COURSE CODE
ABCS 349

COURSE TITLE
ANIMAL ECOLOGY

CREDIT HOURS

THREE

❑Lecture Period & Venue

- **Mondays: 7:30 - 9:25 hrs** and **13:30 - 16:25 hrs**; **Thursday: 10:30 – 12:25 hrs**; DABCS Lecture Theatre 2

❑ Course Instructors

- **Dr. J. K. Quartey;** DABCS Room 40; Office Hours: Monday – Friday: 9:00 – 16:00; E-mail: *joquartey@ug.edu.gh*
- ***Prof. D. K. Attuquayefio;*** Office Location: DABCS Room 17; Office Hours: Tuesday-Friday: 10:00 - 12:00; E-mail: *dattuquayefio@ug.edu.gh*
- ***Mr. Y. Musah;*** Office Location: DABCS/Marine & Fisheries Dept. Room 82; Office Hours: Monday-Friday: 09:00 - 16:00; E-mail: *ymusah@ug.edu.gh*

❑Assessment & Grading

- Continuous Assessment 30% (Interim Assessment, Assignments & Quizzes)
- Examination 70%

Course Outline

➢ Dr. Jones K. Quartey (5 weeks)

- **Introduction to Animal Ecology**: *Scope and Objectives, Ecological Concepts, Definitions and Study Levels*
- **Experimental Methods in Ecology**: *Laboratory, Field and Natural Experiments (Strengths & Limitations)*
- **Niche Theory and Competition**: *Basis of understanding Community Structure and Organisation*
- **Species Diversity Pattern**: *MacArthur's Species Diversity Model, S-Area Relationship, Island-Biogeography*
- **Foraging Ecology:** *Optimum Foraging Theory, Predator-Prey Relationships, Predator-Avoidance Strategies*

➢ Mr. Yahaya Musah (3 weeks)

- **Measuring Ecological Diversity**: *Within- and Between Habitat Diversity Indices, Strengths and Limitations*
- **Comparing Alpha and Beta Indices:** *Shannon-Wiener, Simpson, Margalef, Berger-Parker, Jaccard, Sorenson*

➢ Prof. D. K. Attuquayefio (2 weeks)

- **Behavioural Ecology**: *Decisions, Adaptations, Social Behaviour and Mating Systems and Strategies*

Objectives of lecture 1

➢**Introduction to the major scopes and concepts in Animal Ecology**

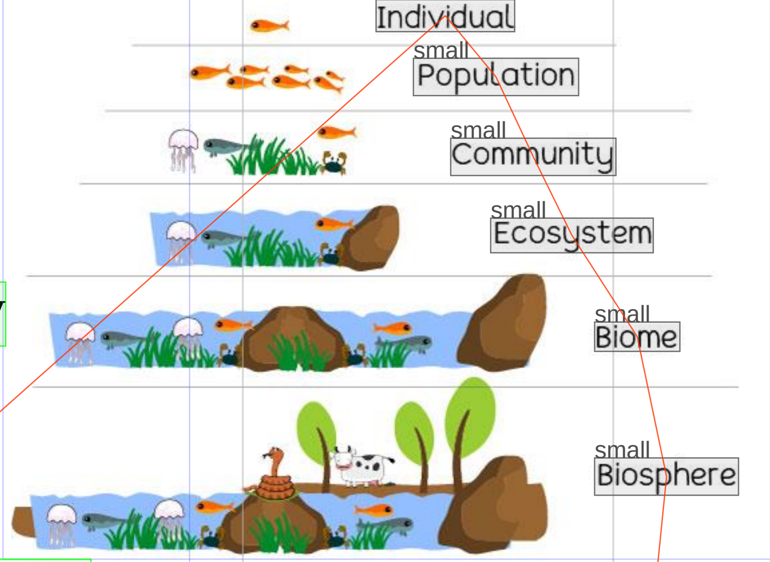
- Trophism, Mobility, Ranges, Behaviour, Reproduction and Dispersion
- Plant-Animal Interactions: Symbiosis and targeted taxa

➢**An overview of 5 major aspects in Animal Ecology**

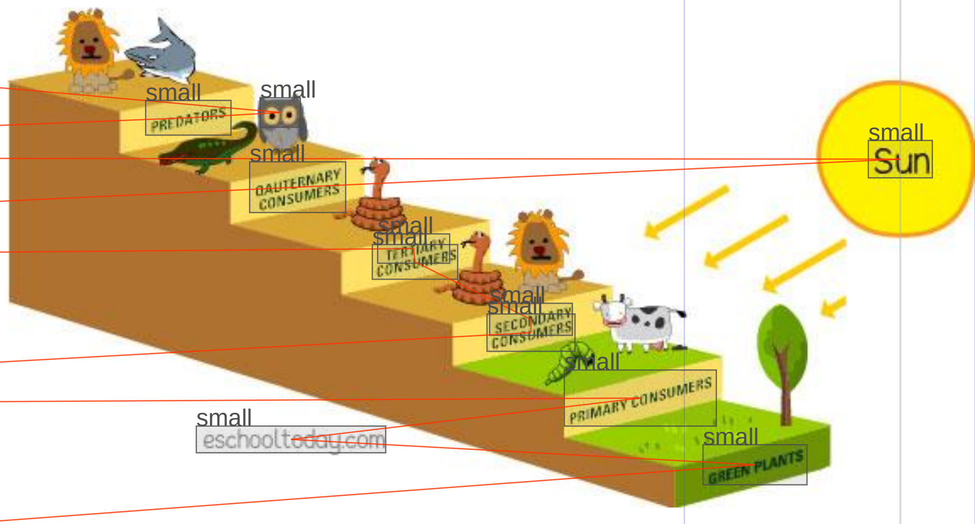
- Evolutionary-Behavioural-Population-Community-Macro-Ecology

➢**Spatial/Organisational levels of Animal Ecology studies**

- **Species**: Genetics (Phenotype/ genotype), niches, habitat requirements
- **Populations**: Growth, structure, regulation and interactions
- **Guilds**: Assemblages of similar species (ecological and/or taxonomical)
- **Communities**: Assemblages of similar and different guilds that interact
- **Ecosystems**: Species, guilds, communities and abiotic factors interacting
- **Biomes**: Highest level with large macro-ecological and geographical regions



Scope and Objectives



❖Basic differences between animals and plants

1. Trophism

- Plants only one trophic level; animals up to 5-7 or more levels (Predators of 6th degree)
- Algae – Copepod – Fish larvae (1) – Dragon fly larvae (2) – Tilapia (3) – Pied kingfisher (4)
- Grass – Locust – Preying mantis (1) – Lizard (2) – Cobra (3) – Mongoose (4) – Python (5) – Leopard (6)
- The relationship between competition and predation in community structuring is far more complex for animals as these can be both prey and predators at the same time (plants are normally only prey for herbivores and few are predatory – carnivorous plants e.g. *Drosera* spp.)

2. Mobility

- Generally, all plants are immobile (except for a few algae) whereas all animals are mobile (except corals and barnacles)
- Field study of animals far more difficult due to seasonal movements, cryptic behaviour etc.
- Implications – challenges in assessing animal population dynamics (distribution, abundance, density and diversity)

3. Ranges

- Animals have larger ranges than plants, especially for migratory animals
- Spatio-temporal (circadian/ circannual) variation in animal ranges poses challenges for describing community structure and interspecific interactions

4. Behaviour

- Animal generally have more complex and diversified behavioural patterns (intra-/ inter- specific interaction, predation, reproduction)

5. Reproduction

- Plants are immobile and reproduction is by fertilization agent (animals, wind or water)
- Many plants depend on animals for their reproduction. E.g. pollinators of pollen and dispersers of seeds
- Mobile animals actively search for reproductive partners, engage in complex courtship behaviour (e.g. vocalization, body display, pheromone attraction, building of structures such as nesting sites, mating chambers) to initiate copulation
- Immobile animals (e.g. marine corals and barnacles) reproduces in a way similar to that of plants (more passive fertilization modes)

6. **Dispersion**

- Plants depends on agents for dispersal whereas animals disperse by themselves by virtue of their mobility
- Good dispersers include flying organisms as well as aquatic organisms that can tolerate a broad temperature range, or highly prolific species with high population turnover

Plant and Animal Interactions

- Plants depend on animals and vice versa
- Examples of animal dependencies on plants: Food (Herbivory), Building materials (Nests), Roosting and shelter (Protection)
- Examples of plant dependencies on animals: Pollination, Seed dispersal, Protection (Predators on Herbivores)

Different aspects of Animal Ecology

- **Evolutionary Ecology** – Focus on how ecology and evolution are linked as inter-related processes. Ecology drives speciation/extinction which again affect community structure
- **Behavioural Ecology** – Focus on how ecology and behaviour is linked. Survival strategies such as Optimal Foraging and Reproductive strategies such as Semelparity/Iteroparity
- **Population Ecology** – Focus on how population grow, are regulated and interaction within and between different species (Competition, Predation, Mutualism, Parasitism)
- **Community Ecology** – Focus on how communities of animals are structured with groups made up of taxonomical and ecological guilds
- **Macro-ecology**: Focus on large scale (global) patterns of animal communities, spatio-temporal patterns of distribution, abundance an diversity on the Earth

Concepts, Definition and Levels

BIOME: All functionally similar ecosystems combined, e.g. West African coastal woodlands

ECOSYSTEM: Biotic and abiotic factors interacting in a specific area (Ghana's coastal woodland)

COMMUNITY: Population of organisms in a specific area, e.g. Legon's Bird Community

GUILD: Assemblage of ecologically and taxonomically related organisms living in a specific, e.g. all sunbirds at Legon

POPULATION: Individuals of same species living in a specific area, e.g. Legon's pied crow

SPECIES: Organisms with same gene pool, e.g. Pied crow

NICHE: Organisms ecological role; an n-dimensional resource hyperspace, e.g. Nectivory

Practical Implications

- Understanding the relationship amongst niches, species, community structure and functioning;

❖**Land and water** – Species-area relationship, habitat heterogeneity, island biogeography models

❖**Crop pests**: Predator-prey relations, anti-predator strategies, invasive species ecology

❖**Design of conservation regions -** Species diversity concentrations, gradients, endemic centres

❖**Vector control of tropical diseases** – Trophic organisations and food webs, predation, competition

❖**World fish stock** – Food webs, predator-prey relations, invasive alien species

In Summary

1. **Animal Ecology is very complex. Plant-Animal interactions important for both**

- *Trophism – Interactions – Mobility – Ranges – Dispersion – Behaviour – Reproduction - Communication*

2. **Five major disciplines in the study of Animal Ecology**

- *Evolutionary ecology, Behavioural ecology, Population ecology, Community ecology and Macro ecology*

3. **Three major interrelated themes**

- *Species abundance, Distribution and Diversity (spatio-temporal)*

4. **Six major organisational/ Spatial levels**

- *Species/Niche – Population – Guild – Community – Ecosystem - Biome*

Lecture 2 – Experimental Methods in Animal Ecology

1. An introduction to the 3 major experimental methodologies in Animal Ecology:

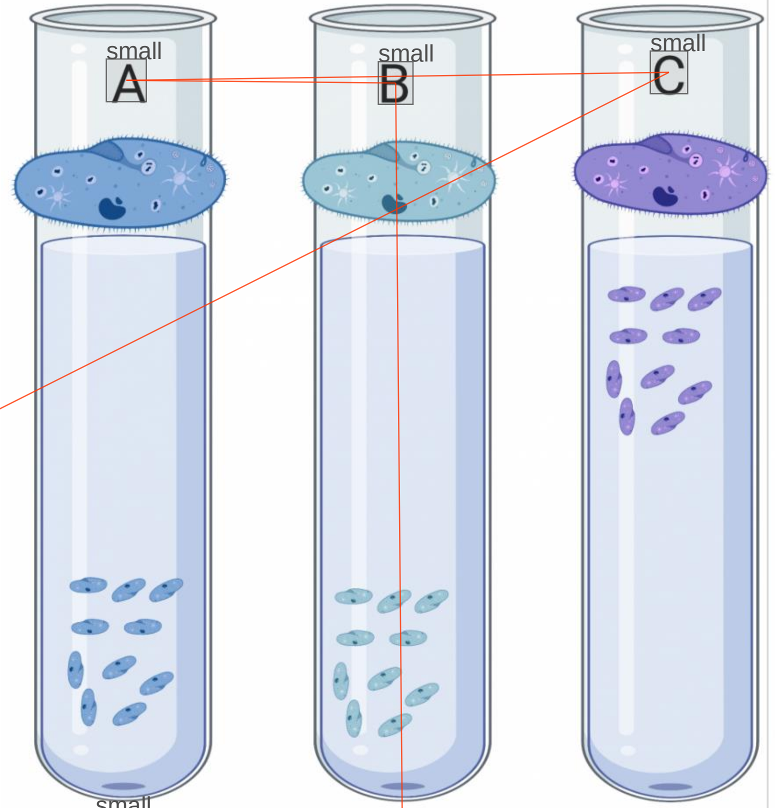
Laboratory tests, Field Experiments, Natural Experiments

