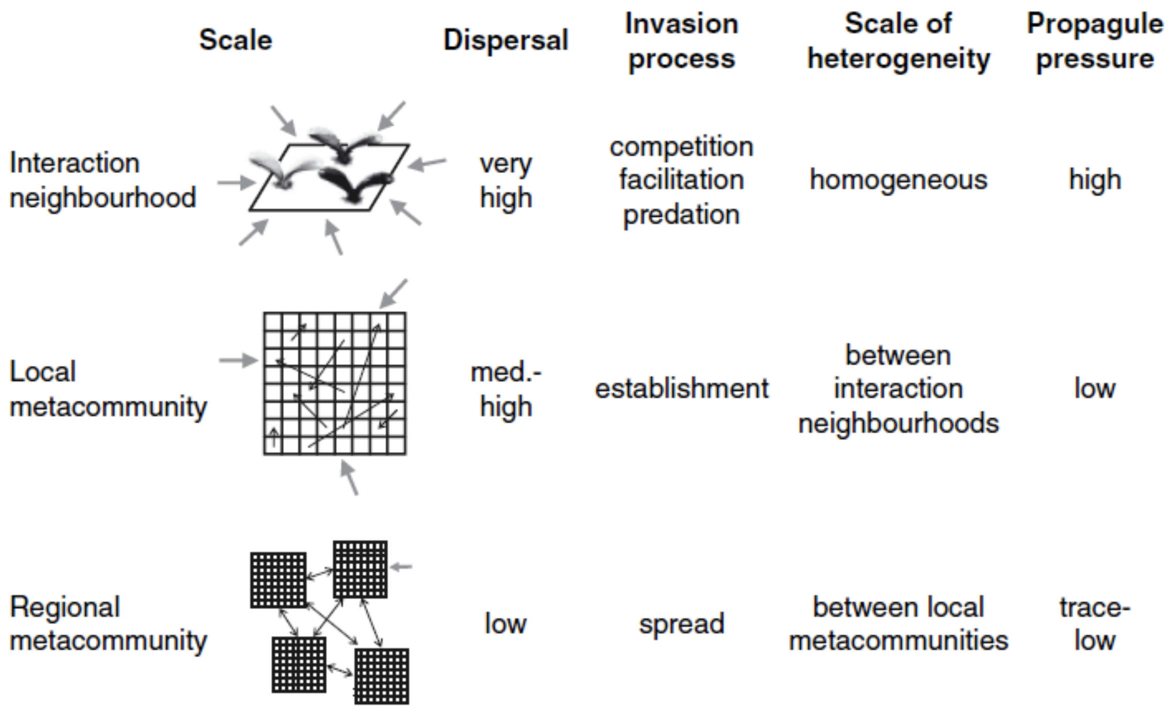
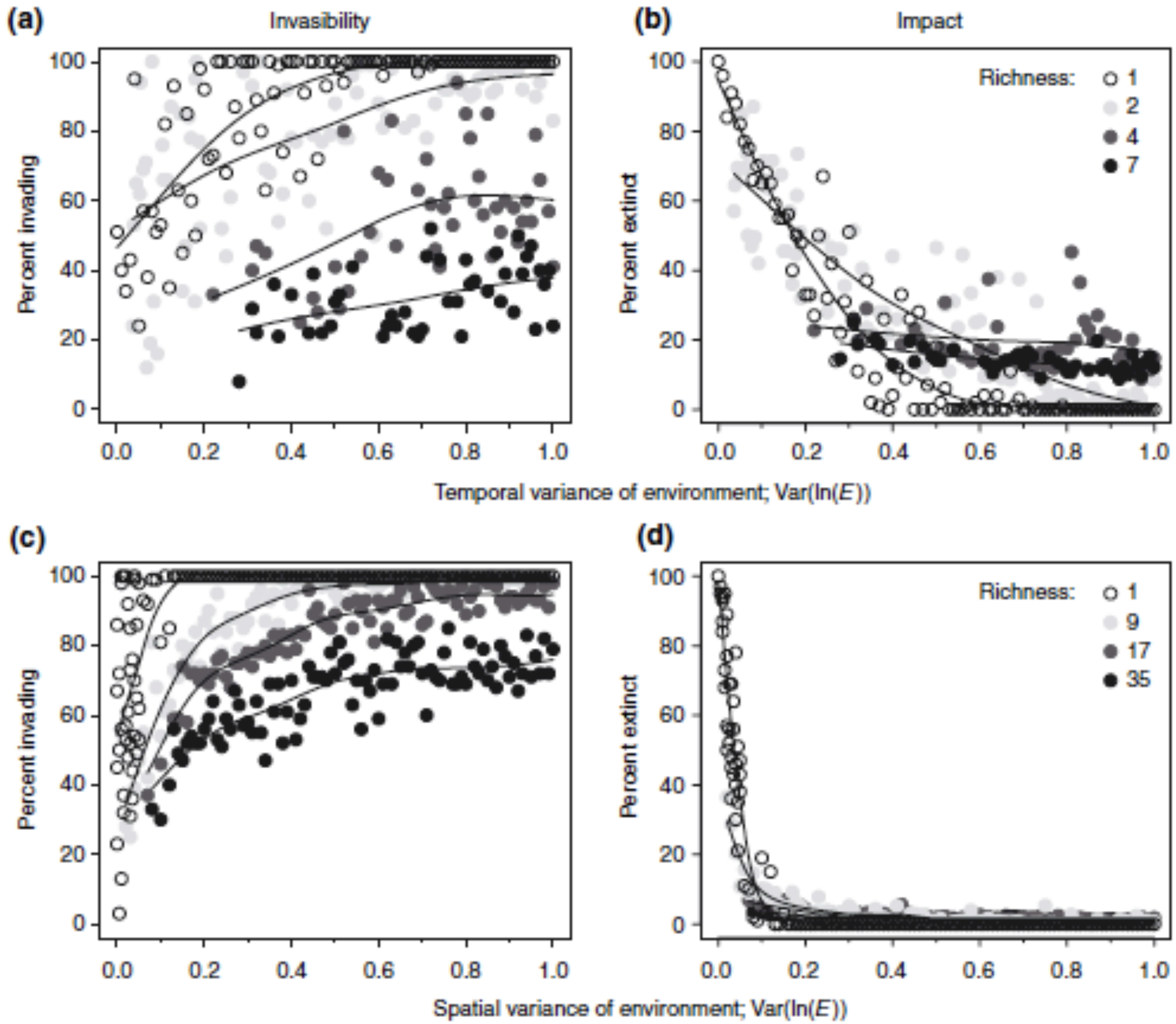
