Species traits as the causal mechanisms underlying interspecific abundance-occupancy relationships

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Structure

Species traits as the causal mechanisms underlying interspecific abundance-occupancy relationships

Biodiversity?

Goal:

How species-specific information can help understand patterns in biodiversity

"If you think ecological science is a bunny hugging luxury, try ignorance"

- J.H. Lawton

Biodiversity

Heuristic concept

Operational measures
(e.g. richness, Shannon-Wiener diversity indices)

Pattern generated across many species

Pattern generated across many individual species

Intuitive idea of its requirements

Mechanistic understanding largely lacking
(beware of empty, circular explanations)

Nuthatch
(*Sitta europaea*)

Heath Fritillary
(*Melitaea athalia*)

Marsh Fritillary
(*Euphydryas aurinia*)

Pattern generated across many individual species

Intuitive idea of its requirements

Mechanistic understanding largely lacking

Species traits as mechanistical explanations

Species traits as mechanistical explanations

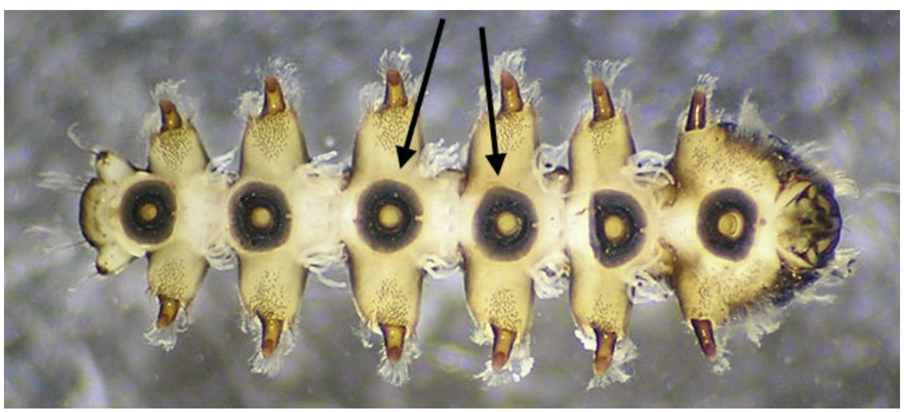
Poor oxygen

Burrowing water beetle
(*Noterus clavicornis*)

Drought

Mosquito
(*Aedes* sp)

High flow velocity



Net-winged midge (*Blepharicera* sp)

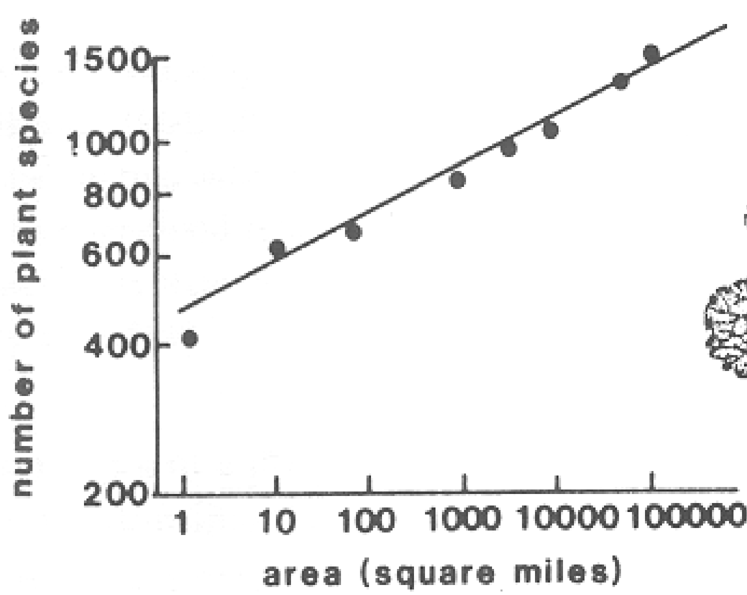
Fish predation

Beautiful Demoiselle (*Calopteryx virgo*)

Pattern generated across many individual species

Problem of accounting species-specific information not solved but circumvented?

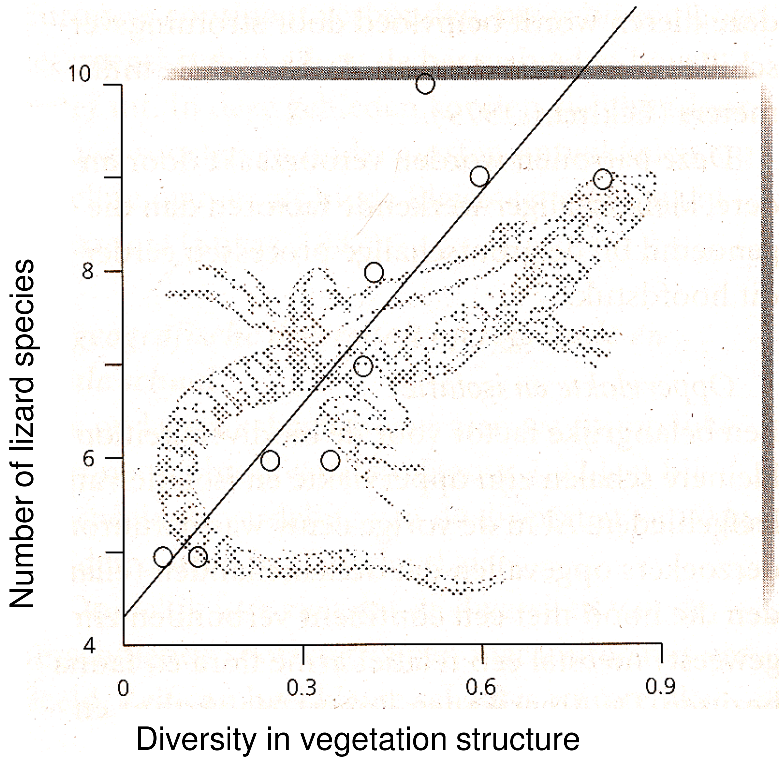
Single Large



Source: Magurran, 1984

Pattern generated across many individual species

Problem of accounting species-specific information not solved but circumvented?



Source: Zoest, 1998

Single Large

or

Several small

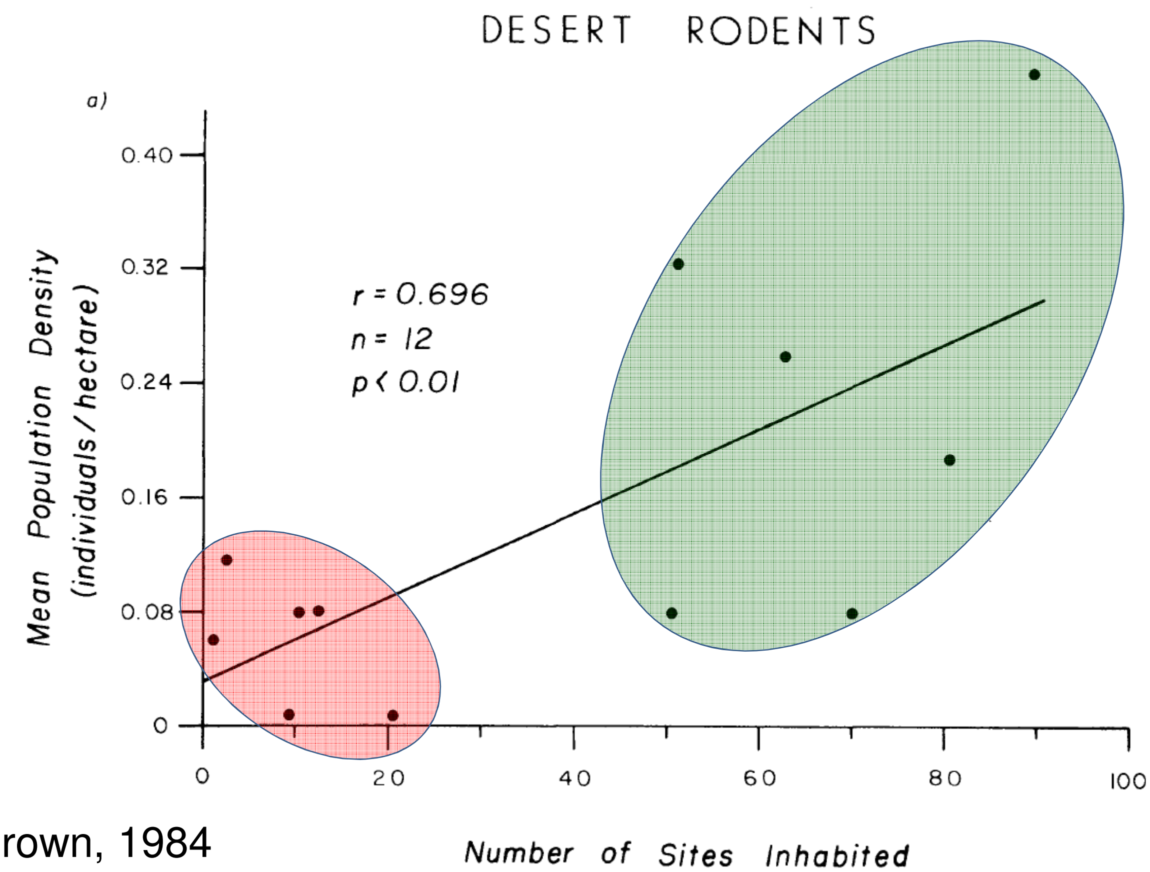
(each of them different)

?

SLOSS

Abundance – Occupancy relationships
(density-distribution relationships)

locally abundant species tend to be widely distributed
whilst locally rare species tend to be narrowly distributed



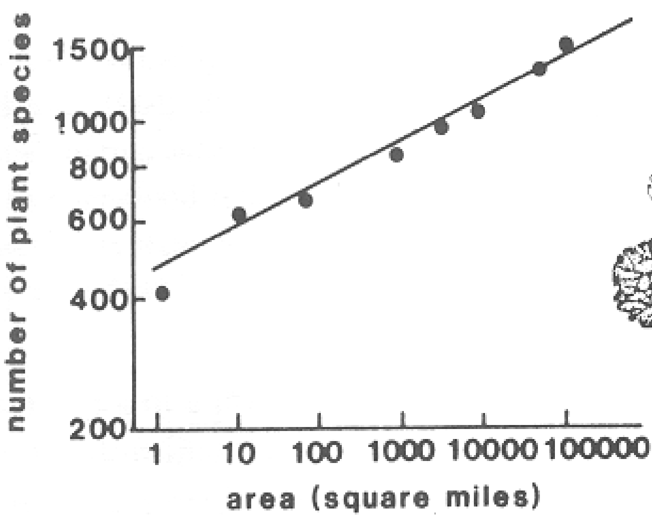
Source: Brown, 1984

Abundance – Occupancy relationships

(density-distribution relationships)

Related to species area relationships

- Lower extinction (abundance)
- Higher colonisation (abundance & occupancy)