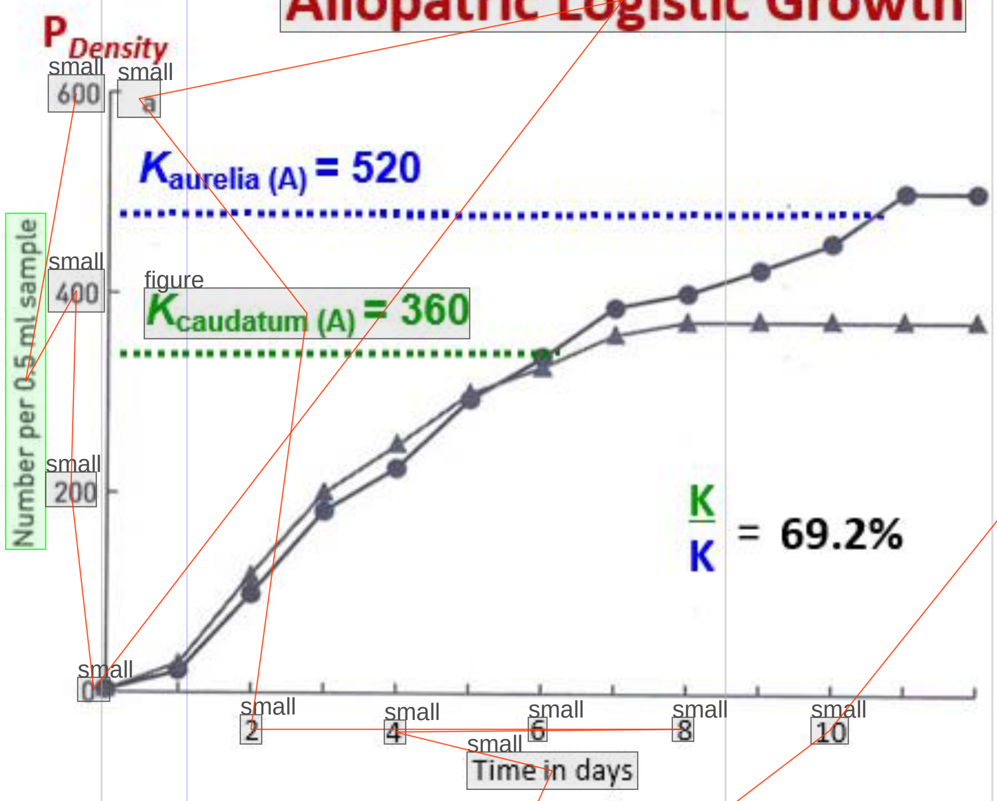
2. An overview of how ecologists use different field approaches to show that **Competitive Exclusion Principle (Gause's Law)** is real
3. A comparison of the strengths and weaknesses of experimental methodologies
4. An account of important ecological concepts related to Gause's Law – **Niche overlap** and **Niche shift**

Method	Famous Examples	Major Advantages	Major Limitations
Laboratory Experiments	• Gause's on cultures of paramecium • Park's on grain beetles	• Better control of confounding factors • Very cheap and fast • Easy to replicate	• Artificial and simplistic environment • Behavioural limitations due to confinement • Only feasible for small or unprotected animals
Field (Manipulation) Experiments	• Connell's on barnacles • Brown and Davidson's on desert mice and ants • Paine's on starfish	• Relatively good controls • Relatively easy to replicate	• Time consuming • Rather expensive • Problematic with large and protected species
Natural Experiments	• Heller's Chipmunks on Californian mountains • Diamond's island ground doves and honey eaters • Nilsson's salmonids in Swedish lakes	• Relatively cheap and fast to replicate • Natural conditions only • Large data samples • No problems with large nor protected species	• Problematic with controls if replicates and samples are small • Confounding factors can compromise validity of patterns

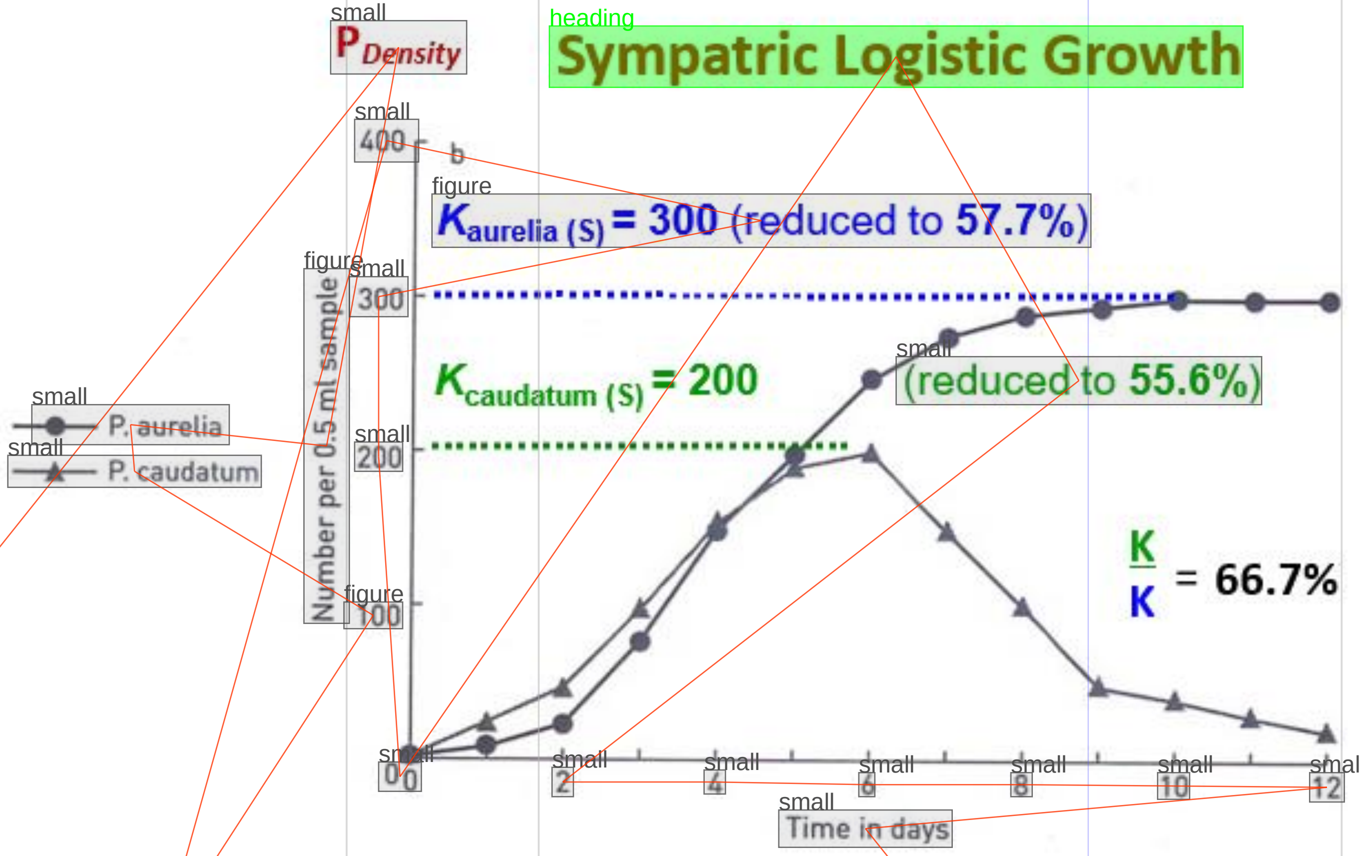
Laboratory Experiments

- Georgy Gause's (1934) Protozoa Cultures (*Paramecium aurelia* & *P. caudatum*)
  - Glass tube experiments
  - Grown separately (allopatric "A & B") or together (sympatric "C")
  - Logistic population growth until carrying capacity (K) reached
  - Carrying capacities (K) measured as volume density of each organism (population density)





Sympatric Logistic Growth



Rockwood, 2006

- Similar decrease in K:
  - ✓ *P. aurelia* = (520-300)/520 = **42.3%**
  - ✓ *P. caudatum* = (360 – 200)/360 = **44.4%**

Laboratory Experiment 2

❑Thomas Park's (1948) Three Grain Beetle species (*Tribolium confusum, T. castaneum* and *Oryzaephilus surinamensis*)

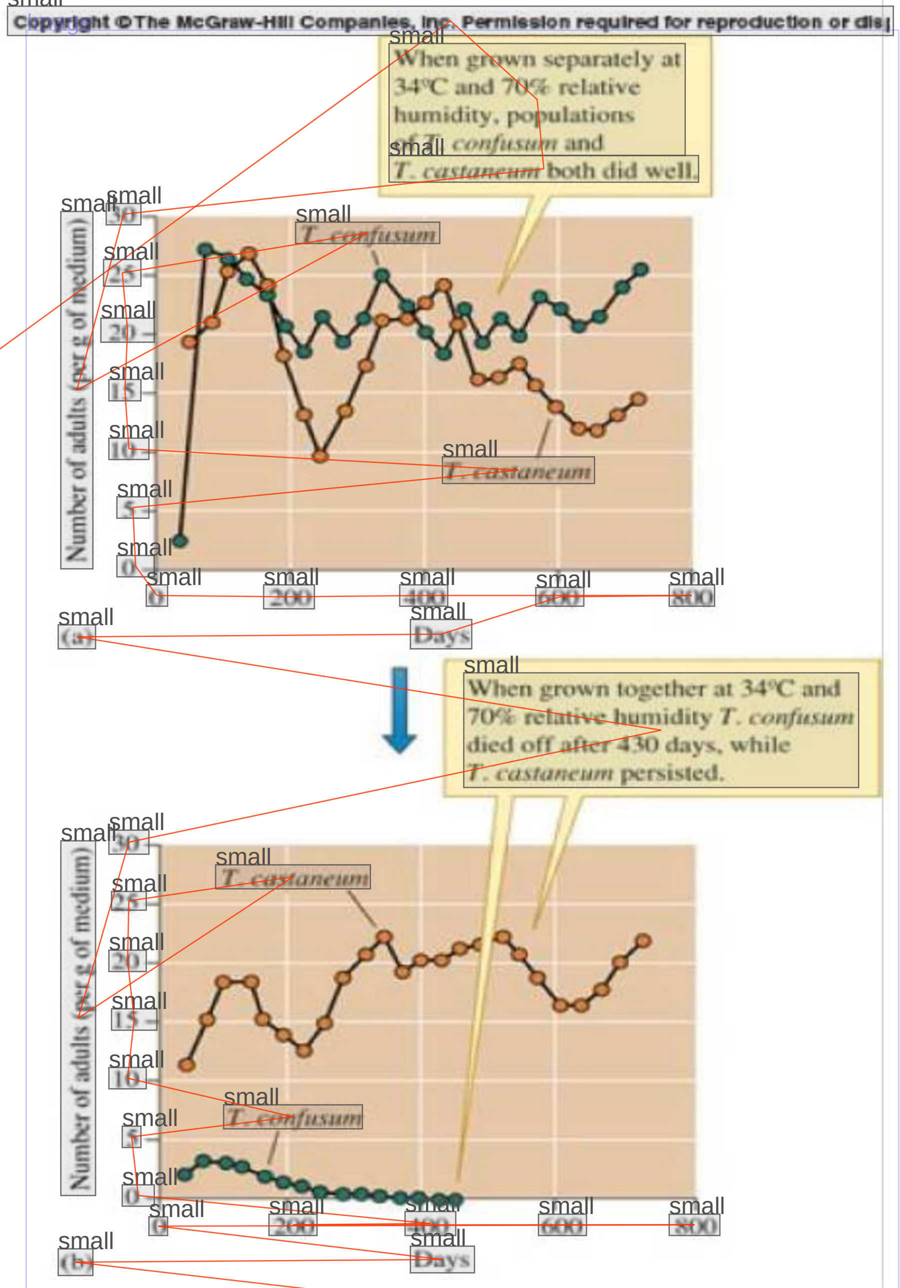
- **Variable** – Climatic conditions (temperature/ moisture) and food availability
- Monitoring of competitive outcome (highest fitness) among 3 grain beetles

✓Moisture gradient: Dry – Moist

✓Temperature gradient: Hot – Warm – Cold

- Demonstrations of Fundamental & Realised niches

Temperature (°C)	Percent relative humidity	"Climate"	Percent of replicates in which one species or the other wins: *T. confusum*	Percent of replicates in which one species or the other wins: *T. castaneum*
34	70	Hot-moist	0	100
34	30	Hot-dry	90	10
29	70	Warm-moist	14	86
29	30	Warm-dry	87	13
24	70	Cold-moist	71	29
24	30	Cold-dry	100	0