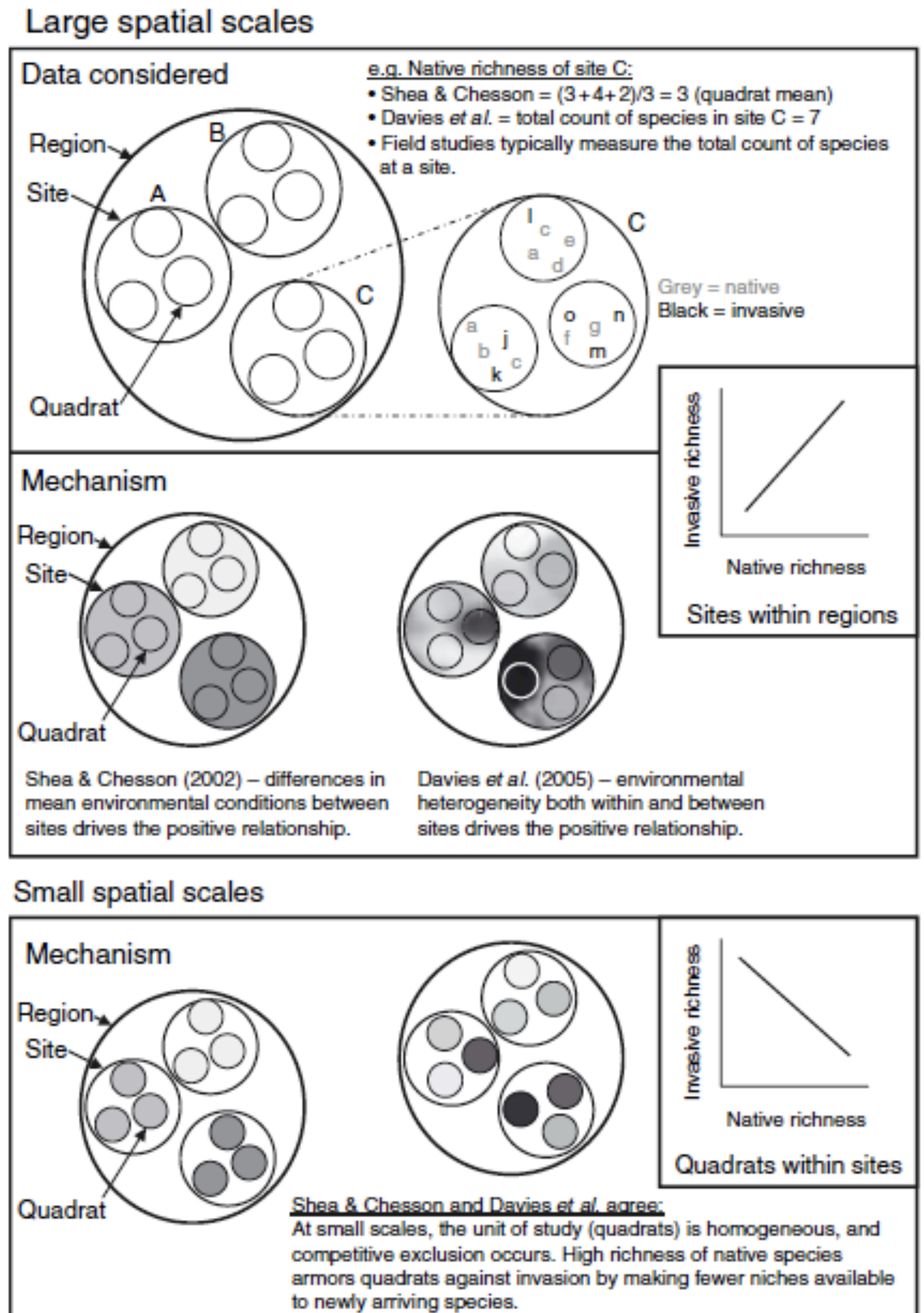