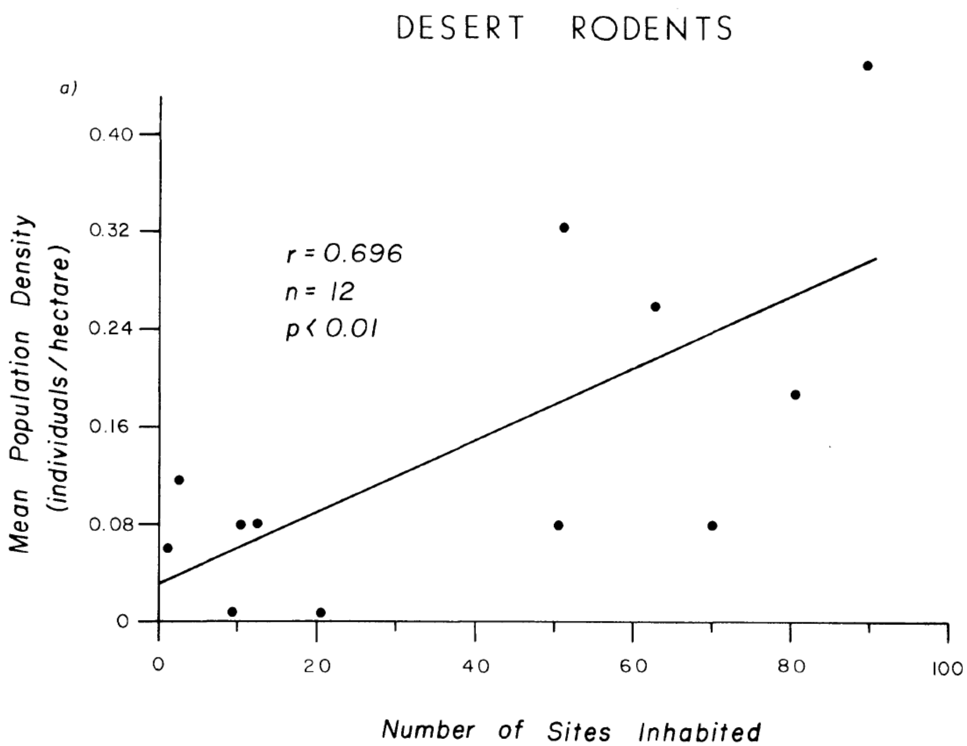
Source: Magurran, 1984

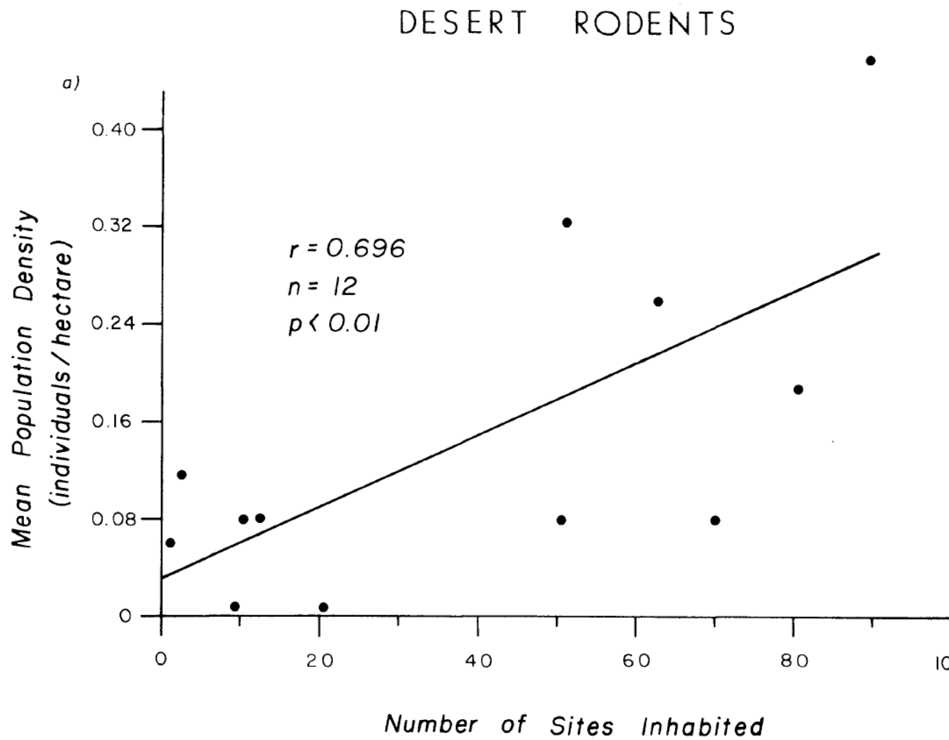
Abundance – Occupancy relationships

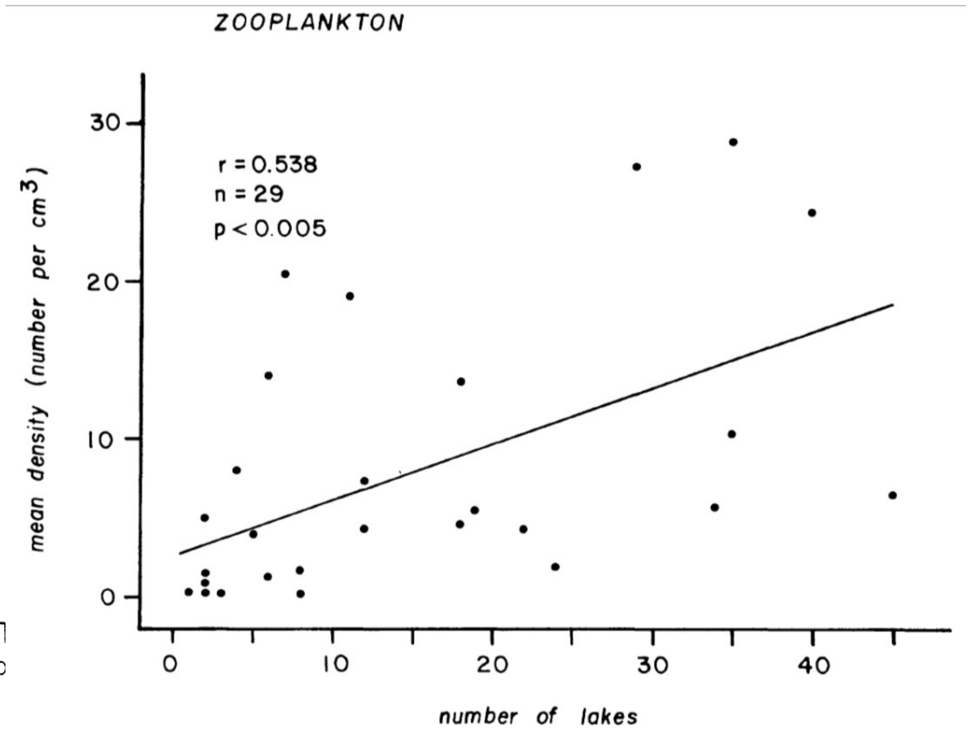
(density-distribution relationships)

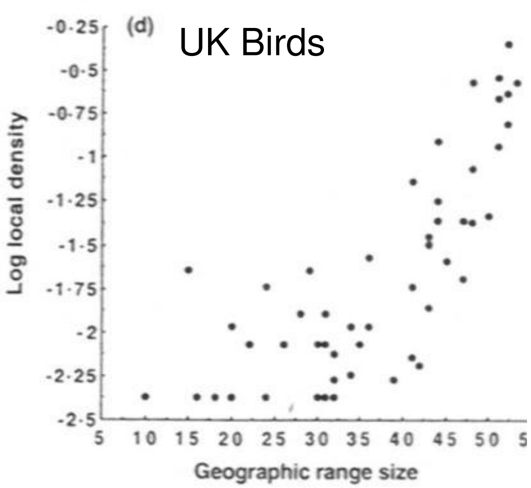
Related to species area relationships

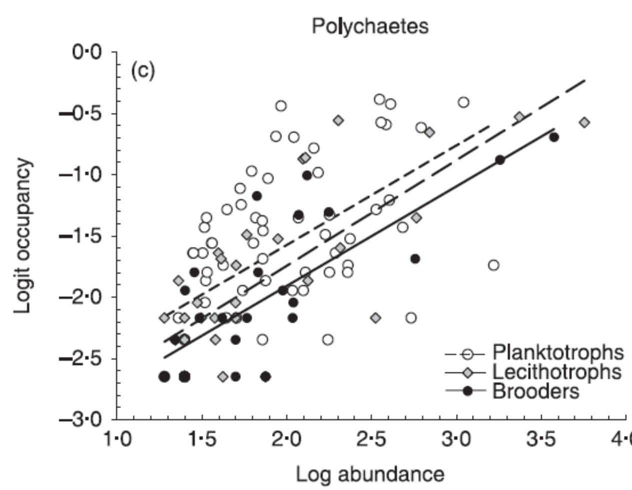
Widespread robust patterns in macroecology

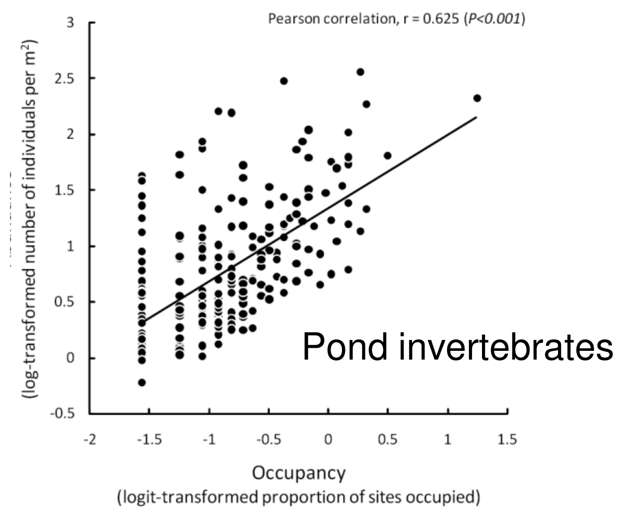












Out of 89 studies: 80% positive, 5% negative, 15 % NS (Gaston 1996)

Abundance – Occupancy relationships

(density-distribution relationships)

Related to species area relationships

Widespread robust patterns in macroecology

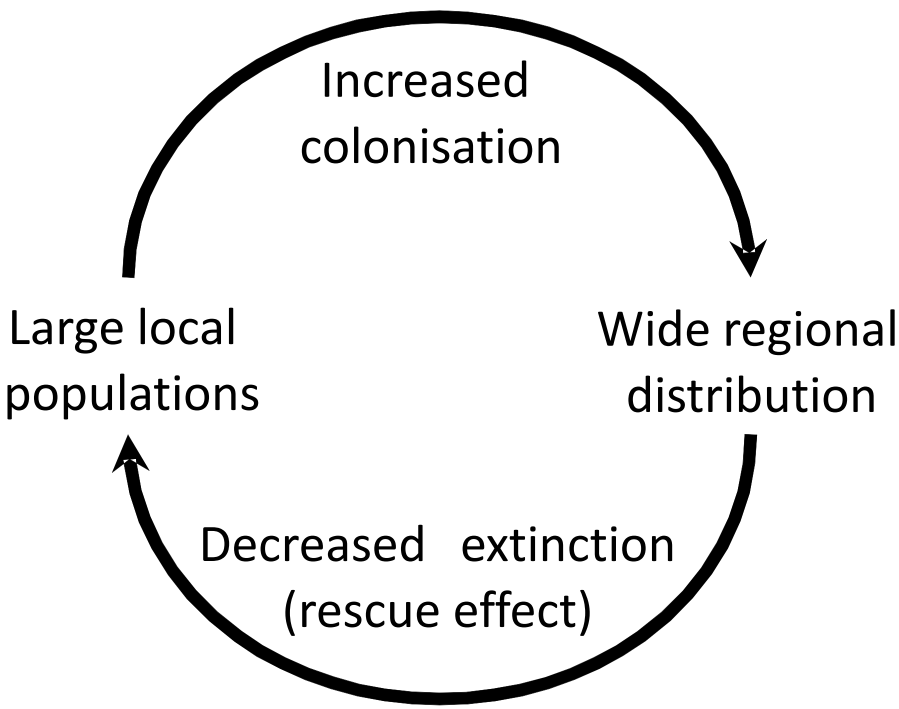
Degree of scatter: 20-30% explained (median values)

Explanations?