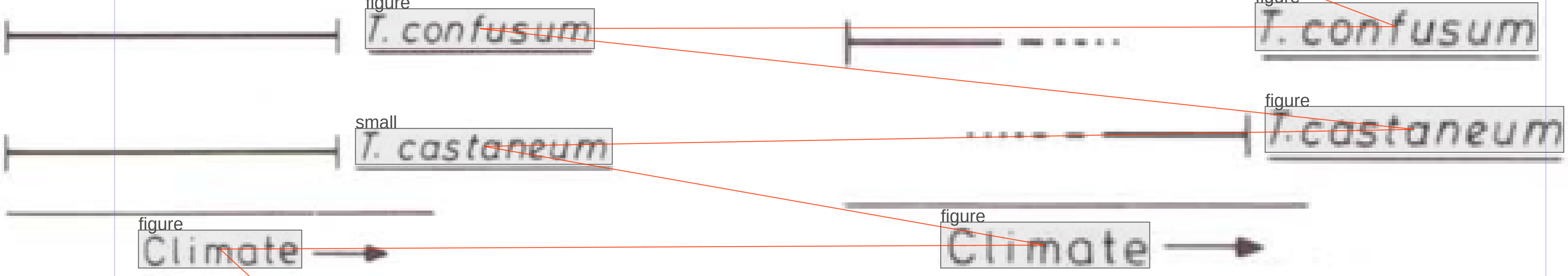


✓ *T. castaneum*: hot-moist specialist

✓ *T. confusum*: cold-dry specialist

Reciprocal competitive exclusion

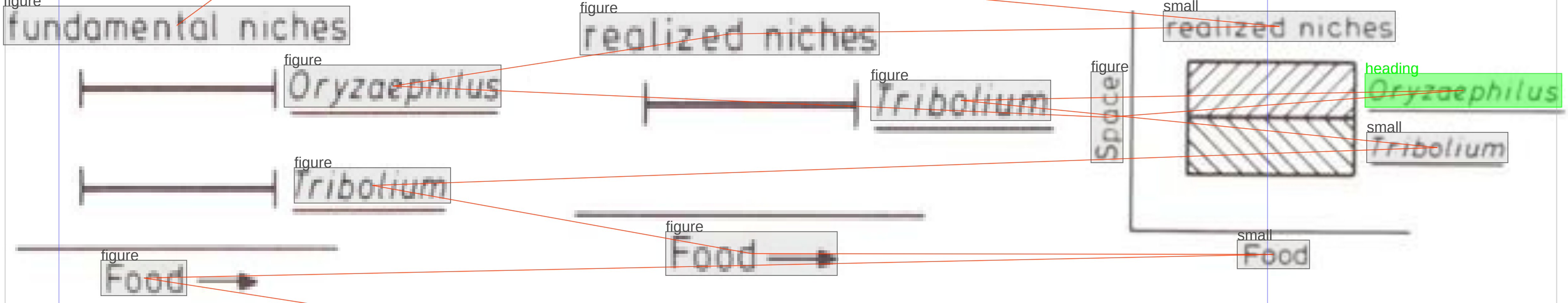
- Fundamental niches
- Realised niches



- Hot-moist vs. cold-dry specialists
- Both species of beetles exhibit identical climate niches in allopatry
- Climatic extremes represented in only one of the two species, with the other species occupying the middle range

- Both *T. confusum* and *Oryzaephilus surinamensis* exhibit similar fundamental niches in allopatry (Crombie, 1974)
- In sympatric medium, *T. confusum* always elimate *O. surinamensis* because of its higher rate of reproduction and better predation ability
- An extra dimension, e.g. space in the form of glass tubes, allow co-existence of the two species

- **Fundamental niche**
- **Realised niche**

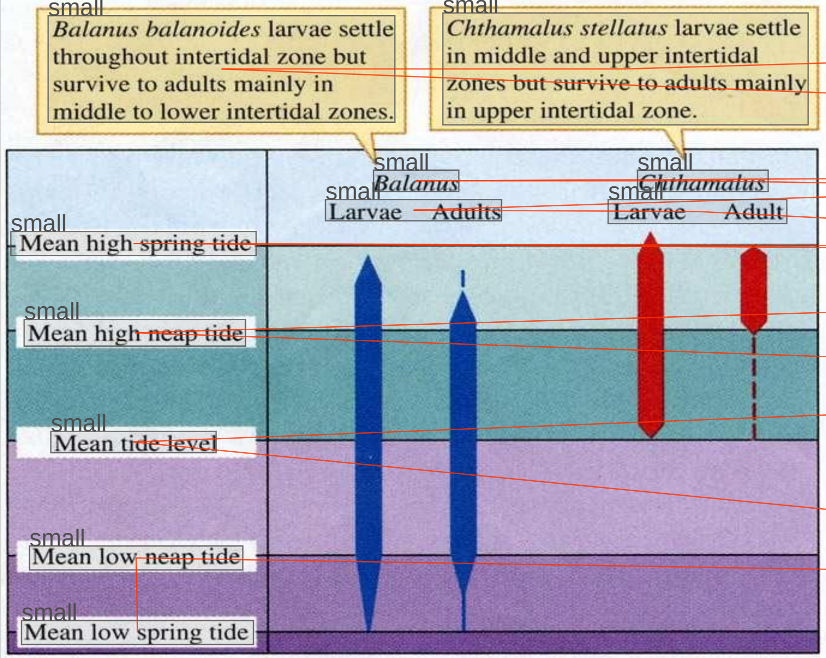


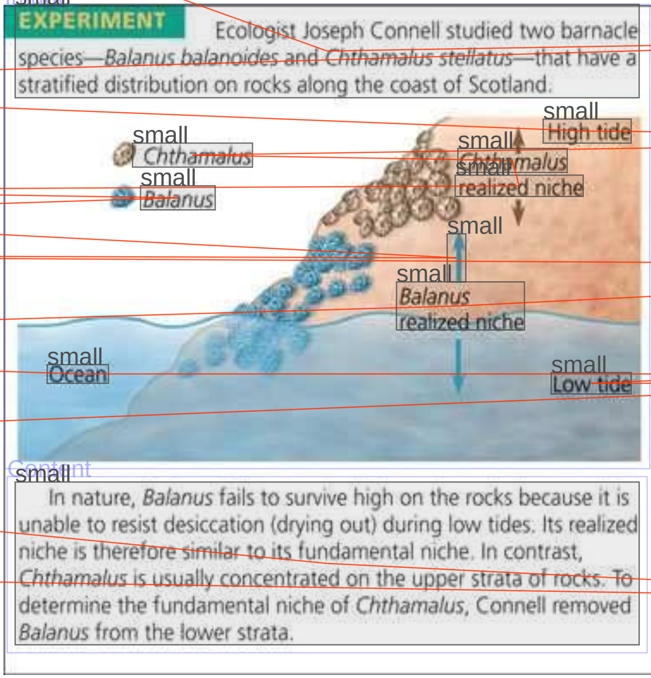
From Begon, Mortimer & Thompson, 1985

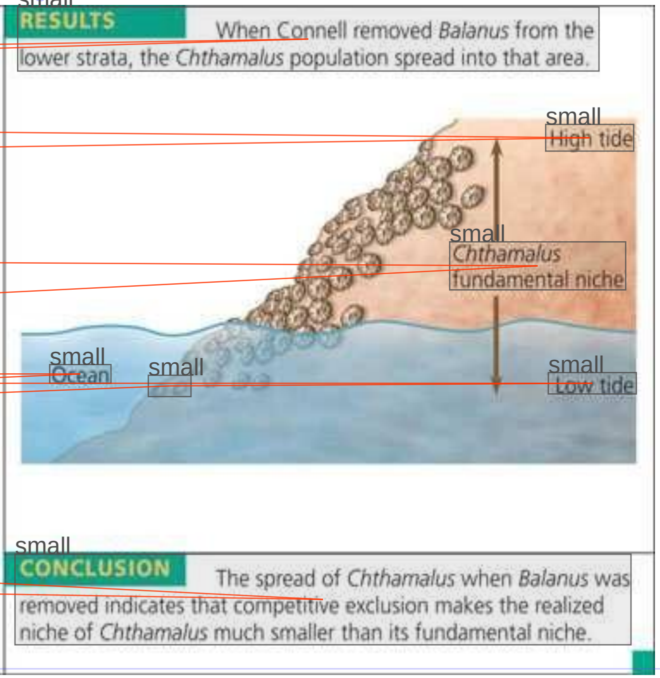
Interspecific Competition – Field Experiments

❑Joseph H. Connell’s (1961) Tidal Barnacles (*Balanus balanoides/ Chthamalus stellatus*)

- Adult *Chthamalus* usually occur above *Balanus*
- *Chthamalus* larvae do settle in *Balanus* Lower Tide Zone (LTZ)
- Adult *Balanus* never in high tide zones (due to desiccation)







- **Methodology** – Connell suspected that adult *Balanus* out competed adult *Chthamalus*. He kept removing *Balanus* adult in lower zones in experimental plots in one set as well as removing *Chthamalus* from upper zone in another

- **Results**

1. Removing *Balanus* from lower zones caused *Chthamalus* to survive

2. *Balanus* never settled in upper zone even as *Chthamalus* was removed there

- **Conclusion**

1. Adult barnacles compete over space in lower zones

2. Balanus is superior (crushing *Chthamalus*) leaving a small realized niche (upper zone) for *Chthamalus*

3. Fundamental niche of *Chthamalus* includes dry upper zones where *Balanus* cannot withstand desiccation

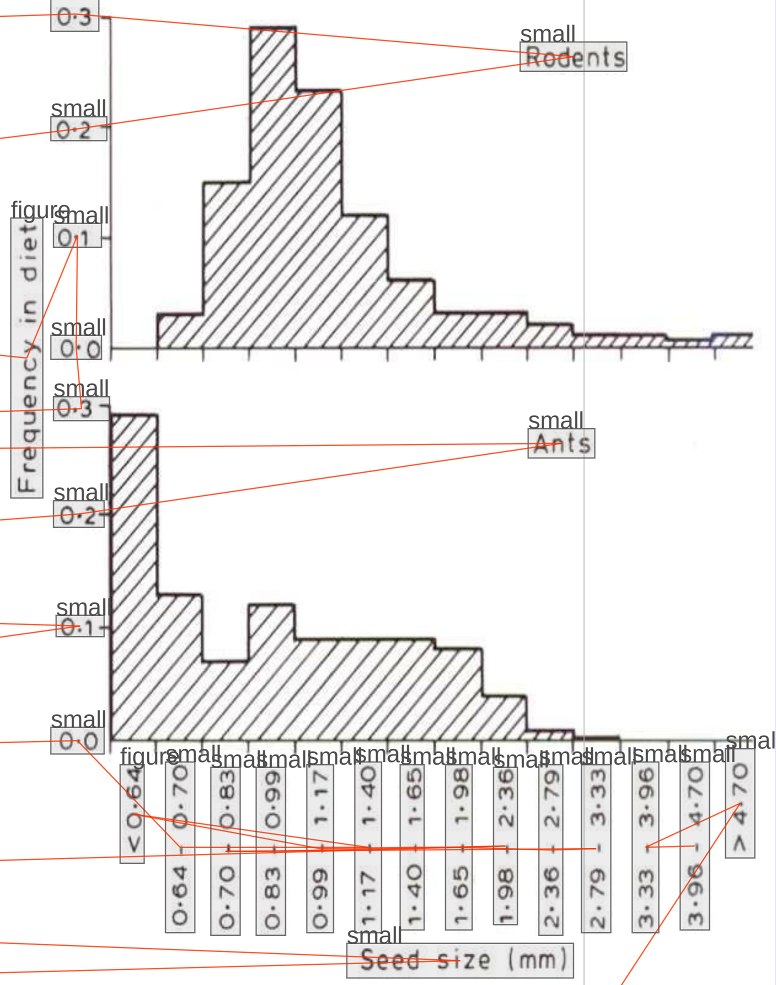
Interspecific competition – Field Experiment 2

- Brown & Davidson’s Granivorous Desert Ants and Rodents in Arizona

- Ants and rodents were observed to overlap in seed utilization, and the question was then: Are they competing for a limited resource (=seeds)?