Figure 2 Hierarchical metacommunity concept of biological invasions. The smallest scale is the interaction neighbourhood. Interaction neighbourhoods are linked by dispersal to form a local metacommunity. Local metacommunities are linked by dispersal to form a regional metacommunity. Shown are: the amount of dispersal between smaller-scale units within the scale; the dominant invasion process at the scale; the scale of spatial heterogeneity important to invasibility and impact; and the propagule pressure exerted on that scale from other units at the same scale. Small black arrows indicate dispersal of invader and resident species between smaller-scale units within the scale. Large grey arrows indicate propagule pressure of the invader and resident species. Large grey arrows are equivalent to the small black arrows at the next largest scale. The amount of dispersal and propagule pressure is relative between scales.



Invasibility is increased and **impact is reduced** by both temporal and spatial heterogeneity. **Invasibility is lower** when species richness of the resident community is higher.


Large spatial scales
Data considered
e.g. Native richness of site C:
• Shea & Chesson = (3+4+2)/3 = 3 (quadrat mean)
• Davies et al. = total count of species in site C = 7
• Field studies typically measure the total count of species at a site.
Region
Site
Quadrat
A
B
C
C
l c e a d
a j b c k
o n f g m
Grey = native
Black = invasive
Invasive richness
Native richness
Sites within regions
Mechanism
Region
Site
Quadrat
Shea & Chesson (2002) – differences in mean environmental conditions between sites drives the positive relationship.
Davies et al. (2005) – environmental heterogeneity both within and between sites drives the positive relationship.
Small spatial scales
Mechanism
Region
Site
Quadrat
Invasive richness
Native richness
Quadrats within sites
Shea & Chesson and Davies et al. agree:
At small scales, the unit of study (quadrats) is homogeneous, and competitive exclusion occurs. High richness of native species armors quadrats against invasion by making fewer niches available to newly arriving species.

Biological Invasions 1: 21–32, 1999.

Positive interactions of nonindigenous species: invasional meltdown?

Daniel Simberloff* & Betsy Von Holle

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**Author for correspondence (e-mail: dsimberloff@utk.edu; fax: +1-423-974-3067)*

There is little evidence that interference among introduced species at levels currently observed significantly impedes further invasions, and synergistic interactions among invaders may well lead to accelerated impacts on native ecosystems – an invasional 'meltdown' process.

Table 1. Numbers of different types of interactions between introduced species cited in 254 articles in seven journals during a five-year period (see text).

Interaction type	Number	Nature of interaction
+/+	10	Disturbance = 6, indirect effects = 3, pollination = 1
+/0	12	Disturbance = 9, commensalism = 1, host/parasite and similar interactions = 2
+/−	156	Predator/prey = 23, phytophagous insect/plant = 131, other = 2
−/−	12	Competition = 12

Simberloff, D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science* 49:87-97.

Observation: island communities have been viewed as more fragile and vulnerable to invasion

- virtually every kind of damage wrought by invaders on islands has been wrought in mainland areas
- it is unlikely that by virtue of low species richness alone, islands have less biotic resistance to invasion
- instead, certain entire groups are more likely to be missing on islands, and these absences predispose islands to certain invaders and to certain impacts

Parker, I.M., et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1:3-19.

Sanders, N.J., et al. 2003. Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences, USA* 100:2474–2477.