- statistical artefacts
- metapopulation dynamics
- niche differences

Abundance – Occupancy relationships

Metapopulation dynamics

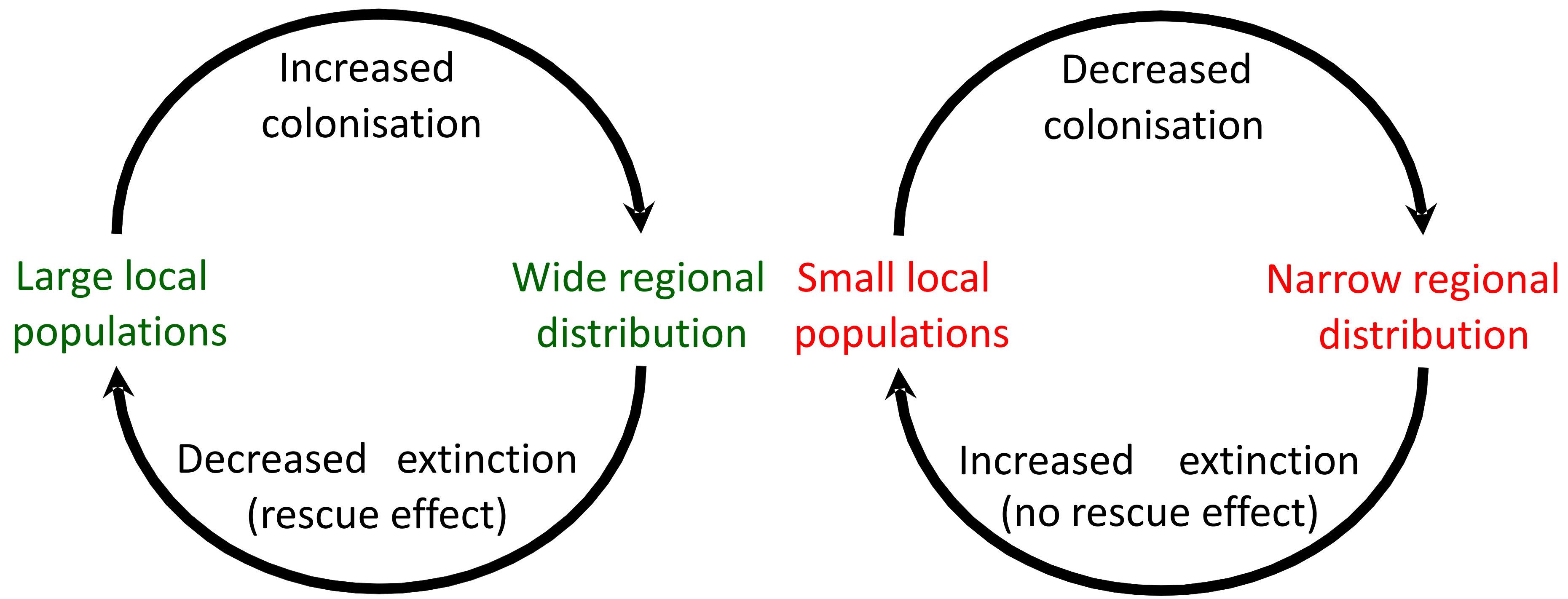


Stochastic

No interspecific differences required

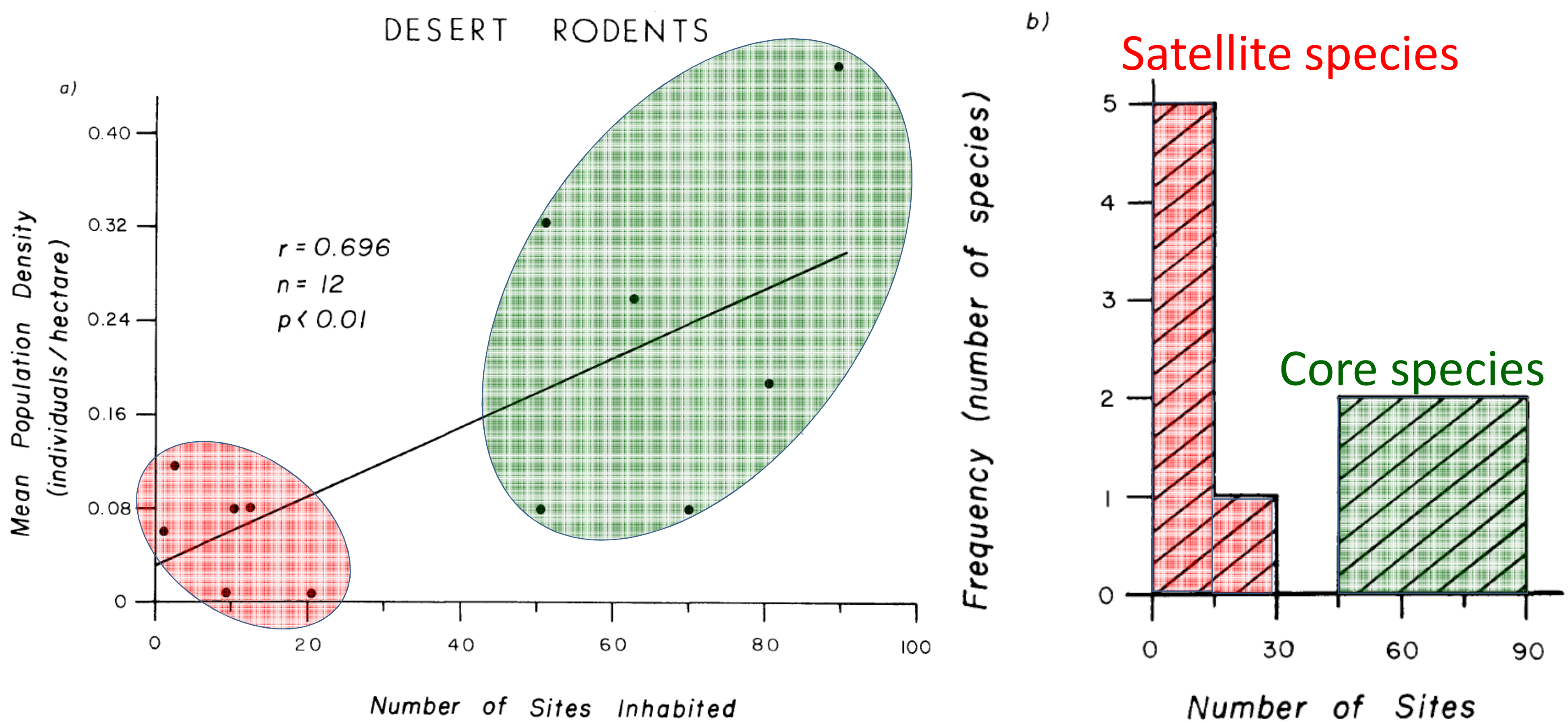
Abundance – Occupancy relationships

Metapopulation dynamics



Abundance – Occupancy relationships

Metapopulation dynamics



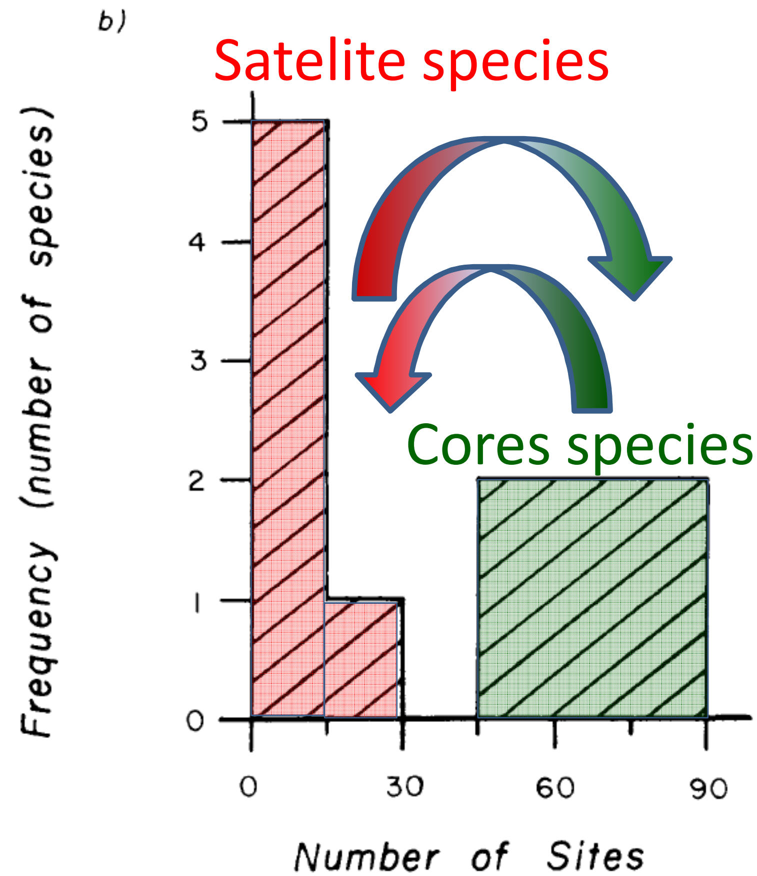
Source: Brown, 1984

Abundance – Occupancy relationships

Metapopulation dynamics

Problems:

- Change in species status?
- Bimodal occ-freq distr?



Abundance – Occupancy relationships

Metapopulation dynamics

Problems:

- Change in species status?
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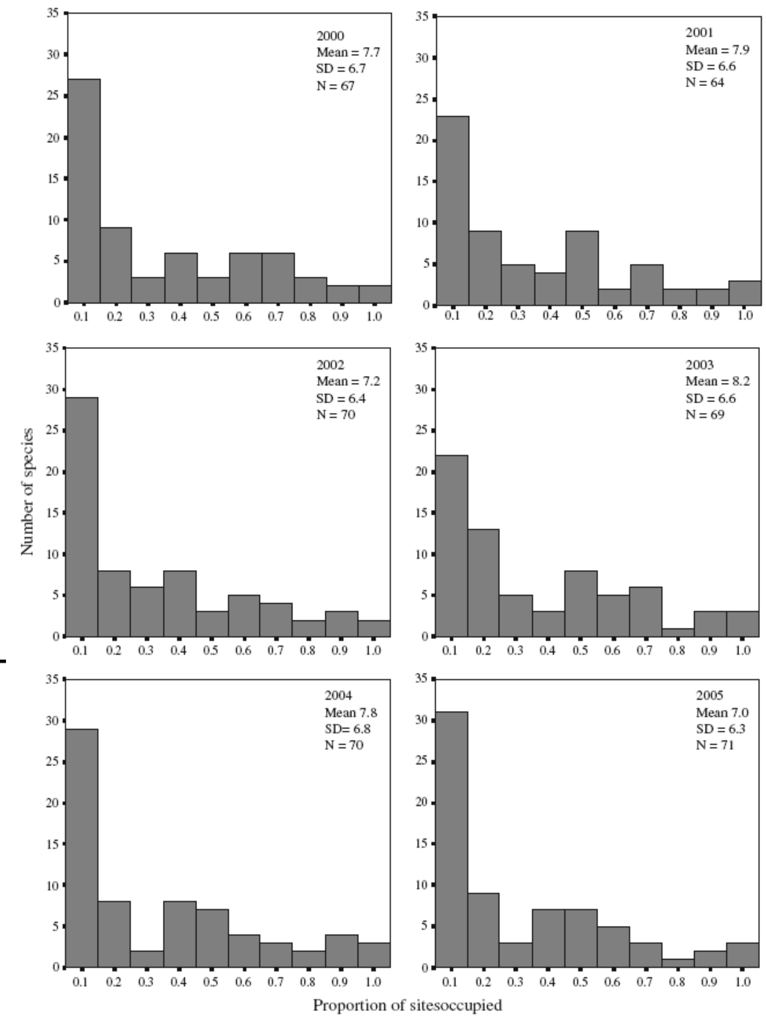