• Experimental Design

1. Ant-Removal Plots were sprayed with pesticides regularly
2. Rodent-Removal Plots were fenced and subjected to intensive trapping protocols
3. Both ants and rodents removed
4. Control Plots with both ants and rodents present



- Results

1. Rodents removed – Ant colonies increase above control plots
2. Ants removed – Rodents densities increase above control plots

	Rodents removed	Ants removed	Rodents and ants removed	Control
Ant colonies	543	—	—	318
Rodent numbers	—	144	—	122
Seed density relative to control	1.0	1.0	5.5	1.0

- **Conclusions**

1. As one competitor is removed the remaining increase. Density Compensation occur – Release of extra resources that is no more utilized by the removed species
2. Ants and rodents have overlapping limited food resource niche (seeds) over which they compete

From Begon, Mortimer & Thompson, 1985

Interspecific Competition – Field Experiment 3

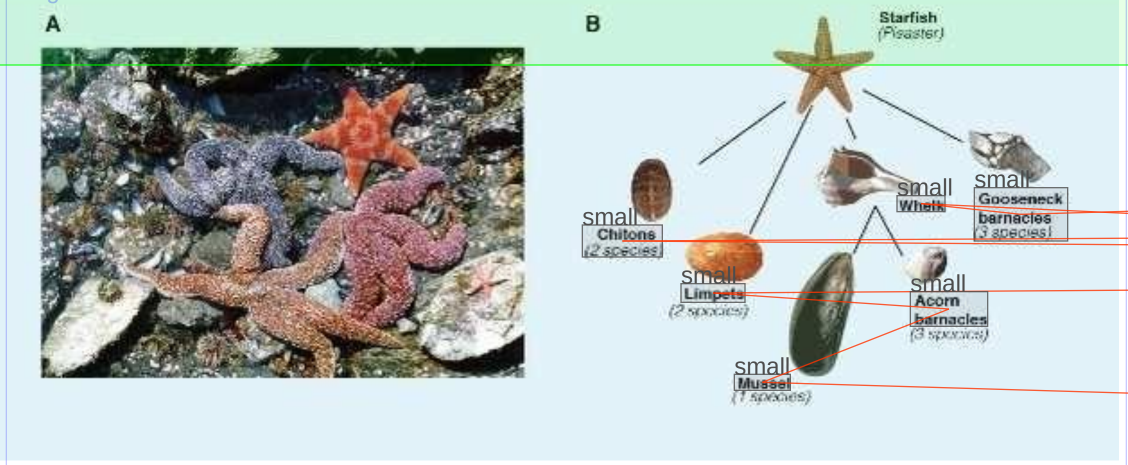
- Paine's (1966) starfish (Pisaster) in rocky intertidal zones of the US: Predator-mediated Coexistence

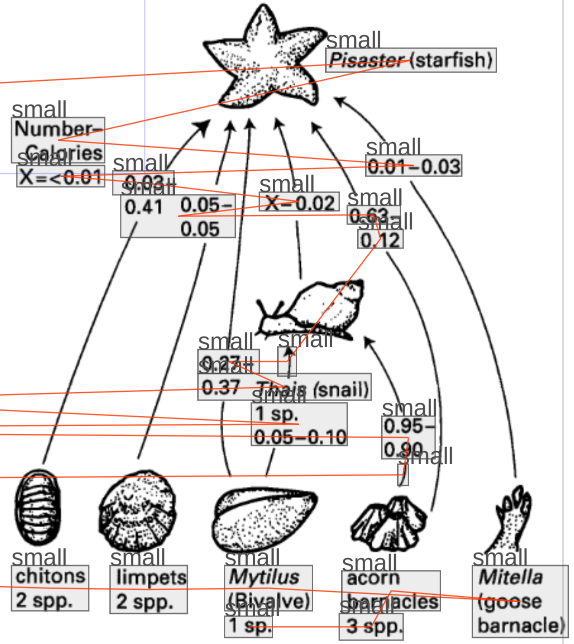
- Picaster (a keystone predator) predates differentially on the dominant competitors (bivalves & acorn barnacles)

- Removal of the predator showed that the more dominant competitors crowded out the inferior species (goose barnacles, limpets and chitons)

- This reduced the total number of coexisting species from 15 to 8

- A classic example of Top-Down control of communities (trophic cascading effects or predator-mediated coexistence at lower trophic levels)

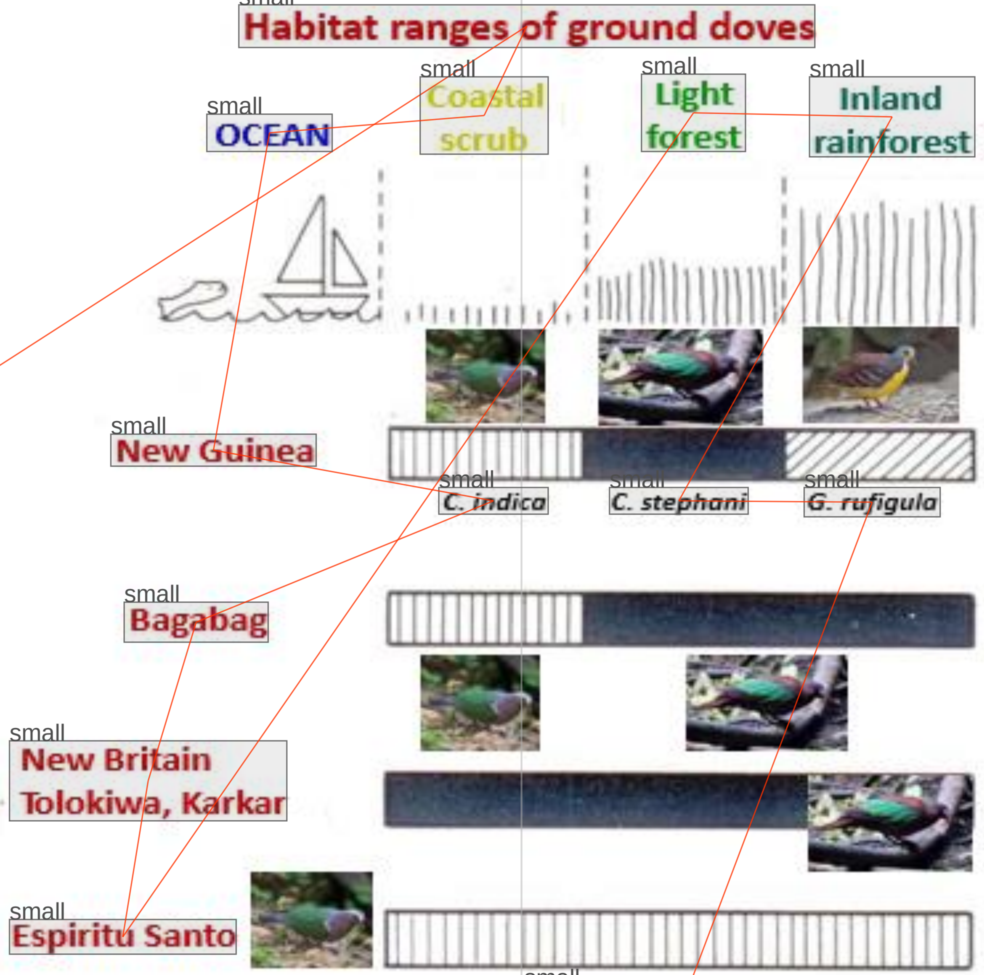




Ecological Release (Habitat) – Natural Experiments 1

❑Jared M. Diamond's (1975) Ground Doves on Papua New Guinea and associated islands (*Chalcophaps indica*, *C. stephani* and *Gallicolumba rufigula*)

- Mainland (New Guinea): All 3 Ground doves living sympatrically in distinct habitats (no overlap)
- Large island (Bagabag): Only 2 species – In the absence of *G. rufigula*, *C. stephani* expands its niche to include inland rainforest
- Very small islands (New Britain, Tolokiwa, Karkar, Espiritu Santo) – Only one species (*C. indica*) present and it's able to occupy all three types



From Begon & Mortimer (1985)

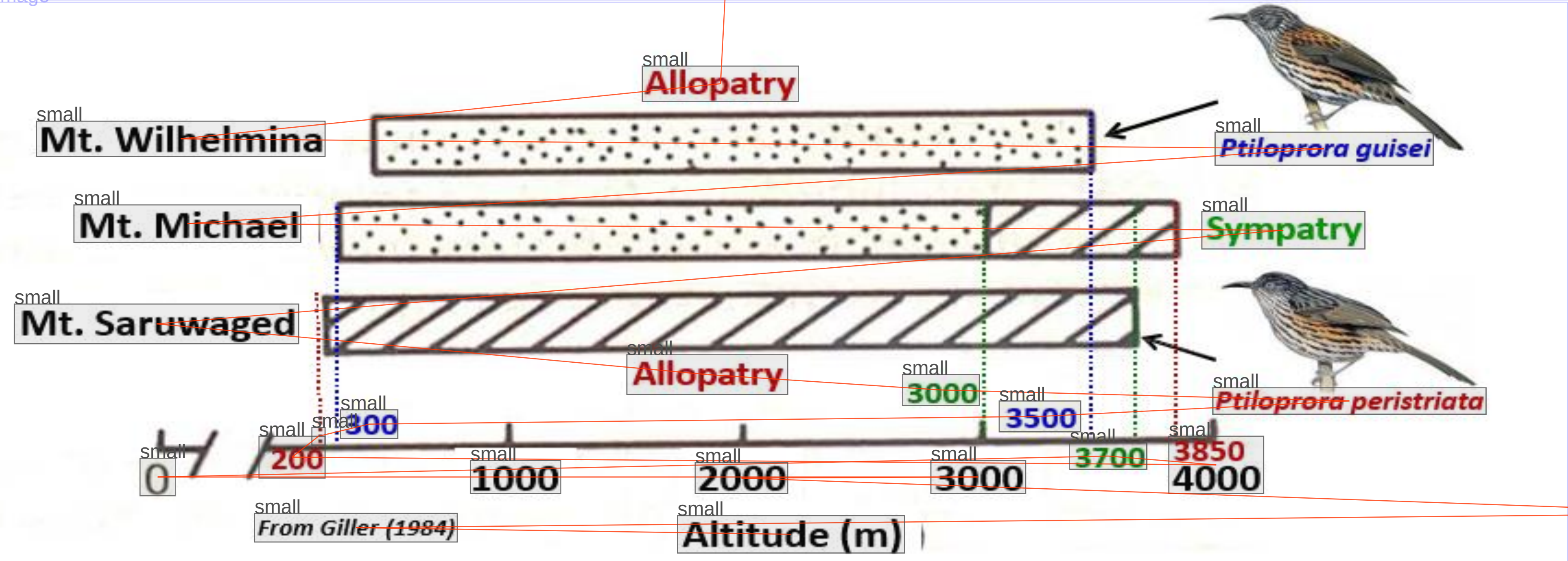
❑Conclusion

- Fundamental niches of the 3 doves shown only when in allopatry
- When in sympatry, each species excludes the other two from its specialized habitat = Contiguous Allopatry
- There is competitive exclusion on New Guinea and competitive release elsewhere

Ecological Release (Habitat) – Natural Experiments 2

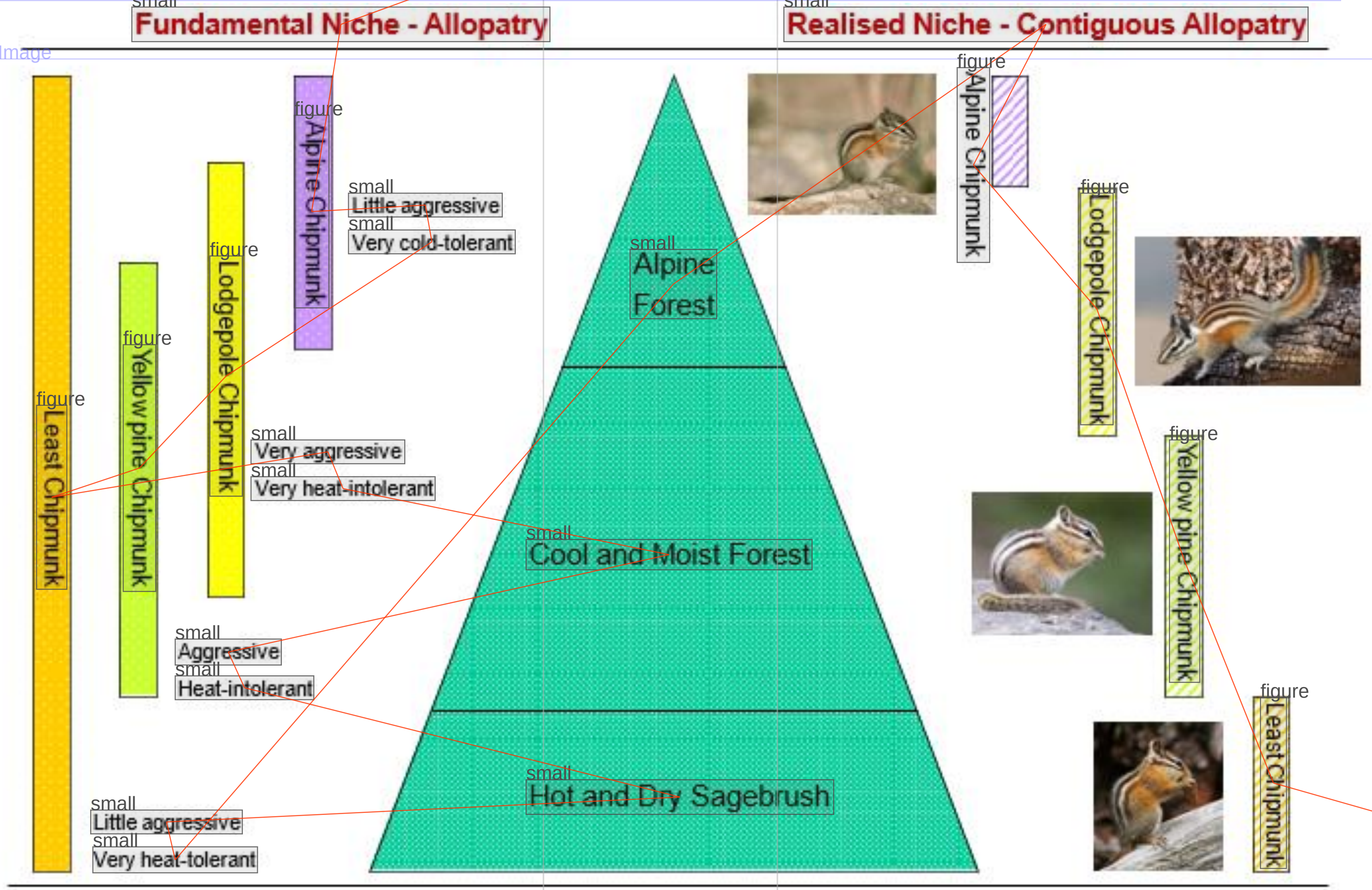
- Jared M. Diamond's (1975) – 2 Honeyeaters on 3 Papua New Guinea mountains