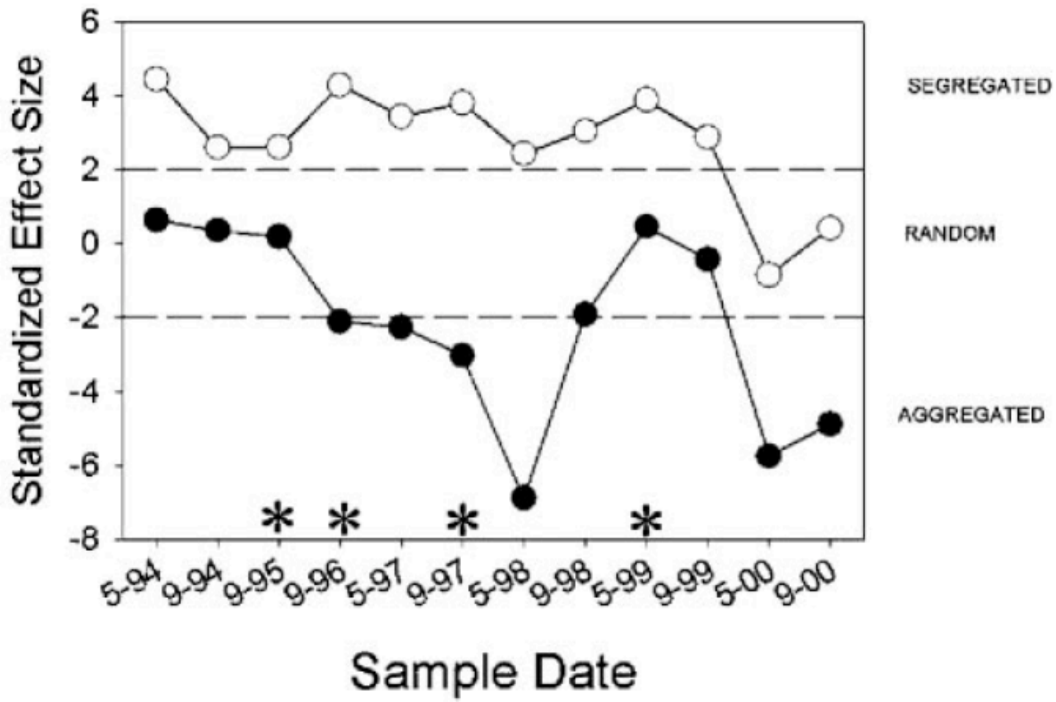


Fig. 1. A comparison of native ant community organization in intact sample plots and sample plots invaded by *L. humile*. The standardized C-score is a measure of the extent to which species co-occur less frequently than expected by chance. Larger C-scores indicate less co-occurrence than in randomly assembled communities. The dotted lines represent 1.96 standard deviations, the approximate level of statistical significance ($P < 0.05$). *, Statistical differences in co-occurrence patterns of intact and invaded plots sampled during the same sampling period (partition test, $P < 0.05$). Paired symbols indicate invaded and intact plots sampled during the same survey. ●, Invaded plots; ○, uninvaded plots.

Metacommunity concepts and **<u>indices of biotic integrity</u>**

- reference community ("healthy condition")

- index transferability

  - from one location to another

    watersheds with different characteristics
    watersheds with different biogeographic histories

  - from one time to another

    variable periods of time following a *natural* disturbance and recovery
    different years with different climatic conditions

Index of Biotic Integrity – Pioneers

Patrick, R. 1949. A proposed biological measure of stream conditions based on a survey of Conestoga Basin, Lancaster County, Pennsylvania. *Proc. Acad. Nat. Sci. Philadelphia, 101:277-341.*

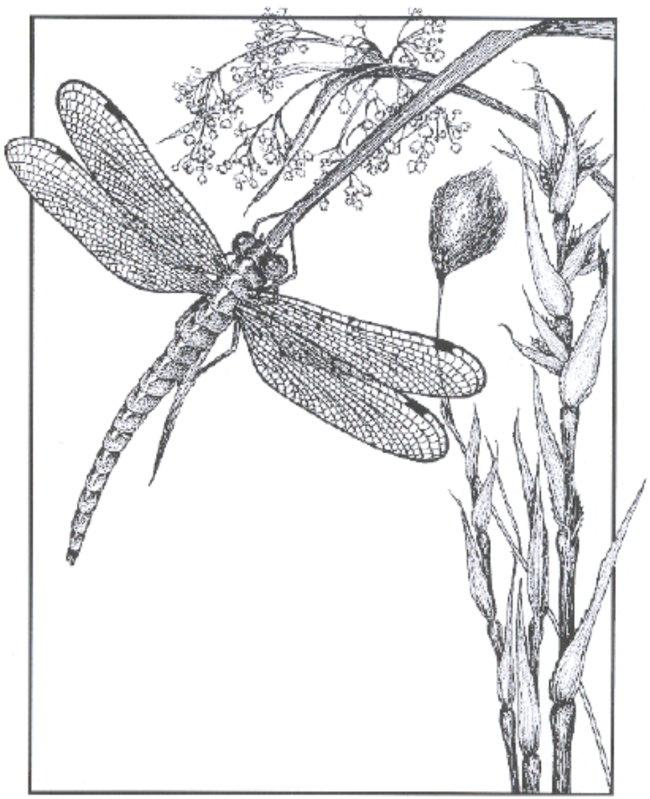
Patrick, R. 1950. Biological measure of stream conditions. *Sewage & Industrial Wastes, 22(7):926-938.*

> A "healthy" stream is one which has a balance of organisms or in which the biodynamic cycle is such that conditions are maintained which are capable of supporting a great variety of organisms. The algae are mostly diatoms and green algae, such as *Cladophora crispata* and *glomerata*, and the insects and fish are represented by a great variety of species.

Karr, J. R. 1981. Assessment of biotic integrity using fish communities. Fisheries 6: 21-27.