Oecologia (2008) 157:337–347
DOI 10.1007/s00442-008-1078-y

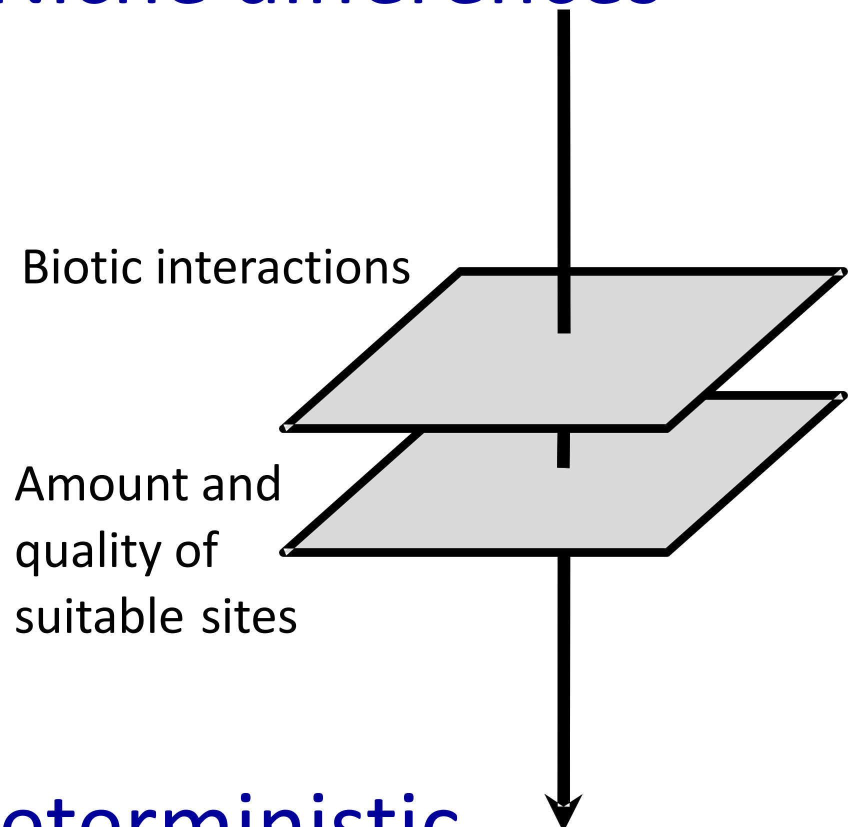
COMMUNITY ECOLOGY - ORIGINAL PAPER

Temporally stable abundance–occupancy relationships and occupancy frequency patterns in stream insects

Jani Heino

Abundance – Occupancy relationships

Niche differences



Species do differ

- habitat requirements
  - diet
  - reproduction
  - dispersal

Deterministic

Requires interspecific differences

Abundance – Occupancy relationships

Niche differences

Resource (Niche) availability hypothesis :

Link between:

- local amount of resources (patch quality)
- regional distribution (proportion of habitable patches)

Source: Gaston *et al*. 1997

Niche breadth hypothesis :

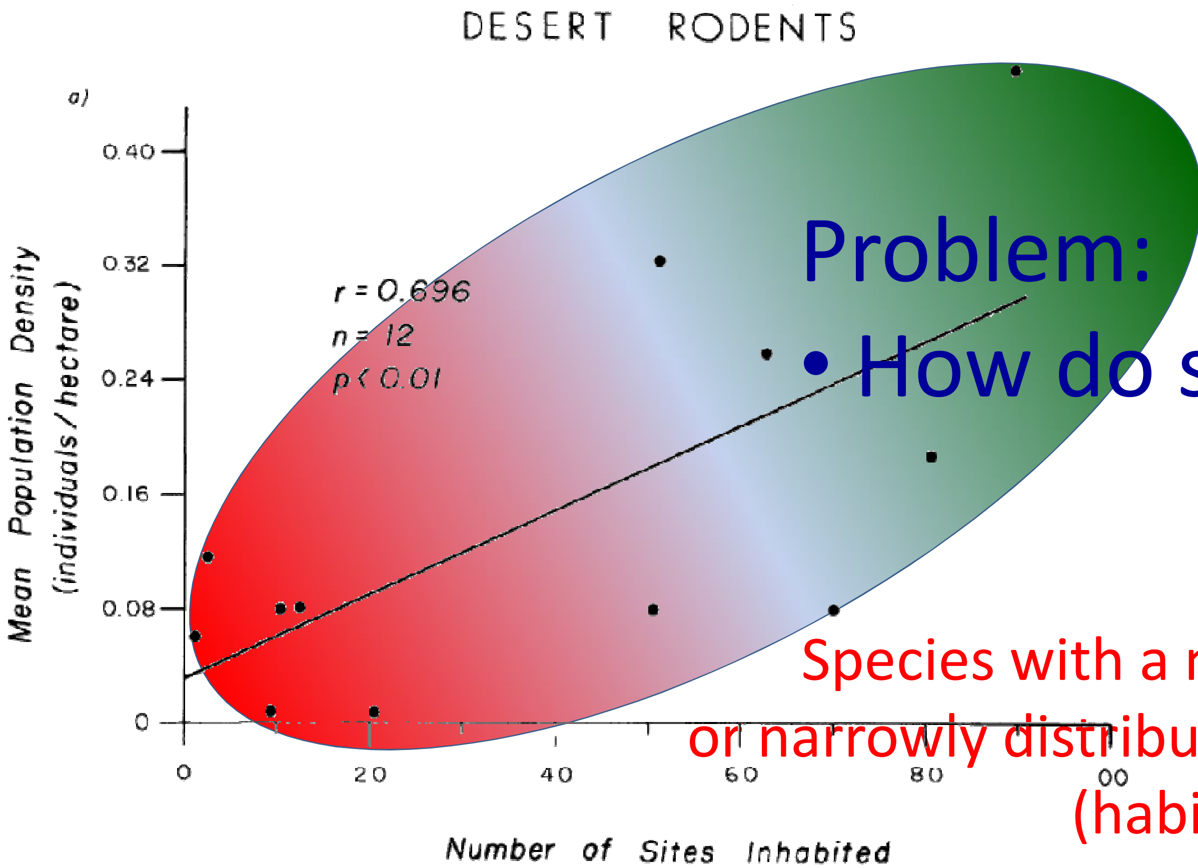
Jack-of-all-trades is master of all

Source: Brown 1984

Abundance – Occupancy relationships

Niche differences

Species with a broad niche
or broadly distributed niches
(habitat generalists)



Problem:
- How do specialists persist?

Species with a narrow niche
or narrowly distributed niches
(habitat specialists)

Source: Brown, 1984

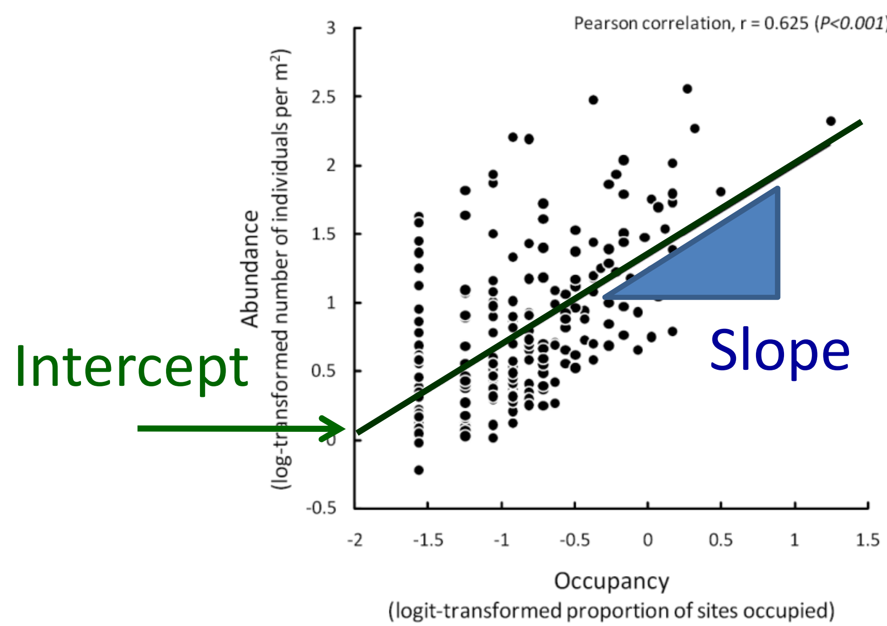
Abundance – Occupancy relationships

Metapopulation dynamics

- Change in species status?
- Bimodal occ-freq distr?

Niche differences

- How do specialists persist?



General

- Degree of scatter: 20-30% explained
- Difficult to disentangle: Both predict a positive relationship
- mismatch between scale of pattern and mechanism

Abundance – Occupancy relationships in pond invertebrates

Ponds

- Clear delineation between suitable and unsuitable habitat
- Aquatic invertebrates include large contrasts in life history

- diet
- reproduction
- dispersal

Life-history strategies:
"sets of coadapted traits solving ecological problems"

Verberk et al. (2008) Freshw Biol 53: 1722-1738

Abundance – Occupancy relationships in pond invertebrates

Life-history strategies:
"sets of coadapted traits solving ecological problems"

Group species
15 traits with three modalities (3^{15} = 14,348,907 combinations)

- Trade-offs
- Alternative suites of traits

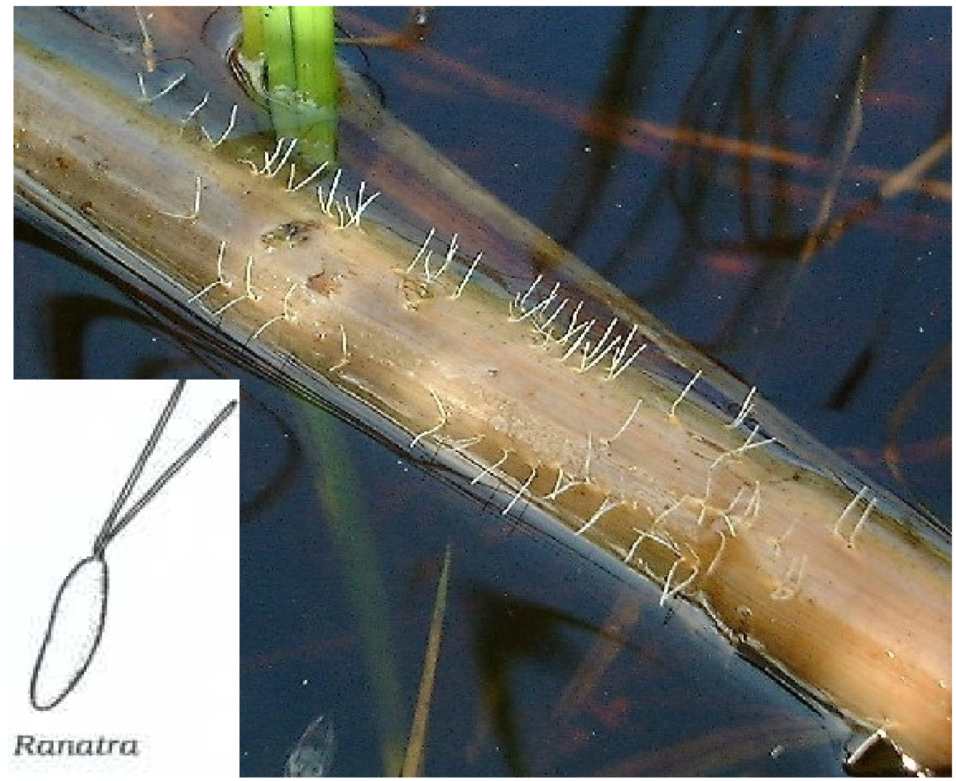
Verberk et al. (2008) Freshw Biol 53: 1722-1738