- **Fundamental niche**: similar – ***P. guisei* = 300 – 3500**m; *P. peristriata* = 200 – 3850m
- **Fundamental niche**: overlap – 3200/3650 ≈ 88%
- Ranged reduced (allopatry to sympatry) from 200-3700 to 3000-3850 m: 850/3500 ≈ 25%
- **Realised niche** of inferior species (*P. peristriata*) only 25% of the fundamental niche
- Another example of habitat related (altitudinal = vertical spatial) Ecological Release



Contiguous Allopatry – Natural Experiment 3

- H. C. Heller's (1971) chipmunks in Sierra Nevada mountains, California



Ecological Release/Niche Shift – Natural Experiment 4

❑Nils-Arvid Nilsson’s (1963) Salmonids in Swedish Lakes (Asymmetric Niche Shift)

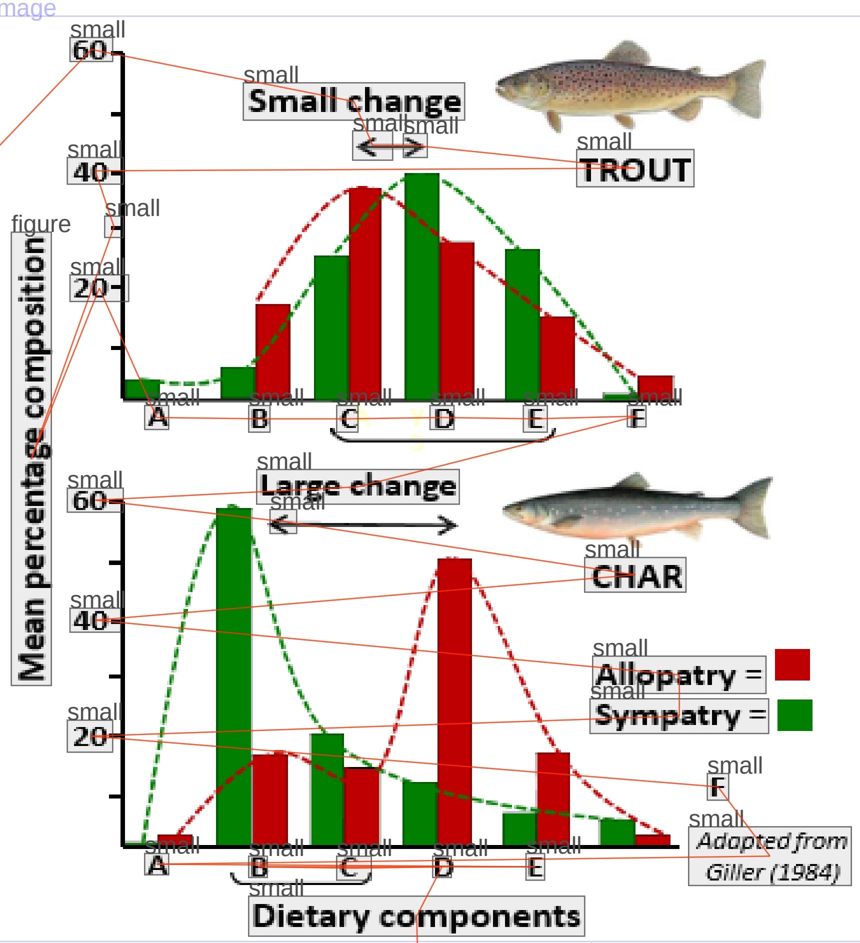
- Assessment of diets (6 food types) of 2 Salmonids
- Great overlap in food utilization in allopatry
- Large crustaceans (C), Insect larvae (D) and terrestrial insects (E) preferred by both species in allopatry
- In sympatry;

✓ **Char** specializes greatly (60%) on small crustaceans (B), greatly reducing consumption of insect larvae (D) and terrestrial insects (E)

✓ **Trout** largely remains a generalist in sympatry

✓ Large crustaceans/molluscs are shared in sympatry

✓ **Char’s** dietary composition greatly changed in sympatry; **Trout’s** not



A = Fish, **B** = Small crustaceans, **C** = Large crustaceans
D = Insect larvae, **E** = Terrestrial insects, **F** = Miscellaneous

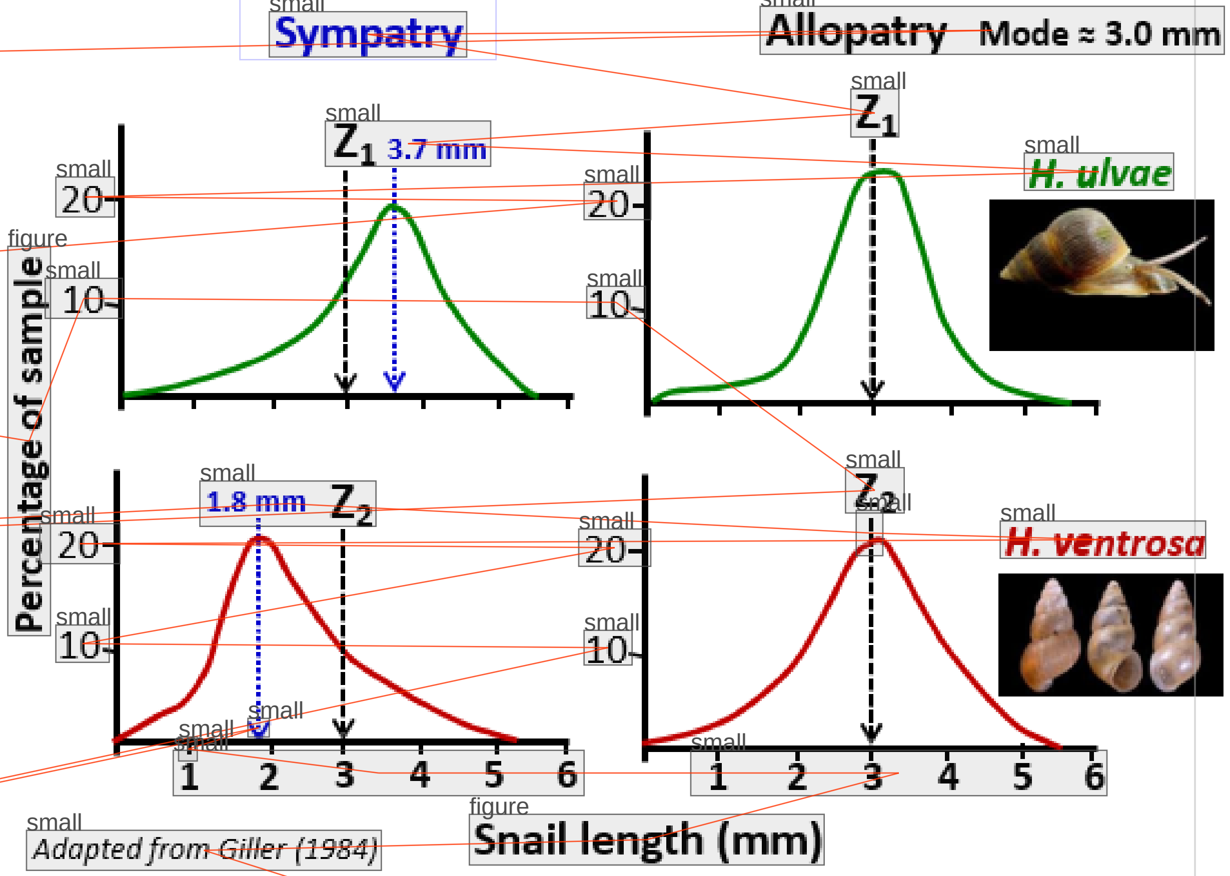
Limiting Similarity – Character Displacement 1

- Tom Fenchel's (1975) Character Displacement in Marine Mud Snails, Denmark

  - Measurement of lengths of 2 species of snails; *Hydrobia ulvae* and *H. ventrosa*
  - Shell length correlated with food size
  - Allopatry: Snail length almost identical, mode ≈ 3.0 mm
  - Sympatry: Snail length distinctively smaller for *H. ventrosa*, mode ≈ 1.8 mm, but bigger for *H. ulvae*, mode ≈ 3.7 mm

Tom Fenchel's (1975) Character Displacement in Marine Mud Snails, Denmark

- Food size of the two species in allopatry very similar
- Allopatry: Both species – mode = c.60 µm in diameter
- Sympatry: *H. ulvae* = c. 100 µm; *H. ventrosa* = c. 60 µm
- **Conclusion**: The snails compete for the same limiting food resource and *H. ulvae* diverge towards the large-sized food hence reducing niche-overlap



Adapted from Giller (1984)

Limiting Similarity – Character Displacement (2)

Community-wide Character Displacement & Hutchinson's Size Ratio Rule

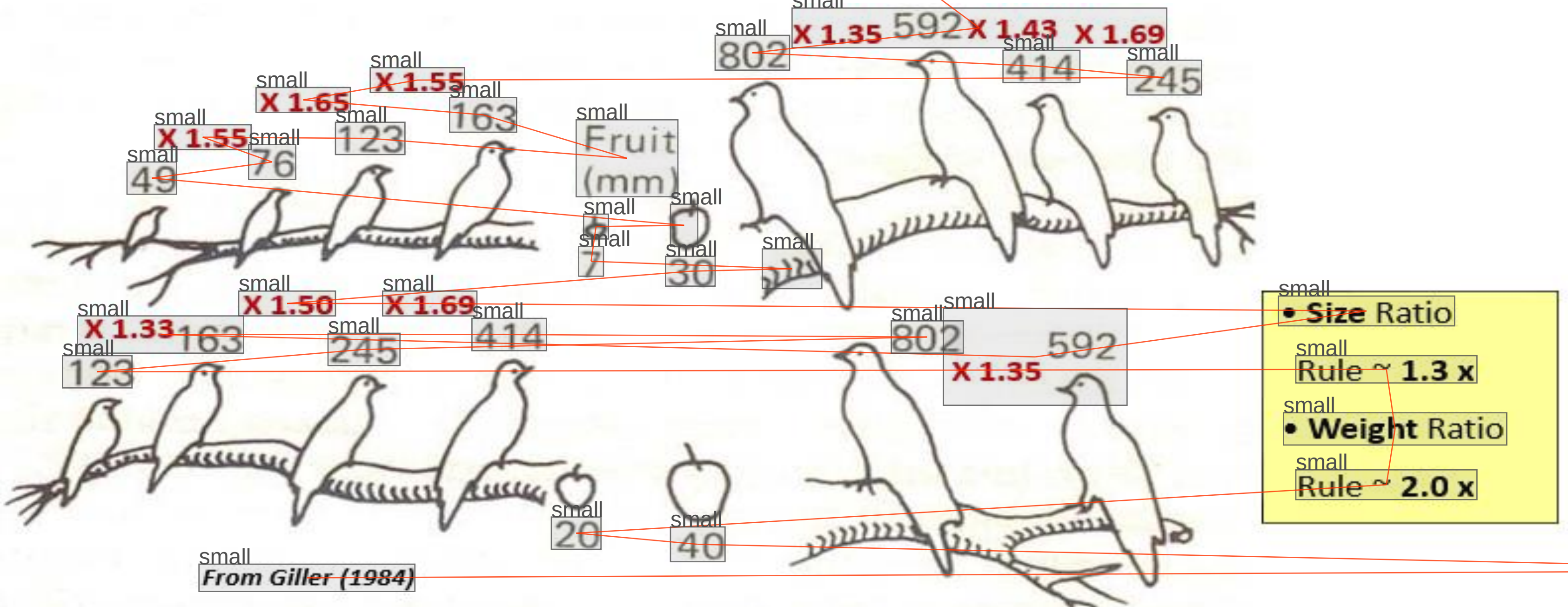
❑ **Niche partitioning among fruit pigeons - 4 key niche dimensions (Diamond 1973):**

1. **Fruit Size**: **Larger species** feed mostly on larger fruits (**large beaks** can handle these)

2. **Bird Size** and **Weight**: **Body size** positively correlated to preferred **fruit sizes eaten**

3. **Thickness** of **Branches**: **Body size** positively correlated with **branch thickness**

4. **Position** on **Branches**: **Small species** foraging on **outer branches** and **twigs** due to lower weight.