United States Environmental Protection Agency | National Heath and Environmental Effects Laboratory Corvallis, OR 97333 | EPA/620/R-04/009 January 2004

Review of Rapid Methods for Assessing Wetland Condition



Environmental Monitoring and Assessment Program

USGS
science for a changing world

National Water-Quality Assessment Program

Prepared in cooperation with The Academy of Natural Sciences, Patrick Center for Environmental Research

Development and Application of Indices to Assess the Condition of Benthic Algal Communities in U.S. Streams and Rivers

By Marina Potapova and Daren M. Carlisle

Open File Report 2011–1126

U.S. Department of the Interior
U.S. Geological Survey

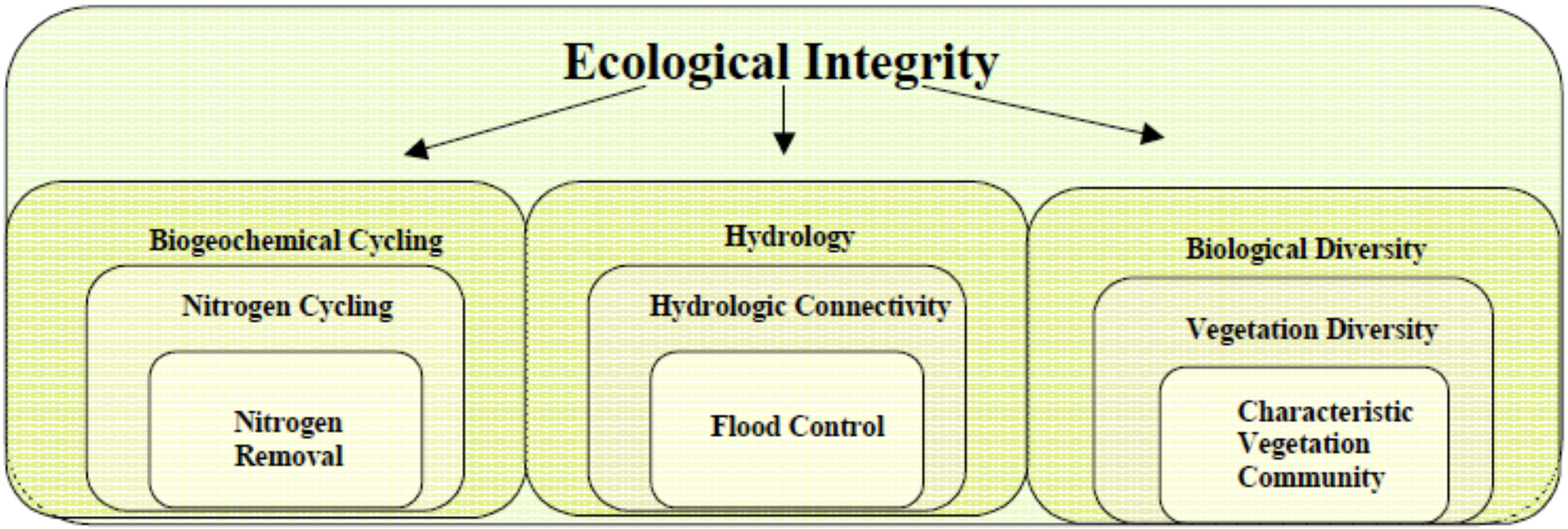
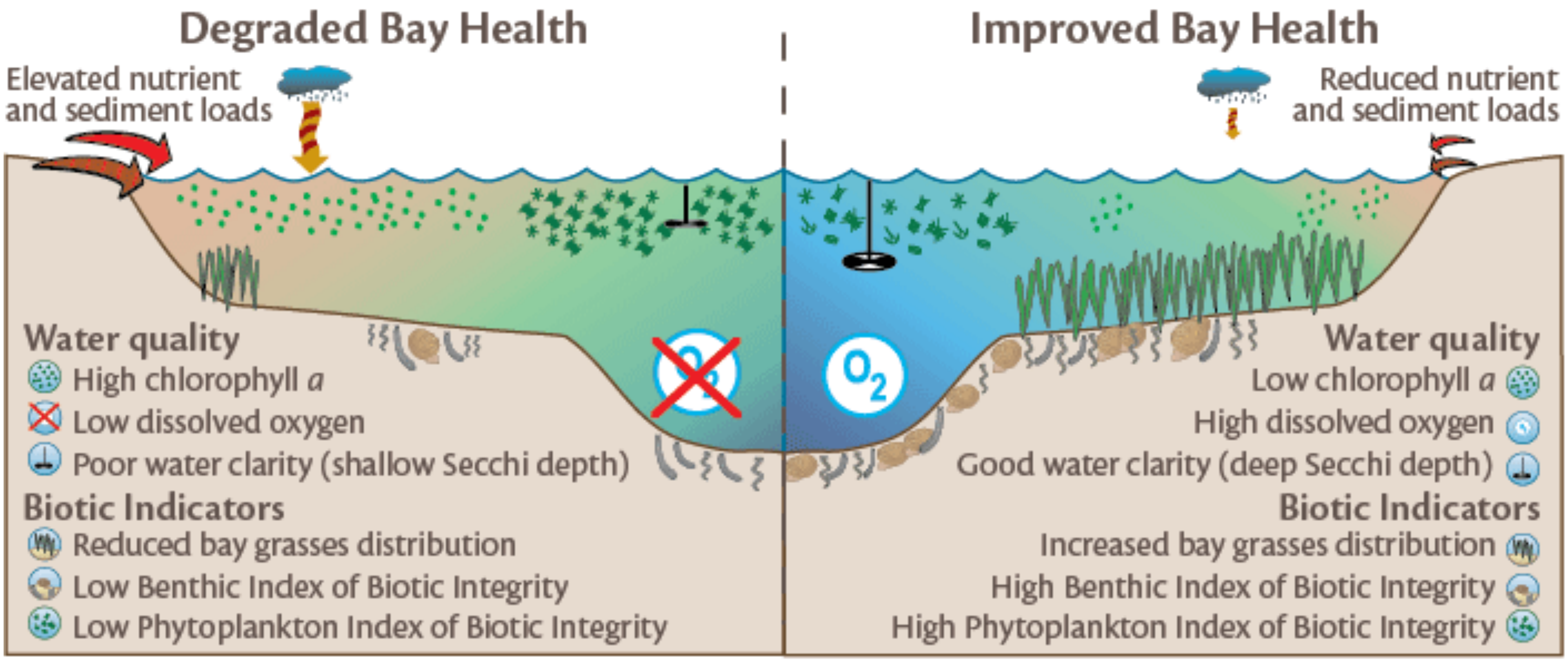
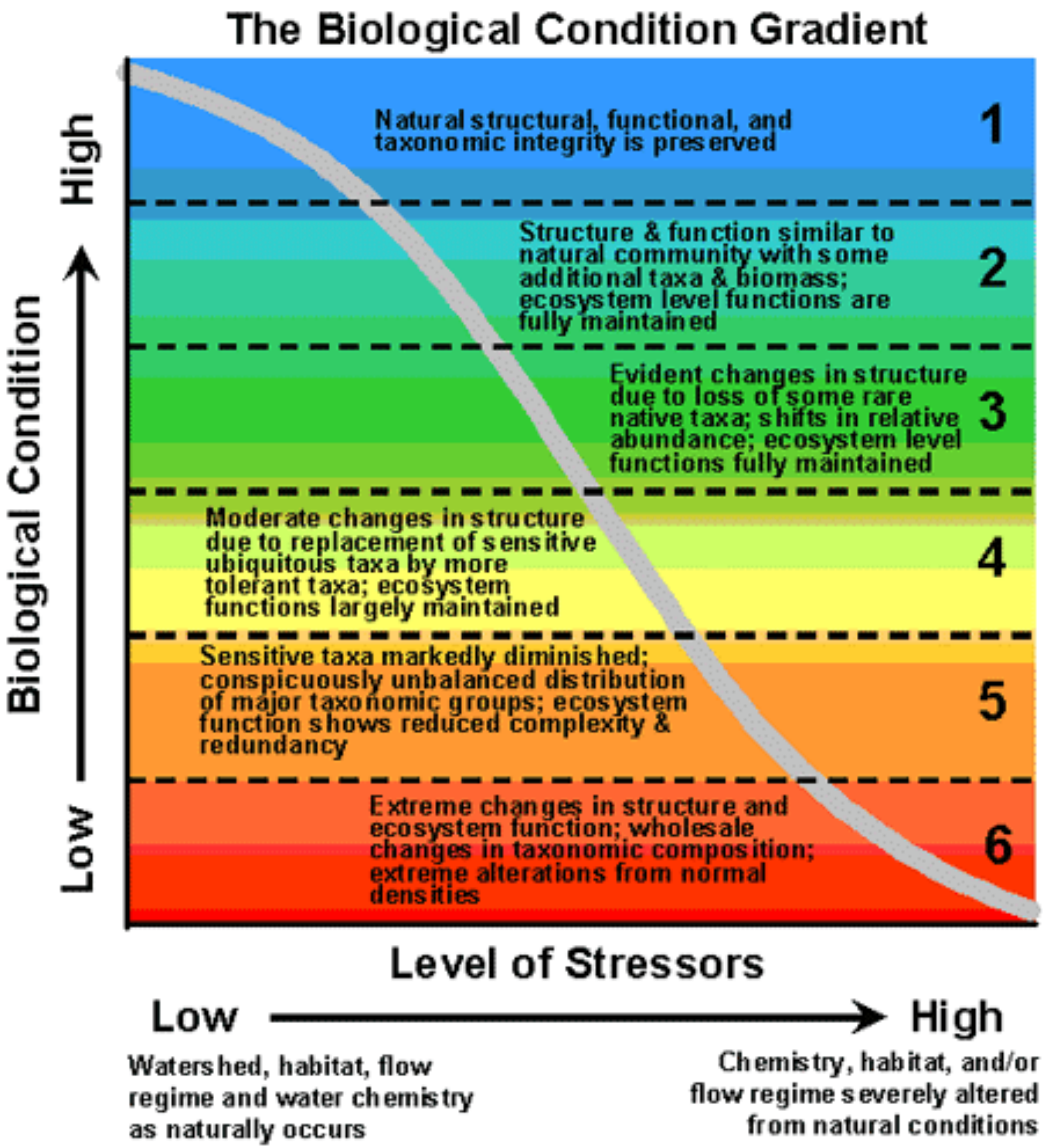