Life-history strategies in aquatic macroinvertebrates

Different traits combinations may be functionally similar

Egg protection:
- endophytical oviposition

Ranatra linearis (Hemiptera)



Life-history strategies in aquatic macroinvertebrates

Different traits combinations may be functionally similar

Egg protection:
- endophytical oviposition
- gelatinous matrix

Limnephilus sp (Trichoptera)

Life-history strategies in aquatic macroinvertebrates

Different traits combinations may be functionally similar

Egg protection:
- endophytical oviposition
- gelatinous matrix
- brood care

Glossiphonia complanata (Hirudinea)

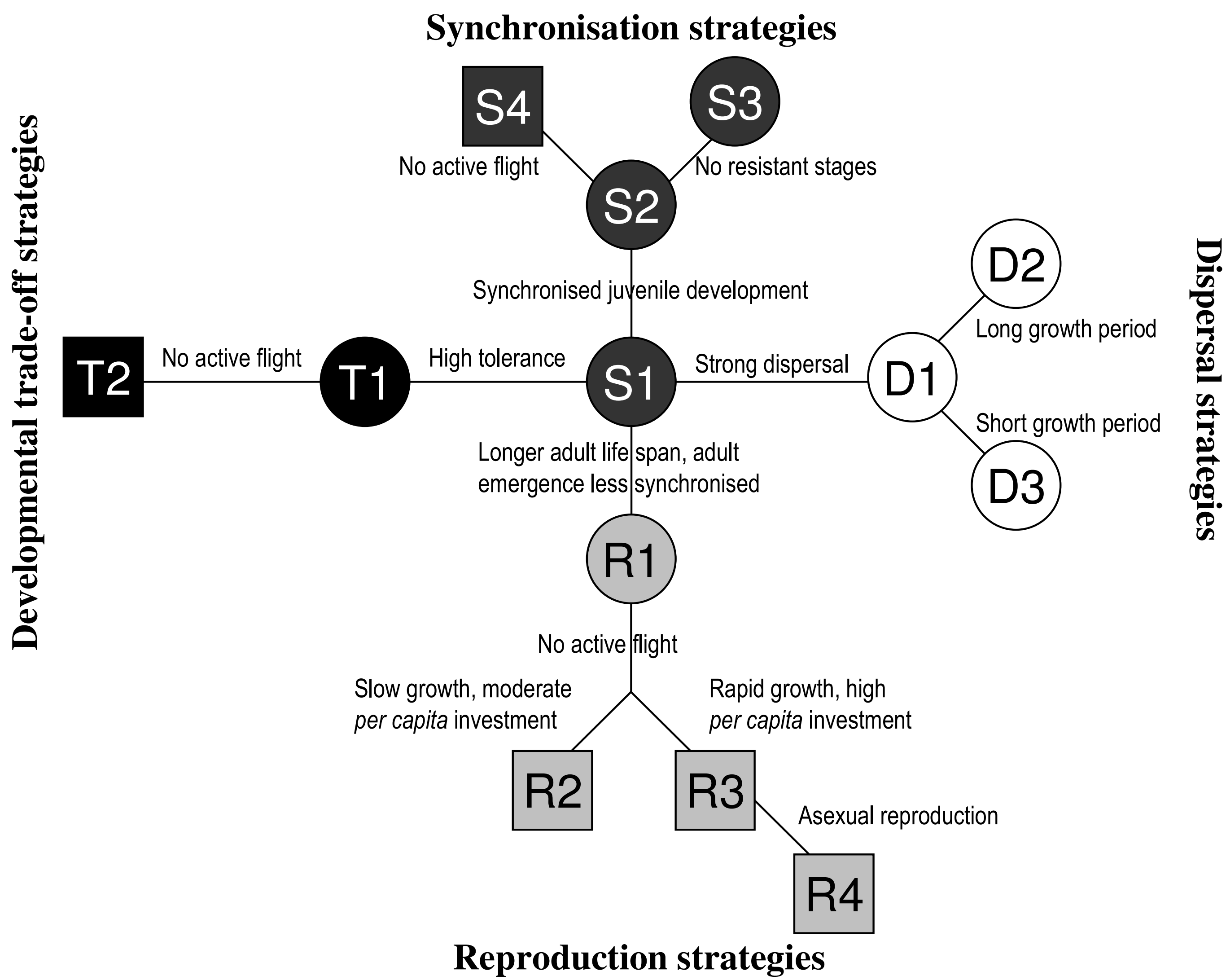
Life-history strategies in aquatic macroinvertebrates

Different traits combinations may be functionally similar

Egg protection:
- endophytical oviposition
- gelatinous matrix
- brood care
- ovoviviparous

Cloeon dipterum (Ephemeroptera)

Life-history strategies in aquatic macroinvertebrates



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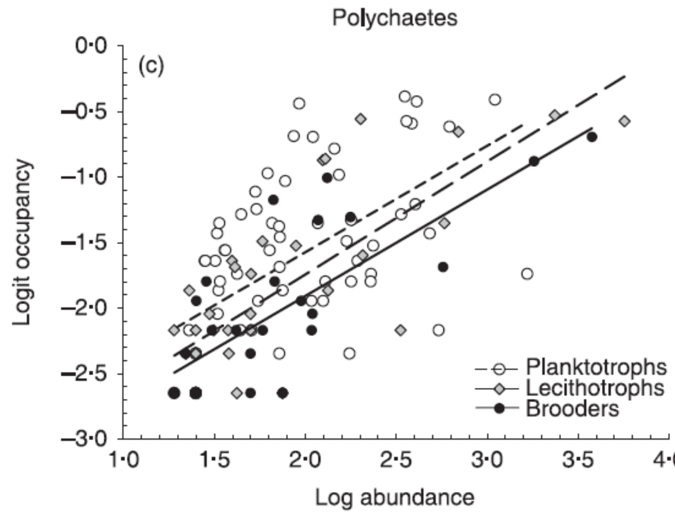
Abundance – Occupancy relationships in pond invertebrates

Ponds

- Clear delineation between suitable and unsuitable habitat
- Aquatic invertebrates include large contrasts in life history



General

- Degree of scatter: 20-30% explained

    incorporate species specific information

Abundance – Occupancy relationships in pond invertebrates

incorporate species specific information

Table 1. Overview of the life-history strategies and their most defining species traits in relation to occupancy and abundance. Less defining species traits and species traits varying within a strategy are left blank. Strategies are ranked from highest to lowest relative abundance (see text). Abbreviations of life-history strategy follow Verberk *et al.* (2008)

Life-history strategy	Number of species	Active dispersal	Rate of juvenile development	Adult longevity	Synchronization of juvenile development	Synchronization of adult emergence	Type of oviposition	Clutch size	High voltinism	Hermaphroditism	Asexual reproduction	Rank order
R4	8	None	Rapid		No	No				x	x	1
T2	7	None	Slow	Months–years	No					x	x	1
R2	3	None	Slow	Months	Some					x		2
R3	3	None	Rapid	Months	Low			Small	x	x		2
D2	4	Strong	Slow			Yes	Clustered	Large				3
D3	11	Moderate	Rapid		No	No	Clustered		x		(x)	3
S1	19	Moderate	Slow	Weeks		Yes	Clustered					3
T1	49	Weak	Slow		Low						(x)	3
S4	13	None	Rapid	Months–years	Yes			Small		x		4
S2	24	Moderate	Rapid		Yes	Yes	Scattered					5
S3	21	Moderate	Rapid	Months–years	Yes	Yes	Scattered					5
D1	45	Strong	Rapid	Months–years		Some	Scattered					6
R1	27	Moderate	Rapid	Months–years			Scattered	Small				6

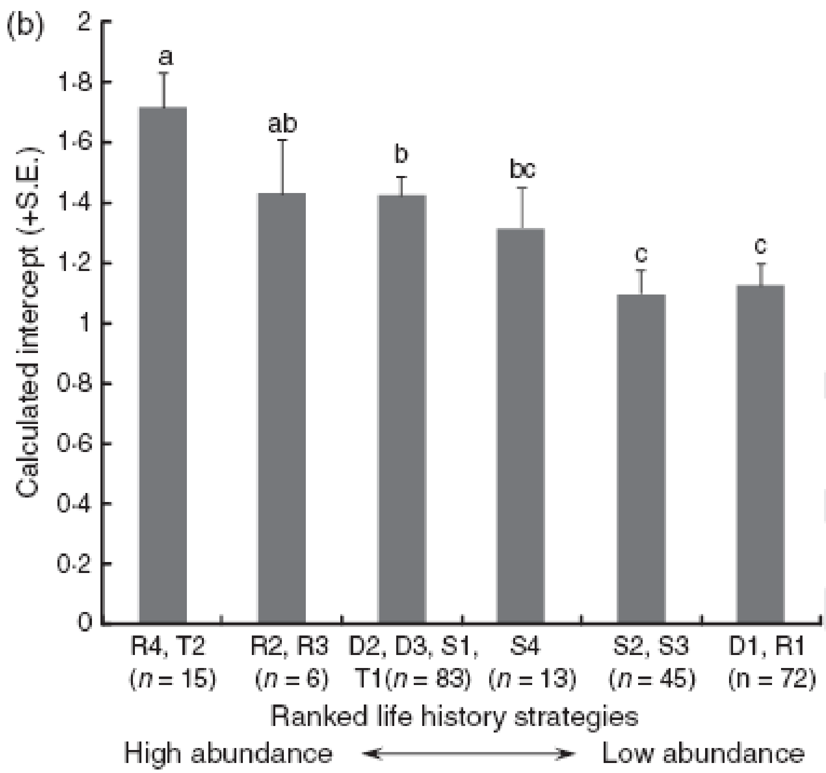
Dispersal

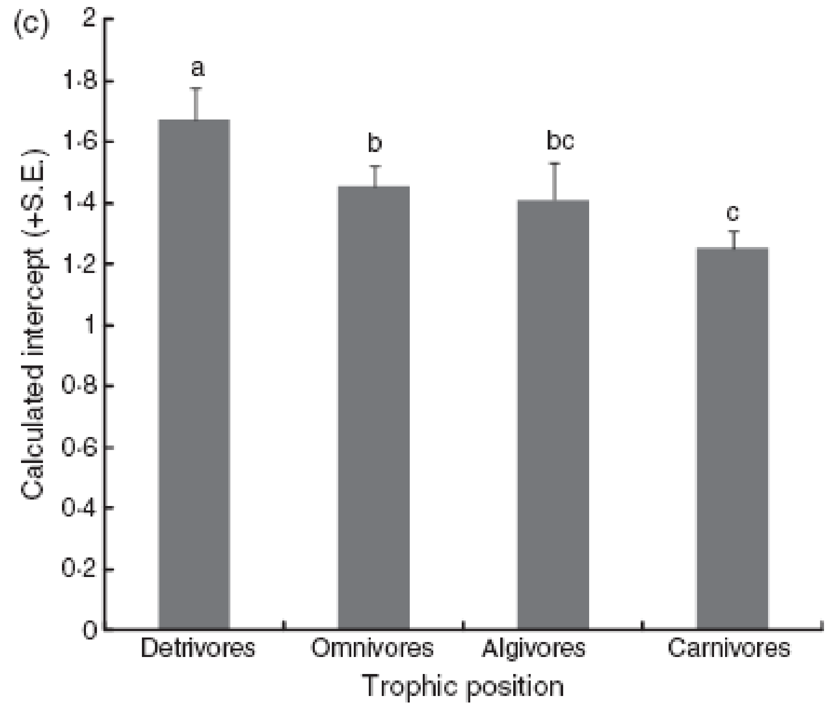
Fecundity & voltinism

Type of oviposition (scattered – clustered)