From Giller (1984)

Summary – Animal Ecology Experimental Methods

1. Three Animal Ecology Experimental Methods

- **Laboratory**: small animals, simple principles, strong controls
- **Field Experiments**: small-medium sized, advanced set-up, limited control
- **Natural Experiments**: any size of animal, large sample size, poor controls

2. Seven Major Ways to demonstrate competitive interactions

- **Competitive Exclusion**: Yeast and grain beetle competition for space
- **Niche shift**: Dietary shift between two salmonids (allopatry-sympatry)
- **Ecological release**: Barnacle competition for space (Displacement)
- **Density compensation**: Rodent-ant competition for seed (Displacement)
- **Contiguous allopatry**: Chipmunk habitat occupation (allopatry-sympatry)
- **Character displacement**: Food partitioning – Fruit pigeons, mud snails
- **Predator-mediated co-existence**: Starfish predation (Displacement)

Summary – Animal Ecology Experimental Methods

3. Three Manipulation Methods to demonstrate competitive interactions

- Removals
- Displacement
- Occupational Comparative (allopatry-sympatry)

4. The Explanatory Concept for competition: Fundamental vs Realised Niche

Lecture 3: The Basis of the Ecological Niche Concept

1. Definitions of important terminologies in Ecological Niche Concept

- **Habitat component**: Grinnell (1917)
- **Trophic component**: Elton (1927)
- **Multi-dimensional**: Hutchinson (1957)
- **Abiotic-biotic multidimensional**: Begon-Krebs-Ricklefs (1986-1997)

2. Overview of perception of niche dimensionality

- **Niche dimensions**: Biotic and abiotic components interacting
- **Graphical depiction**: One-, two-, three-, multi-dimensional visualization
- **Dimensional interaction**: Dimensions can be unrelated or inter-dependent

Lecture 3: The Basis of the Ecological Niche Concept

3. Comparison of 2 niches types and the eco-potential of a species

- **Eco-potential**: Genotype determined/ limited maximum potential
- **Fundamental**: Optimum niche, phenotype limited by environmental factors
- **Realised**: Limited by biotic interactions: competition, predation, parasitism

4. Foraging Niche concept and fitness of animals

- **Fitness**: Population size, reproductive and survivorship rates
- **Utilization and Response Curves**: Bell-shaped, normal distribution, idealized
- **Three Levels**: Trophic (what-), Spatial (where-), Temporal (when) to eat

- According to Joseph Grinnel, an American ecologist, **Ecological Niche** is defined it as **“The ultimate distributional unit of a species”**

- Grinnel implied that niches **do not overlap**, but are **disjunct**. Species display their fundamental niches; hence there is no apparent competition among them.

- Charles S. Elton (1927), a British ecologist, went further by using a more **functional view concept**, and defined **Ecological niche** as: “**The trophic position of a species in the biotic environment”**.

- Elton viewed the niche as a **simplistic subdivision** within the traditional trophic grouping as herbivores, carnivores etc., i.e. the mere **feeding habits** or **dietary trait** of a species.

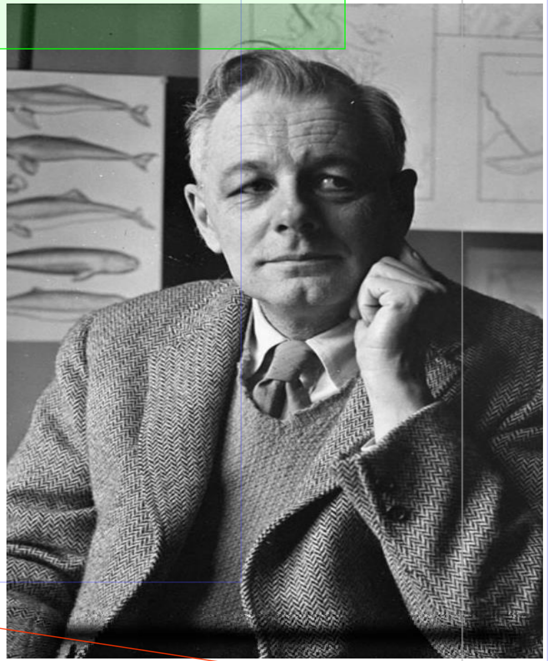
- George Evelyn Hutchinson (1957), after 30 years, proposed the most comprehensive concept to date

“The n-dimensiona hypervolume or hyperspace of a species”

- The Hutchinsonian concept implies the total range of environmental variables to which a species must be adapted, and under which a species population lives and reproduces indefinitely.

- The Hutchinsonian concept therefore involves both habitat and functional aspects

- The environmental variables include physical, chemical and biotic parameters



- These variables can be viewed as a **gradient** along which species utilize with different intensities, and each gradient is considered as an **n-dimensional space**. Adding up all these forms the **niche hyperspace**

- The niche can be viewed as **an n-sided** flexible ball that can take any form in an **n-dimensional coordinate system** and represents the responses of the species population to all **environmental variables**.

- In multidimensional geometry with **n-number of axes**, the niche of an organism is graphically depicted, when all **relevant environmental variables** are included and these are **independent** of each other

- Begon *et al.* (1986): “The limits, for all important environmental features, within which all individuals of a species can survive, grow and reproduce”

- Krebs (1994): “The **role** or **profession** of an organism in the environment; its activities and relationships in the community”

  ✓A very broad definition comprising all biotic interactions (competition, mutualism etc)

- Ricklefs (1997): Formal Definition – “The ranges of many conditions and resource qualities within which the organism or species persists” (i.e. perceived as the multi-dimensional space)

  ✓Informal Definition – “The ecological role of a species in the community”

- Polechová & Storch (2008): “Ecological niche indicates the position of a species within an ecosystem, describing both the range of conditions necessary for persistence of species, and its ecological role in the ecosystem

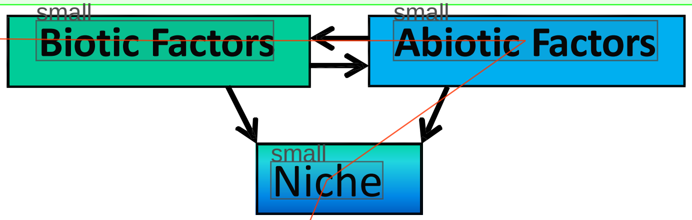
- The diversity of definitions illustrates to what extent the niche is perceived as a species or community property: Is the niche created by the species itself, or by its surroundings?
    - Or as a dynamic mutual interaction? Let us examine an example – The Beaver

The Niche Concept - Dynamics

- The Beaver (*Castor Canadensis*, *C. fiber*) creates dams by felling trees across fast-flowing rivers, hence creating a new environment of **stagnant water** in which they build their nests.

• Hence beavers **create their own habitat** which is conducive both for itself and for many other organisms - i.e. beavers impact their habitat by virtue of a specialised niche of dam building.

We can generalise that:



• **Eco- or Biotic Potential**: The full **genetic potential** of a species population in all ecological matters (Note: ***Genotype limited***; not necessarily expressed in the **phenotype**).

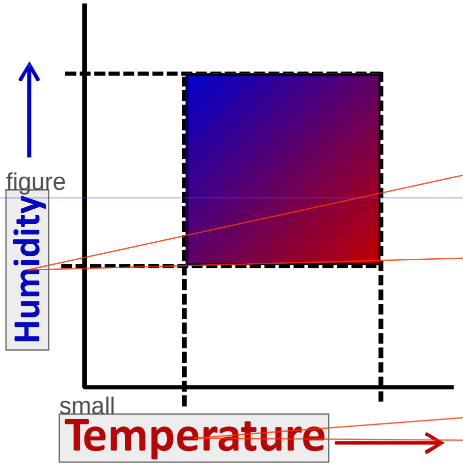
- **Fundamental Niche**: Phenotype limited by environmental factors and physical constraints currently shaping the genotype; e.g. the temperature or food type range of an organism.

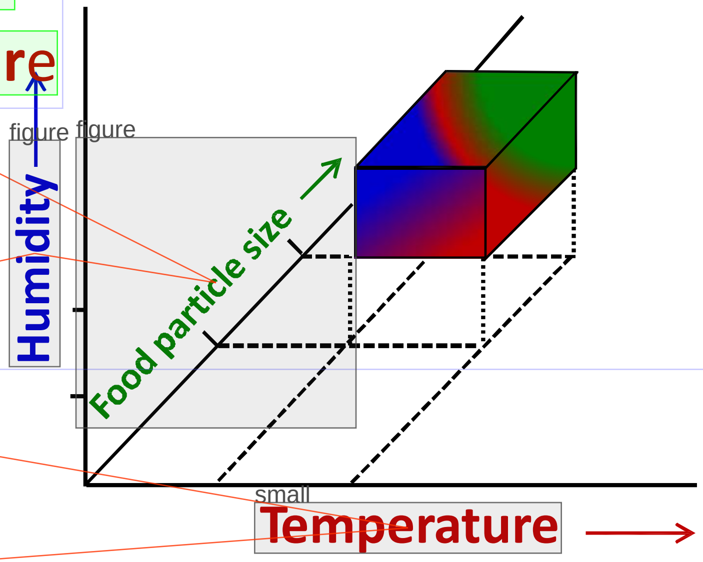
- **Realized Niche**: Phenotype limited by biotic interactions = competition, predation, parasitism; e.g. the population growth of an organism after predators have reduced it.

The Niche Theory – Niche Dimensions & Fitness

(a) One Dimension:

Abiotic: Temperature





Adapted from Begon & Mortimer (1985)

(b) Two Dimensions:

Abiotic: Temperature and Moisture

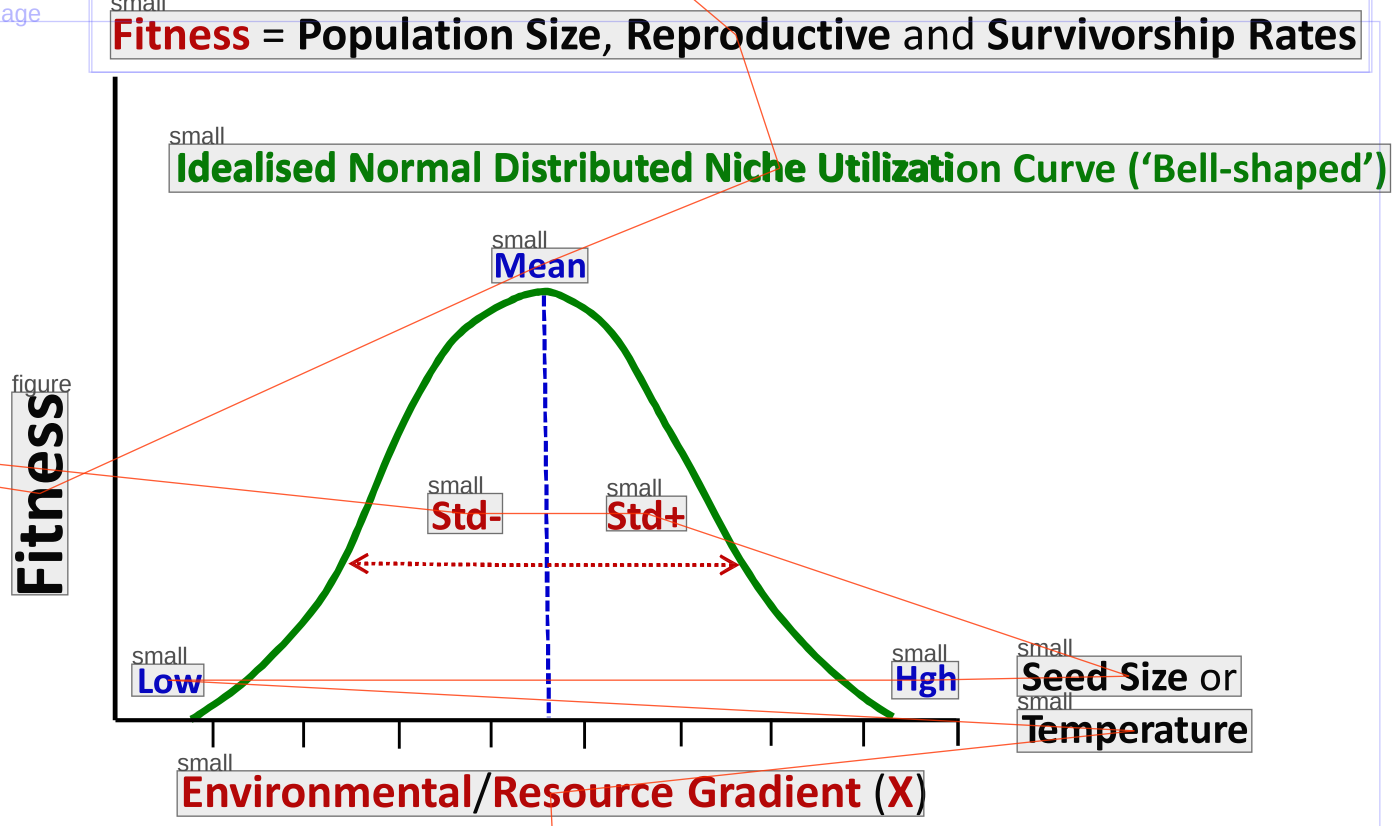
(c) Three dimensions:

Abiotic: Temperature and Moisture

Biotic: Food Size

- It is difficult to **graphically depict** more than three dimensions simultaneously
- When assessing competition, ecologists often focus on the **assumingly most important** and **easiest to measure dimensions**, and analyse these one by one.

The Niche Theory – Niche Dimensions & Fitness



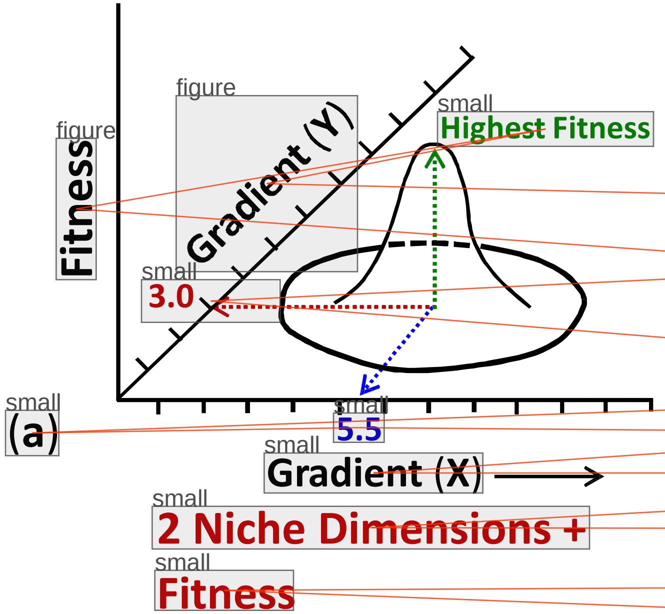
From Giller (1984)

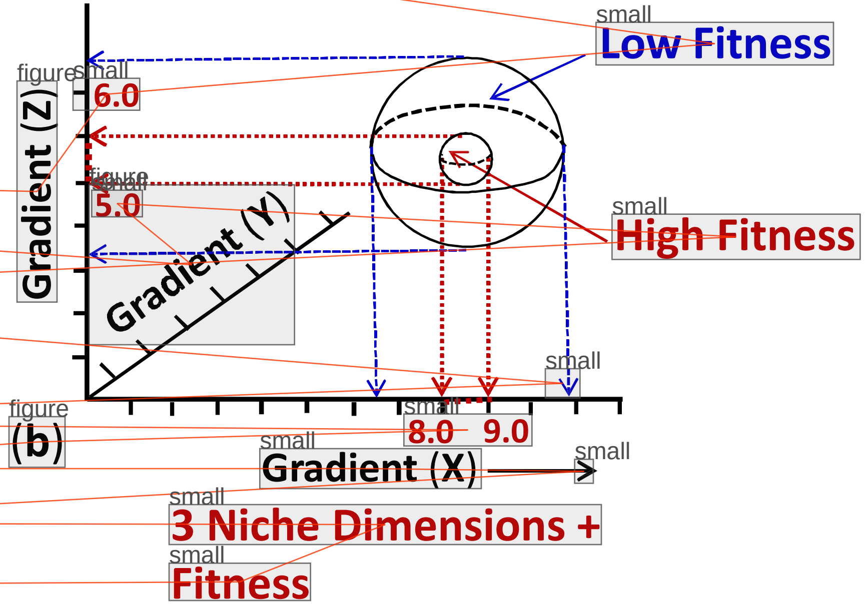
- **Resource Utilisation Curve** (Resource Gradient = Seed size, Fruit ripeness, Tree height etc.)
- **Species Response Curve** (Environmental Gradient = Temperature, pH, Salinity etc.)
- Note that only ***one dimension*** is shown on these '**bell-shaped curves**'.

The Niche Theory – Niche Dimensions & Fitness

- **Graphical expressions of multidimensional niches** can also incorporate fitness
- Again with more than three niche dimensions this becomes increasingly problematic to show in graphic diagrams.
- **Examples are shown below**: (**a**) Fitness highest at **X** = **5.5** units; **Y** = **3.0**
- (**b**) Fitness highest at **X** = **8.0 - 9.0**; **Z** = **5.0 - 6.0**

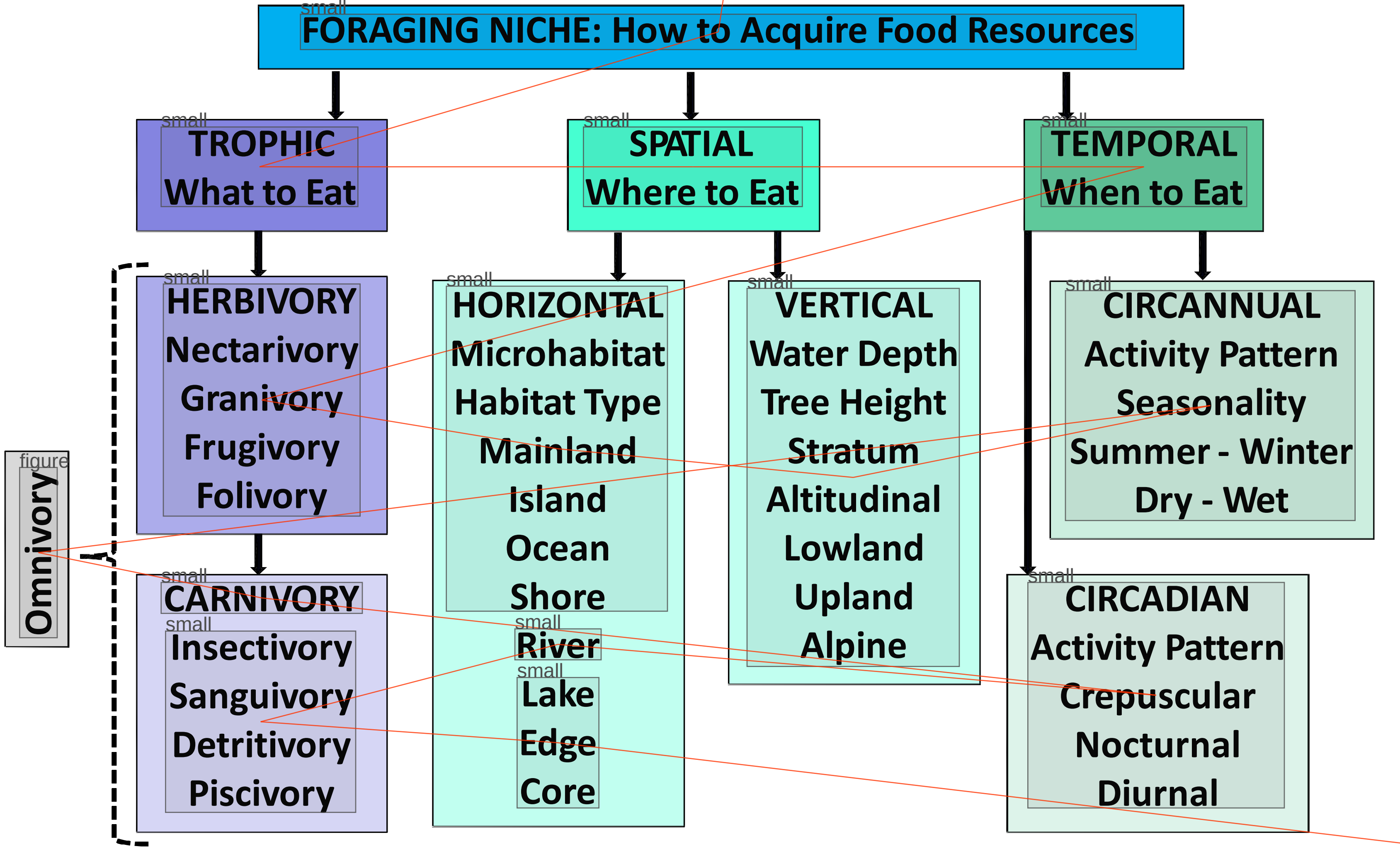
Adapted from Giller (1984)





The Niche Theory – Niche Dimensions & Fitness

Summarizing the Overall Levels of Ecological (Foraging) Niche Dimensions



Summary of Lecture 3 – The Basis of the Ecological Niche Concept

1. **Historically** the **Niche Concept** was initiated and developed about 100 years ago
   - **Grinnel (1917)**: **Geographical-spatial** distributional unit of a species
   - **Elton (1927): Trophic-foraging positioning** of a species in the ecosystems
   - **Hutchinson (1957):** The first comprehensive **n-dimensional hyper volume**
   - **Begon-Krebs-Ricklefs (1986-1997):** Further advancing of Hutchinson's
   - **Polechová & Storch (2008): Duality** – both **position** and **role** in ecosystems

2. Species Niches are controlled by Dynamic Ecological Interactions:

- **Abiotic components**: **Climatic** conditions, **chemical-physical** environment
- **Biotic components**: Competitors, parasites, predators-prey, disease

Summary of Lecture 3 – The Basis of the Ecological Niche Concept

3. Three types defined within the Theory of the ecological Niche Concept:
    - Eco/Biotic Potential: Absolute maximum potentiality – genotype determined
    - Fundamental: Actual uncontested, resource unlimited – phenotype determined
    - Realized: Actual in the presence of other biotic interactors – resource limited

4. Three major Niche Dimensions: Trophic (food), Spatial (area), Temporal (time)

Objectives of lecture 4 - Theory & Concept of the Ecological Niche

1. An introduction to **Niche Width** - populations and individual morphs:

- What is the effect of **phenotypic traits** on niche width and shape?
- What is the resulting effect of **all morphs** on niche width and shape?

2. **An Overview** of **interspecies niche relationship** and **positioning**:

- **Included niches:** Which are **inferior** and which are **superior**?
- **Disjunct niches**: How **distant** are niches – can **competition** be neglected?
- **Abutting niches**: How limited is **competition** such as in **Contiguous Allopatry**?
- **Overlapping niches**: How much can **niches overlap** before **exclusion** results?