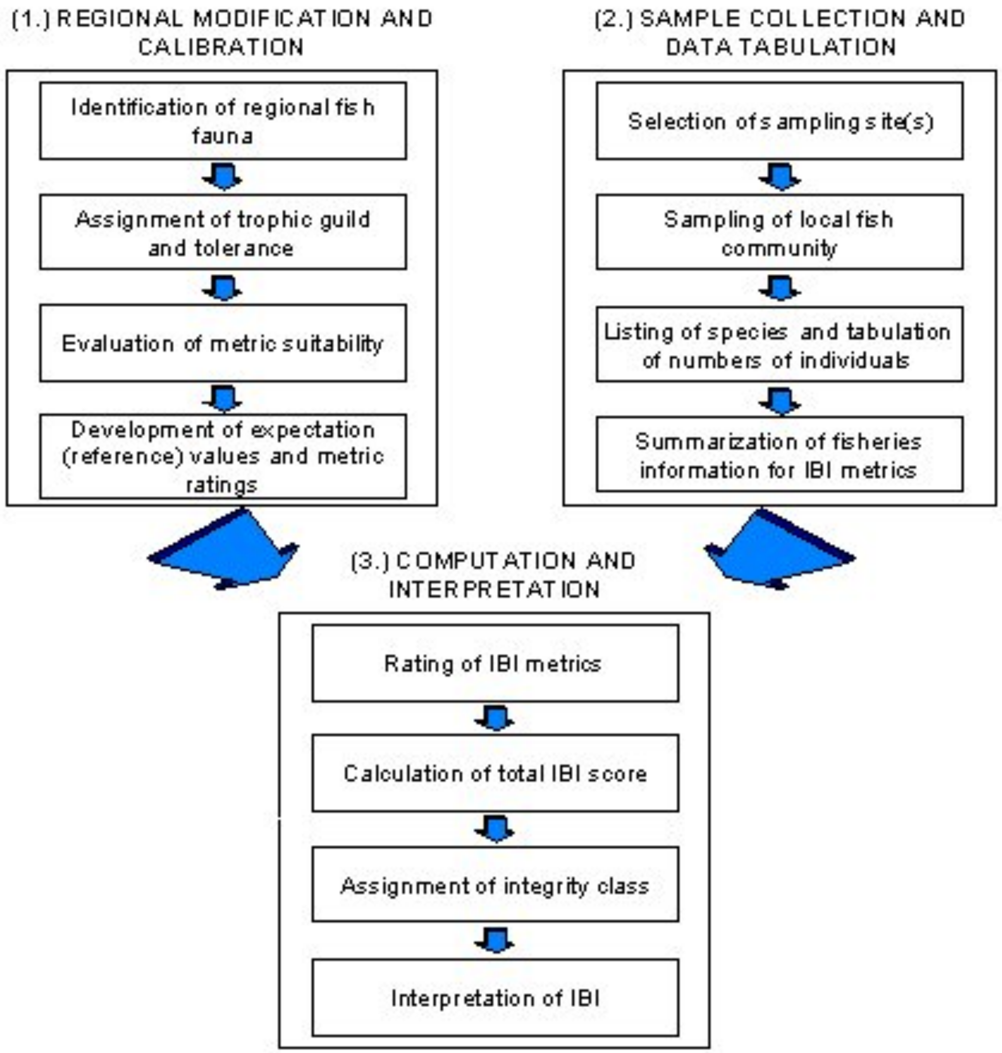
Figure 2. A schematic to illustrate the concept of ecological integrity as the integrating function of wetlands, encompassing both ecosystem structure and processes. In this case integrity is shown to include biogeochemical processes that lead to functions such as nitrogen removal and hydrological processes that lead to the flood control function, and habitat functions (based on Smith et. al., 1995).