Abundance – Occupancy relationships in pond invertebrates

incorporate species specific information





Occupancy +

Life-history strategy + Diet = 80.9%

Abundance – Occupancy relationships in pond invertebrates

Ponds

- Clear delineation between suitable and unsuitable habitat
- Aquatic invertebrates include large contrasts in life history

General

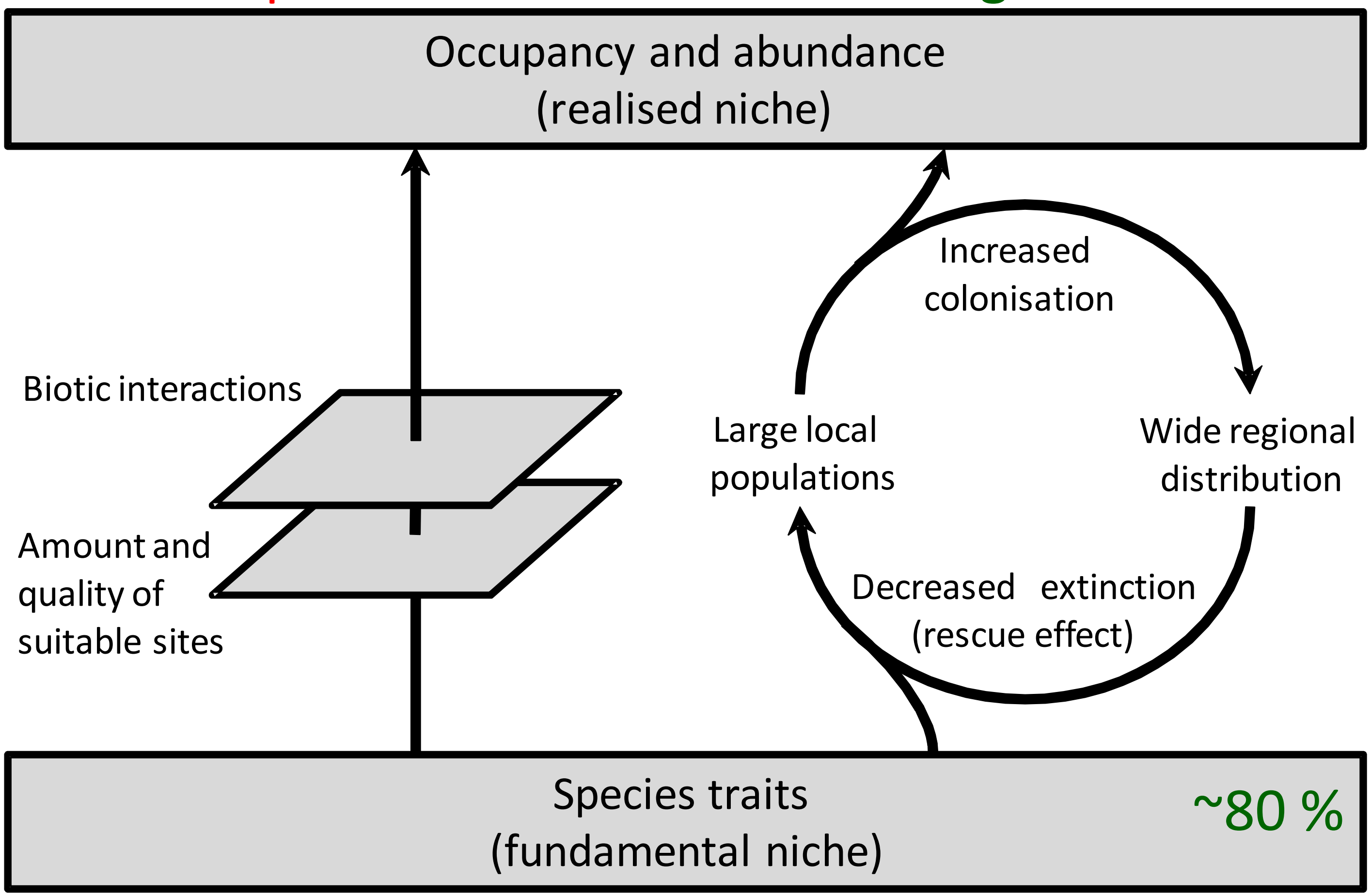
- Degree of scatter: 20-30% explained

  incorporate species specific information: ~ 80%
- Difficult to disentangle: Both predict a positive relationship

  apply to different species

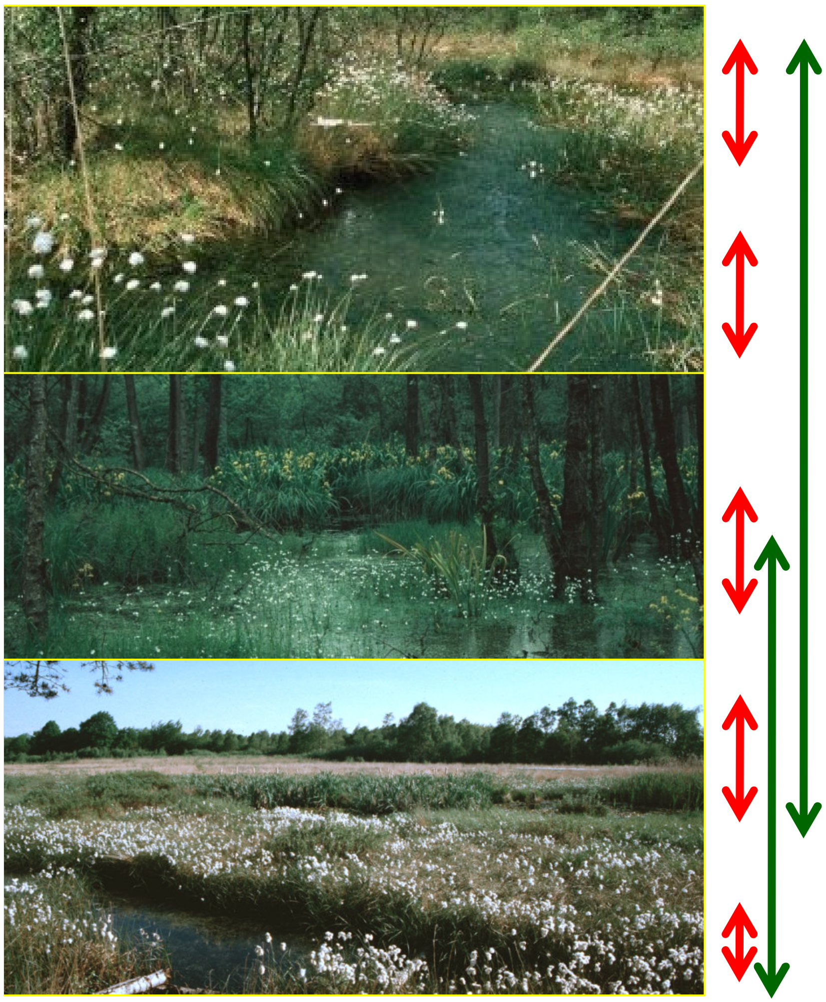
Abundance – Occupancy relationships in pond invertebrates

habitat specialists habitat generalists



Source: Verberk, van der Velde & Esselink *in press*

Abundance – Occupancy relationships in pond invertebrates

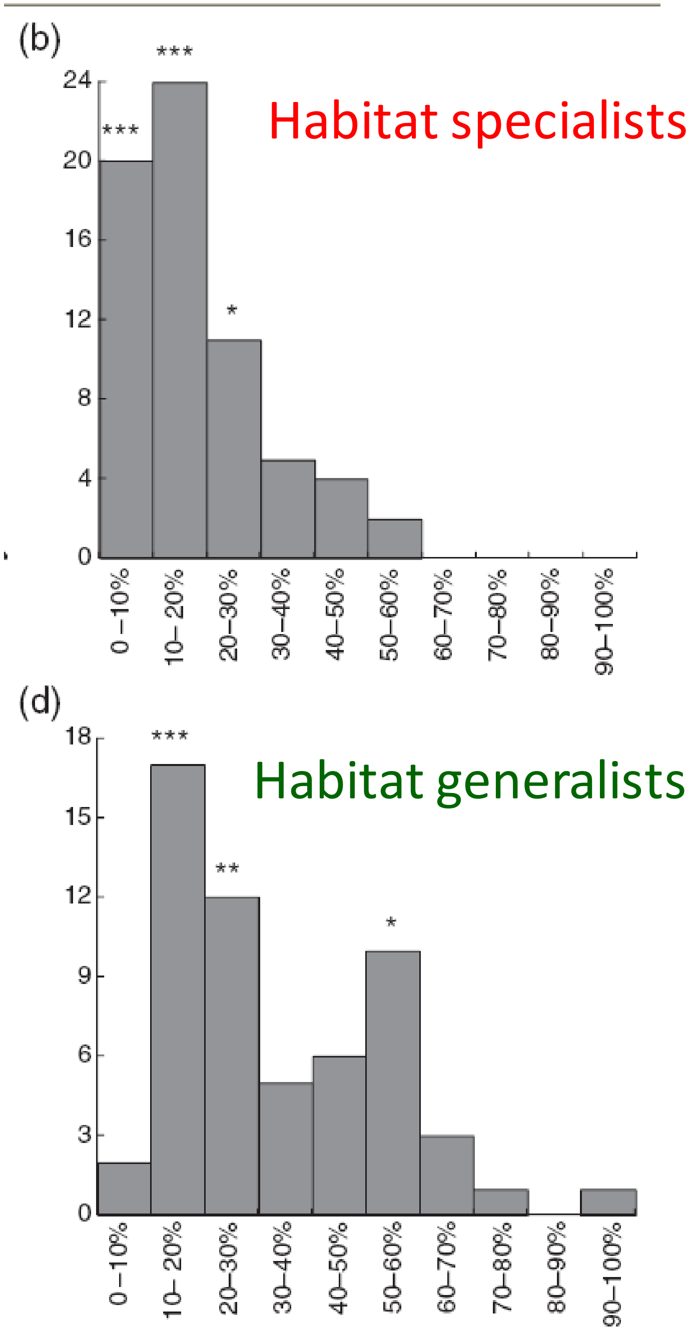


habitat specialists

habitat generalists

$$\text{PS index} = 1 - 0{\cdot}5 \sum_i |p_i - q_i|$$

Source: Verberk, van der Velde & Esselink *in press*



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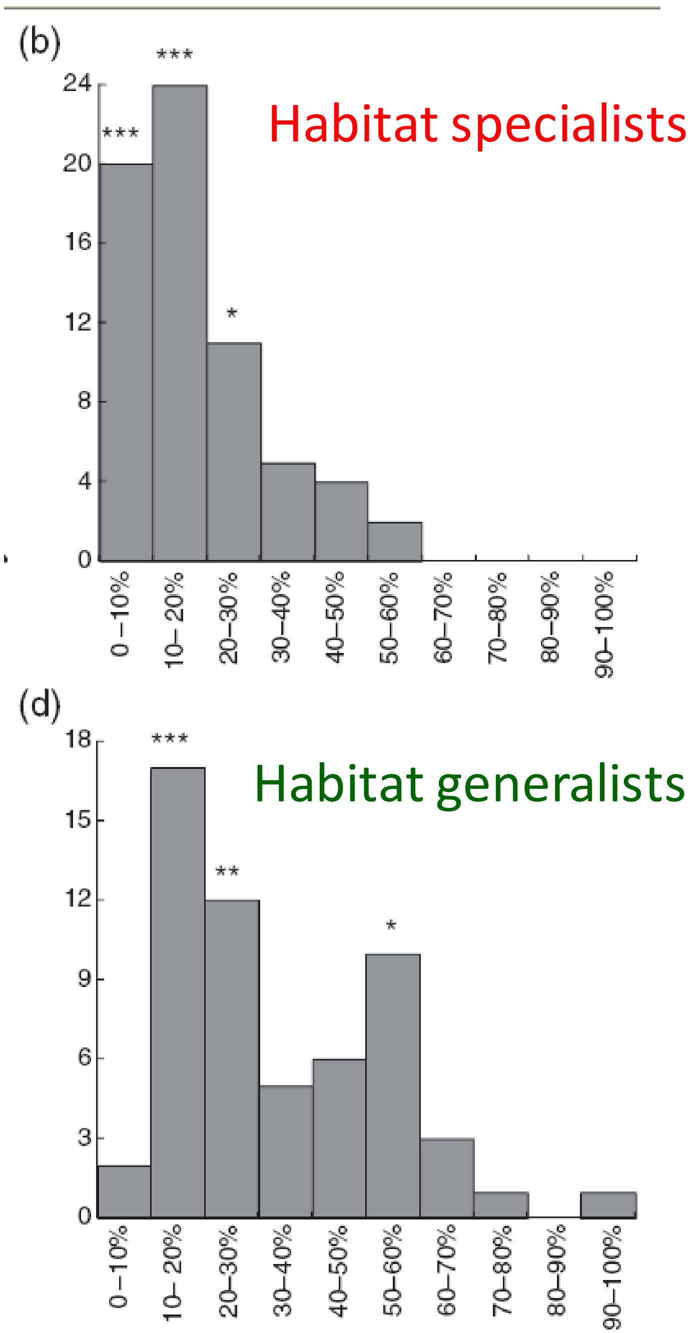

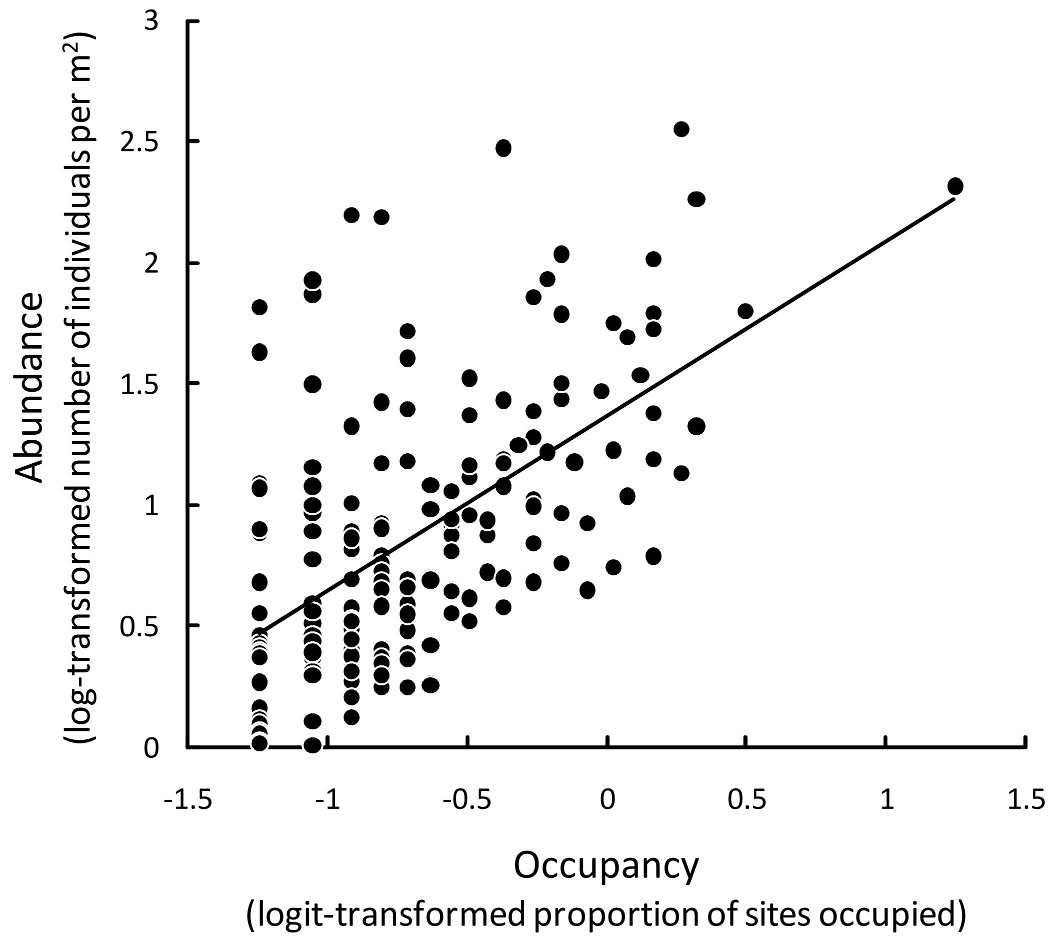

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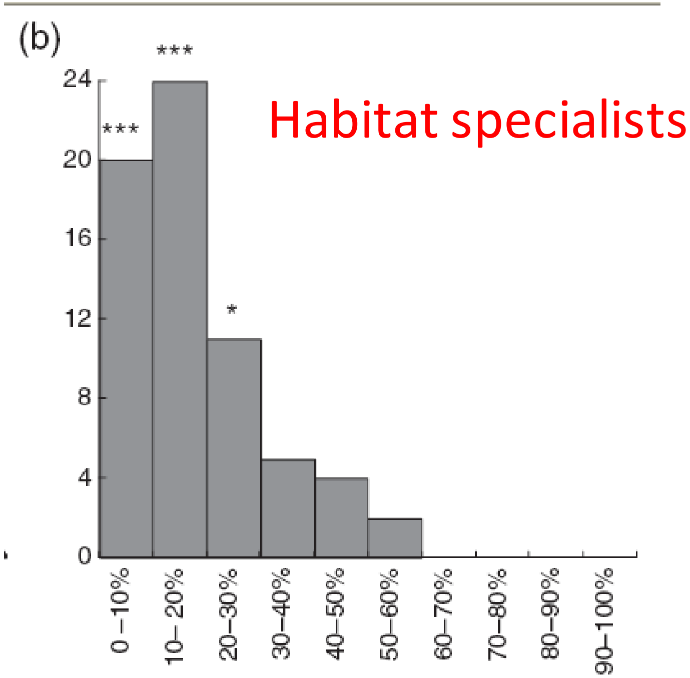