Degraded Bay Health
Improved Bay Health
Elevated nutrient and sediment loads
Reduced nutrient and sediment loads
O_2
O_2
Water quality
High chlorophyll *a*
Low dissolved oxygen
Poor water clarity (shallow Secchi depth)
Biotic Indicators
Reduced bay grasses distribution
Low Benthic Index of Biotic Integrity
Low Phytoplankton Index of Biotic Integrity
Water quality
Low chlorophyll *a*
High dissolved oxygen
Good water clarity (deep Secchi depth)
Biotic Indicators
Increased bay grasses distribution
High Benthic Index of Biotic Integrity
High Phytoplankton Index of Biotic Integrity



The Biological Condition Gradient
Natural structural, functional, and taxonomic integrity is preserved
1
Structure & function similar to natural community with some additional taxa & biomass; ecosystem level functions are fully maintained
2
Evident changes in structure due to loss of some rare native taxa; shifts in relative abundance; ecosystem level functions fully maintained
3
Moderate changes in structure due to replacement of sensitive ubiquitous taxa by more tolerant taxa; ecosystem functions largely maintained
4
Sensitive taxa markedly diminished; conspicuously unbalanced distribution of major taxonomic groups; ecosystem function shows reduced complexity & redundancy
5
Extreme changes in structure and ecosystem function; wholesale changes in taxonomic composition; extreme alterations from normal densities
6
Biological Condition
High
Low
Level of Stressors
Low
High
Watershed, habitat, flow regime and water chemistry as naturally occurs
Chemistry, habitat, and/or flow regime severely altered from natural conditions

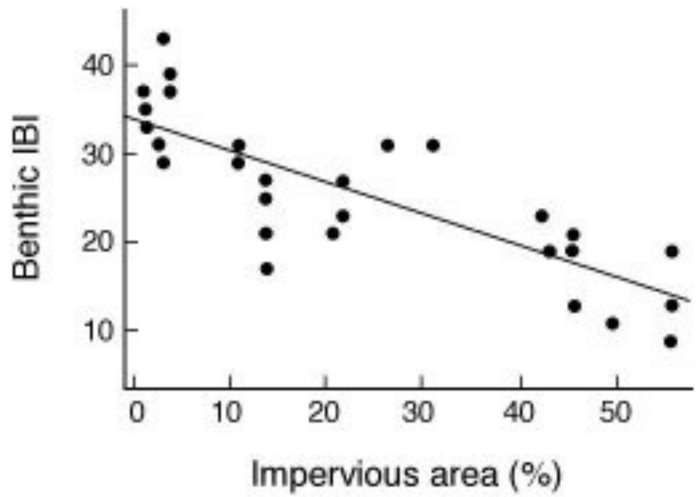

(1.) REGIONAL MODIFICATION AND CALIBRATION
Identification of regional fish fauna
Assignment of trophic guild and tolerance
Evaluation of metric suitability
Development of expectation (reference) values and metric ratings
(2.) SAMPLE COLLECTION AND DATA TABULATION
Selection of sampling site(s)
Sampling of local fish community
Listing of species and tabulation of numbers of individuals
Summarization of fisheries information for IBI metrics
(3.) COMPUTATION AND INTERPRETATION
Rating of IBI metrics
Calculation of total IBI score
Assignment of integrity class
Interpretation of IBI

Alternative IBI Metrics
1. Total Number of Species
#native fish species
salmonid age classes[b]
2. Number of Darter Species
sculpin species
benthic insectivore species
darter and sculpin species
darter, sculpin, and madtom species
salmonid juveniles (individuals)[b]
% round-bodied suckers
sculpins (individuals)
benthic species
3. Number of Sunfish Species
cyprinid species
water column species
sunfish and trout species
salmonid species
headwater species
% headwater species
4. Number of Sucker Species
adult trout species[b]
minnow species
sucker and catfish species
5. Number of Intolerant Species
sensitive species
amphibian species
presence of brook trout
% stenothermal cool and cold water species
% of salmonid ind. as brook trout
6. % Green Sunfish
% common carp
% white sucker
% tolerant species
% creek chub
% dace species
% eastern mudminnow
7. % Omnivores
% generalist feeders
% generalists, omnivores, and invertivores
8. % Insectivorous Cyprinids
% insectivores
% specialized insectivores
juvenile trout
% insectivorous species
9. % Top Carnivores
% catchable salmonids
% catchable trout
% pioneering species
Density catchable wild trout
10. Number of Individuals (or catch per effort)
Density of individuals
% abundance of dominant species
Biomass (per m^2)
11. % Hybrids
% introduced species
% simple lithophills
simple lithophills species
% native species
% native wild individuals
% silt-intolerant spawners
12. % Diseased Individuals (deformities, eroded fins, lesions, and tumors)

Metric*	Scoring Values			
	5	3	1	0
1. Taxa Richness	> 80%	80 - 60%	59 - 40%	< 40%
2. EPT Index	> 90%	89 - 70%	69 - 50%	< 50%
3. IAI	0.8 - 1.0	0.65 - 0.79	0.5 - 0.64	< 0.5
4. % Dominant Taxon	< 20%	20 - 30%	31 - 40%	> 40%
5. NCBI	> 85%	85 - 70%	69 - 50%	< 50%
6. % Shredders	> 50%	50 - 35%	35 - 20%	< 20%
7. Total Habitat Score	> 90%	89 - 75%	74 - 60%	< 59%

Integrity Class	Excellent	Good	Fair	Poor	Very Poor
Scoring Range	60 - 52	50 - 44	42 - 34	32 - 26	24 - 8

biotic index of watershed impairment



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