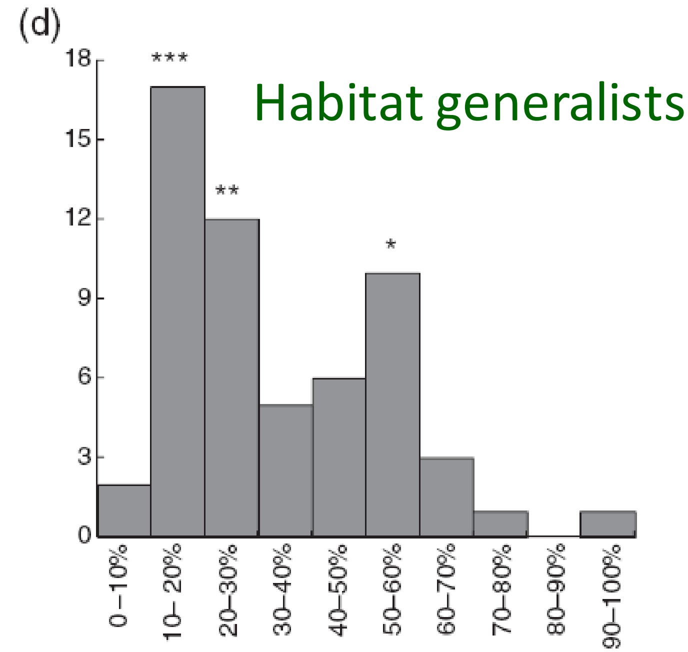

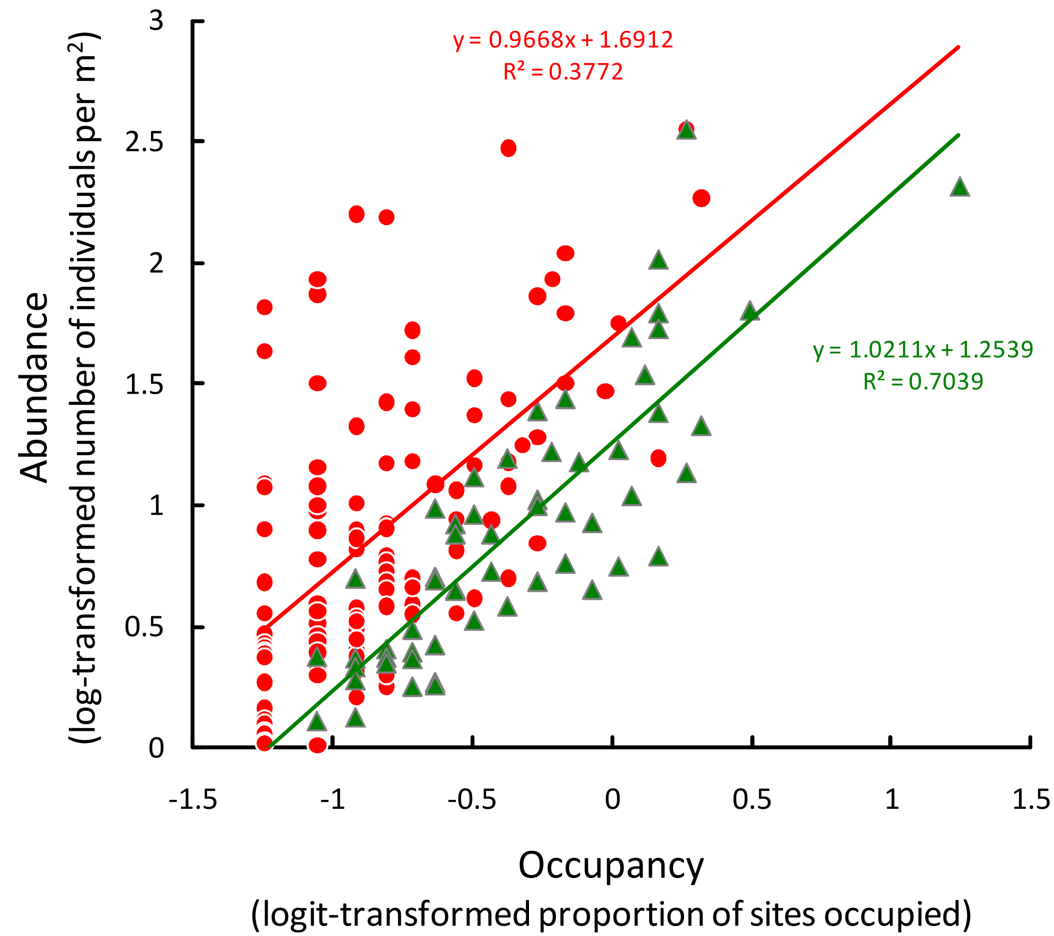

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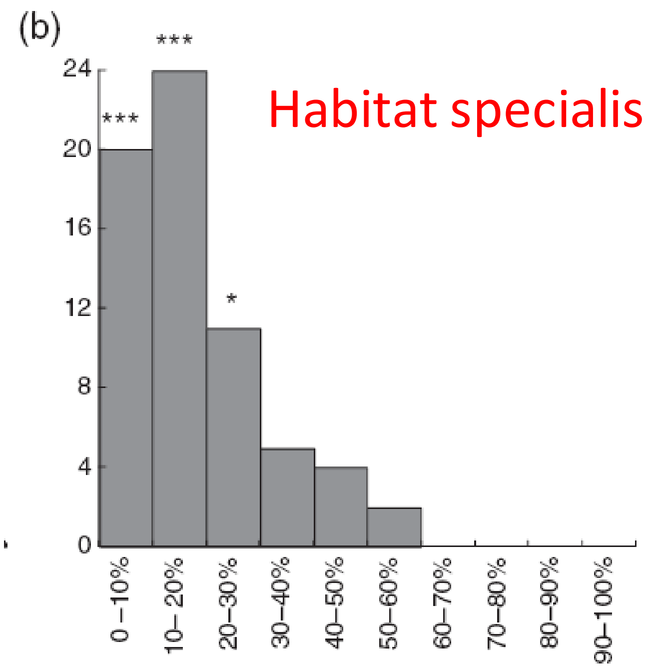
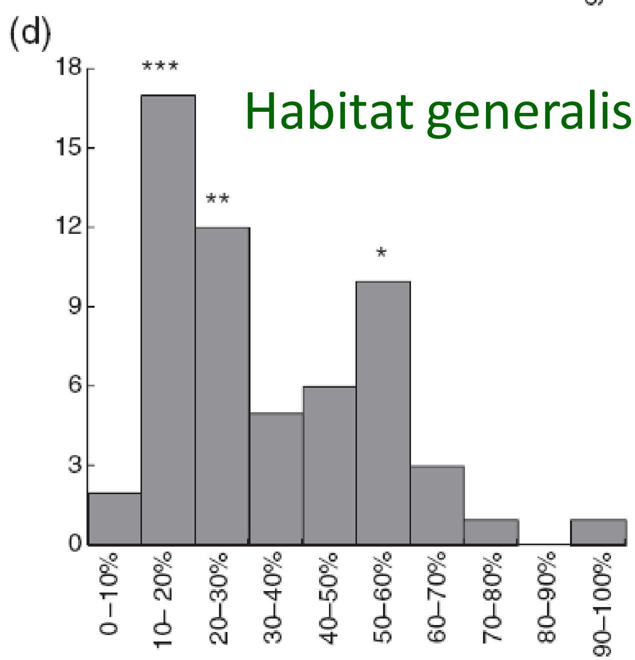
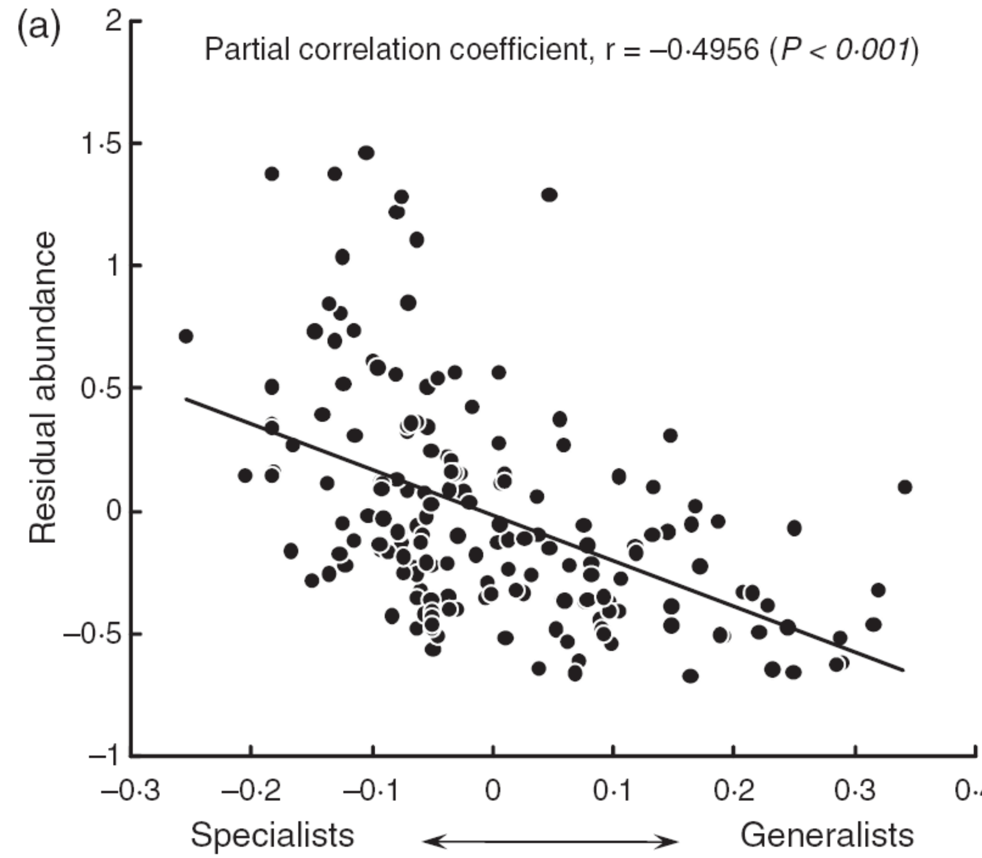


Habitat specialists



Habitat generalists

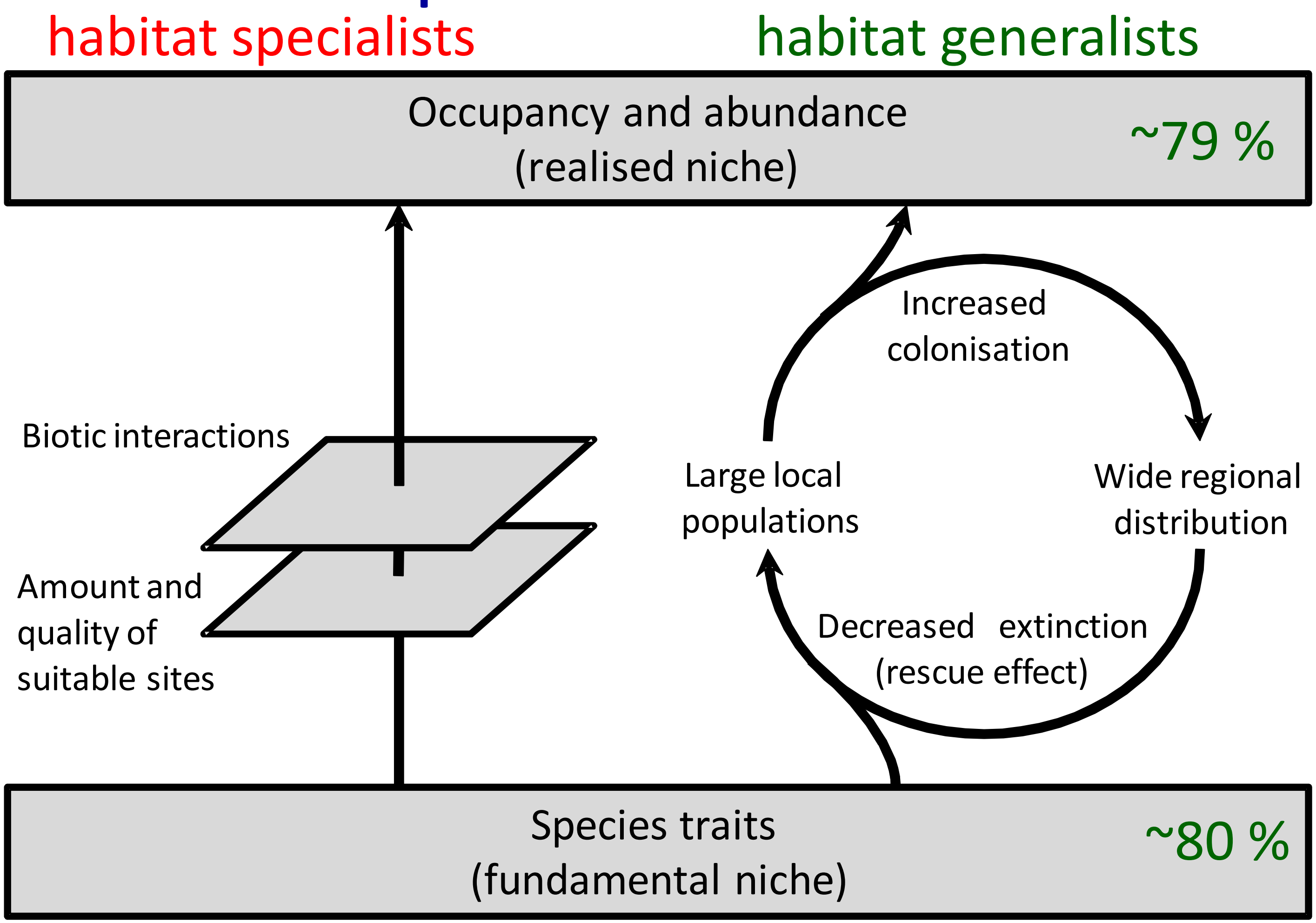


Jack-of-all-trades is master of none

Occupancy + Habitat specialisation = 79.3%

Source: Verberk, van der Velde & Esselink *in press*

Abundance – Occupancy relationships in pond invertebrates



Source: Verberk, van der Velde & Esselink *in press*

Habitat generalists

- Long-lived adults
- Spread reproductive effort
- Adapted to unpredictable habitats

Stochastic element of colonisation and extinction

Persist regionally through risk-spreading
Likely to benefit from improving connectivity

SLOSS

Habitat specialists

- Synchronised life-cycles
- Clustered oviposition or low dispersal capacity
- Adapted to predictable habitat

Interplay between requirements (rooted in traits) and underlying spatial distribution of environmental conditions

Persist locally through numerically large populations
Likely to benefit from improving nature quality (Natura 2000, EU-WFD)

Importance of species-specific information

Large variety in species-environment relationships

(no general rules due to contingency)

At large scales across many species this contingency is less important?

Lack of mechanistic understanding (causality mismatch)

Species-specific information to inform on causality (life-history, physiology)

Problem of how to aggregate information

Life-history strategies

(aggregate similar causal relationships)

General rules? Perhaps, but at least a better understanding

(even for large scale patterns)

Advance both applied and fundamental science

Information sources

Brown, J.H. (1984) On the relationship between abundance and distribution of species. *The American Naturalist*, **124**, 255-279.

Foggo, A., Bilton, D.T. & Rundle, S.D. (2007) Do developmental mode and dispersal shape abundance-occupancy relationships in marine macroinvertebrates? *Journal of Animal Ecology*, **76**, 695-702.

Gaston, K.J. (1996) The multiple forms of the interspecific abundance-distribution relationship. *Oikos*, **76**, 211-220.

Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1997) Interspecific abundance-range-size relationships: an appraisal of mechanisms. *Journal of Animal Ecology*, **66**, 579-601.

Hanski, I. (1982) On patterns of temporal and spatial variation in animal populations. *Annales Zoologici Fennici*, **19**, 21-37.

Heino, J. (2008) Temporally stable abundance-occupancy relationships and occupancy frequency patterns in stream insects. *Oecologia*, **157**, 337-347.

Verberk, W.C.E.P., Siepel, H. & Esselink, H. (2008) Life history tactics in freshwater macroinvertebrates. *Freshwater Biology,* **53**, 1722-1738.

Verberk, W.C.E.P., van der Velde, G. & Esselink, H. (2010) Explaining abundance-occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters. *Journal of Animal Ecology*, **79**, 589-601.