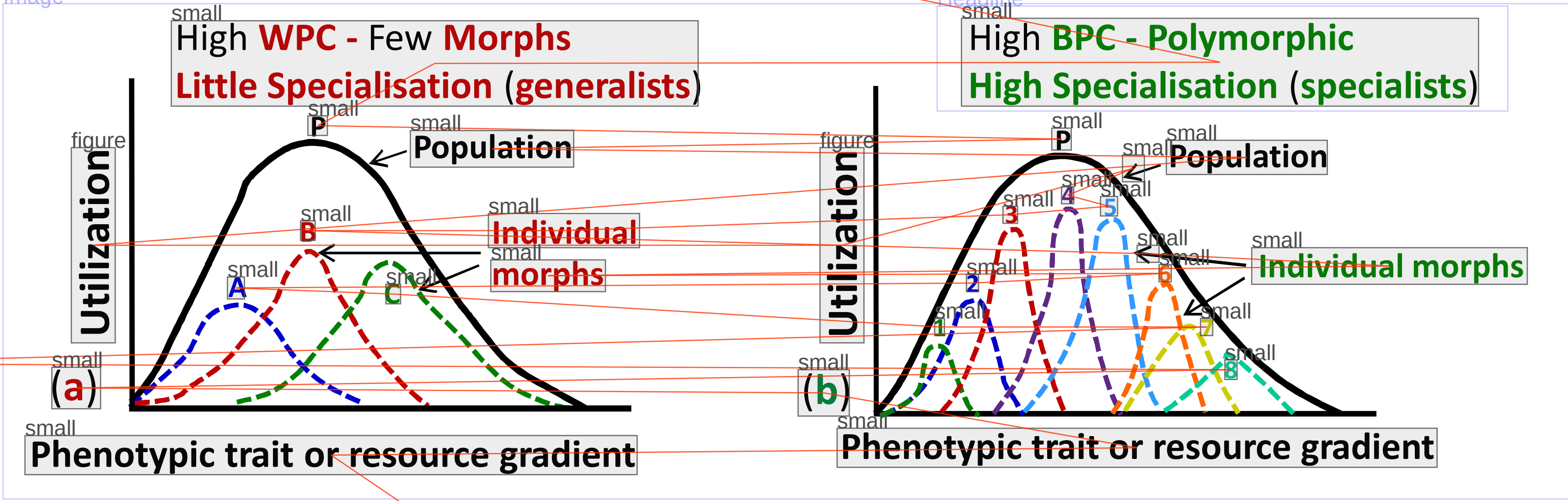
3. **A Comparison** of **Niche Overlap** and **Competition**:

- **Intraspecific**: The relationship between **population density** and **niche width**
- **Interspecific**: The relationship between **species density** and **niche width**.

4. **An Account** of the rules for **Niche Width**, **Overlap** and **Limiting Similarity**:

- **Thresholds** for: **Exclusion**, **Coexistence**, **Disjunct Niches**, **Invasion** of **species**.
- **Diffuse Competition**: **Additive competitors** may drive exclusion from Niche.

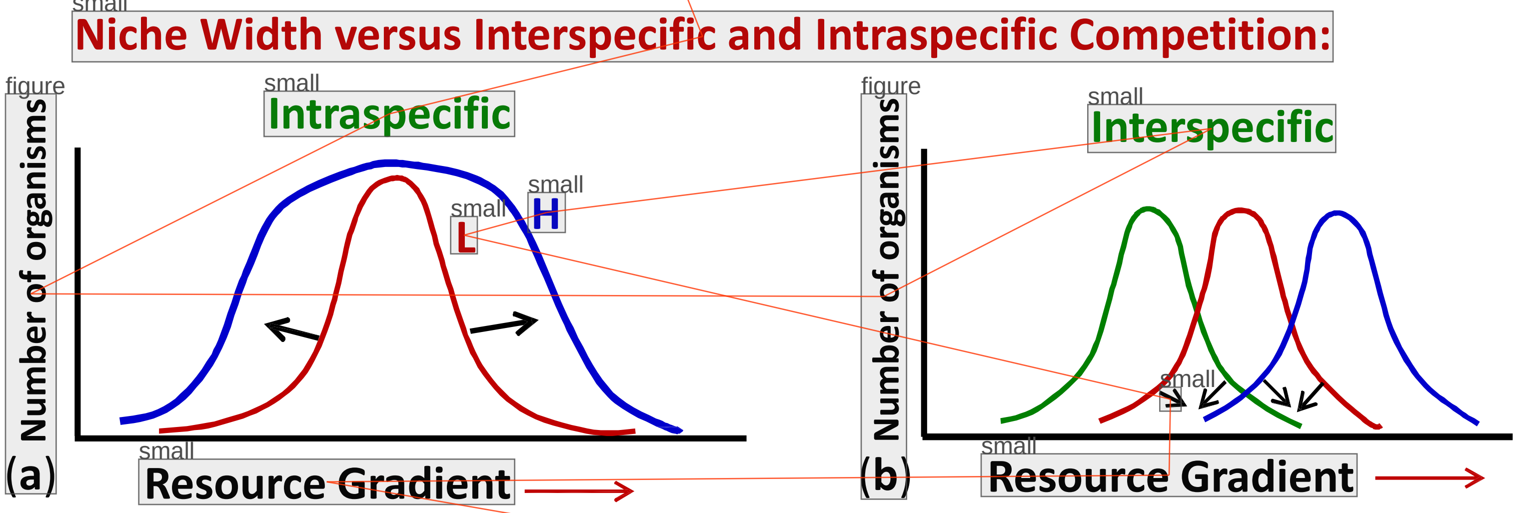
Niche Theory - Niche Width & Overlap (1)



Adapted from Giller (1984)

- **Natural populations** have variability in both **resource use** and **diversity of morphs**
- (a) **Within Phenotype Component** (**WPC**): the way resources are used by all the individuals in the total species population - how wide is their resource use
- (b) **Between Phenotype Component** (**BPC**): morphological diversity of a population.
- **Niche width** (**W**) = **WPC** + **BPC**
- If **WPC** is **high** then the population consists of **mono/oligo-morph generalists** (**a**)
- If **BPC** is **high** then the population consists of **poly-morph specialists** (**b**)

ABCS349-AnimalEcology.Lecture4:NicheTheory-NicheWidth&Overlap(2)

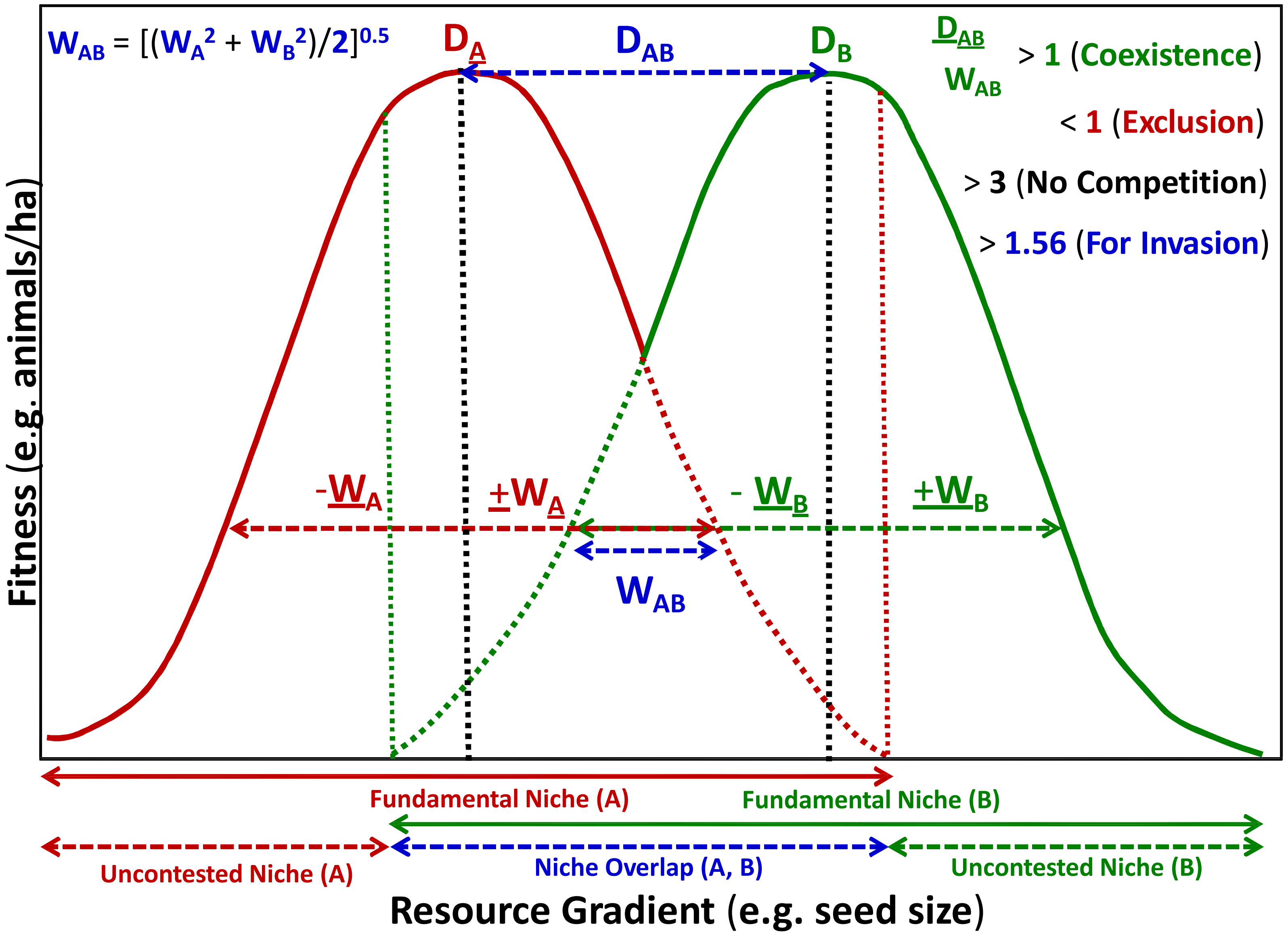


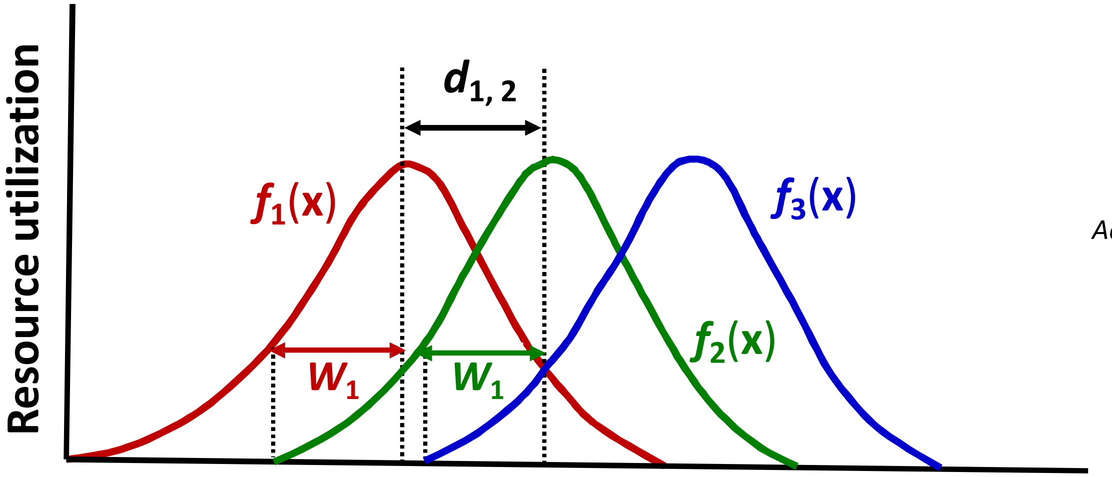
Adapted from Giller (1984)

(a) **Intraspecific**: Increased population density (**L→H**) increases competition among individuals for limited resources (**food** and **space**), forcing individuals to **search for** and **adapt** to other **opportunities** = **increasing niche width**.

(b) **Interspecific**: Increased competition between species force these to reduce niche overlap or segregate niches by virtue of **specialisation** = **decreasing niche width** (**narrow niches** allow more dense packing of species in communities).

ABCS349 - Animal Ecology. Lecture 4: Niche Width & Limiting Similarity (2)





Adapted from Giller (1984)

- **3 competing species** ($S_{1\text{-}3}$) with overlapping idealised niche curves $f_{1\text{-}3}(x)$
- S_1 and S_3 both have a wide refuge niche
- S_2 has a much narrower uncontested refuge niche
- The niche width (**W** = *STD*) in relation to the distance (***d***) between the resource utilisation curve maximum denotes the magnitude of competition among the two species: **d/w** > **1 = coexistence**; **d/w** < **1** = **exclusion**; **d/w** > **3 no competition** (= **disjunct niches**). Note: **D/W = 1** (then it can go either way!).

ABCS349 - Animal Ecology. Lecture 4: Niche Width & Limiting Similarity (3)

Question1: Can the two flycatchers coexist? – is the D/W value greater than 1?

D = 12 - 8 = 4

$W_{AB} = [(W_A^2 + W_B^2)/2]^{0.5} = [(3^2 + 3^2)/2]^{0.5} = [(9 + 9)/2]^{0.5} = (18/2)^{0.5} = \sqrt{9} = 3$

D/W = 4/3 = 1.33

Answer: Yes they can coexist as D/W > 1.00

Question2: Can a 3rd flycatcher wedge itself in between the Grey and Little Flycatchers?

Answer: No, because D/W < 1.56

Little Flycatcher:

Fundamental niche = **1-15 mm**

Uncontested niche = **1-5 mm**

Superior niche = **5-10 mm**

Curve maximum (mean) = **8 mm**

Niche width STD (W) = **3 mm**

Grey Flycatcher:

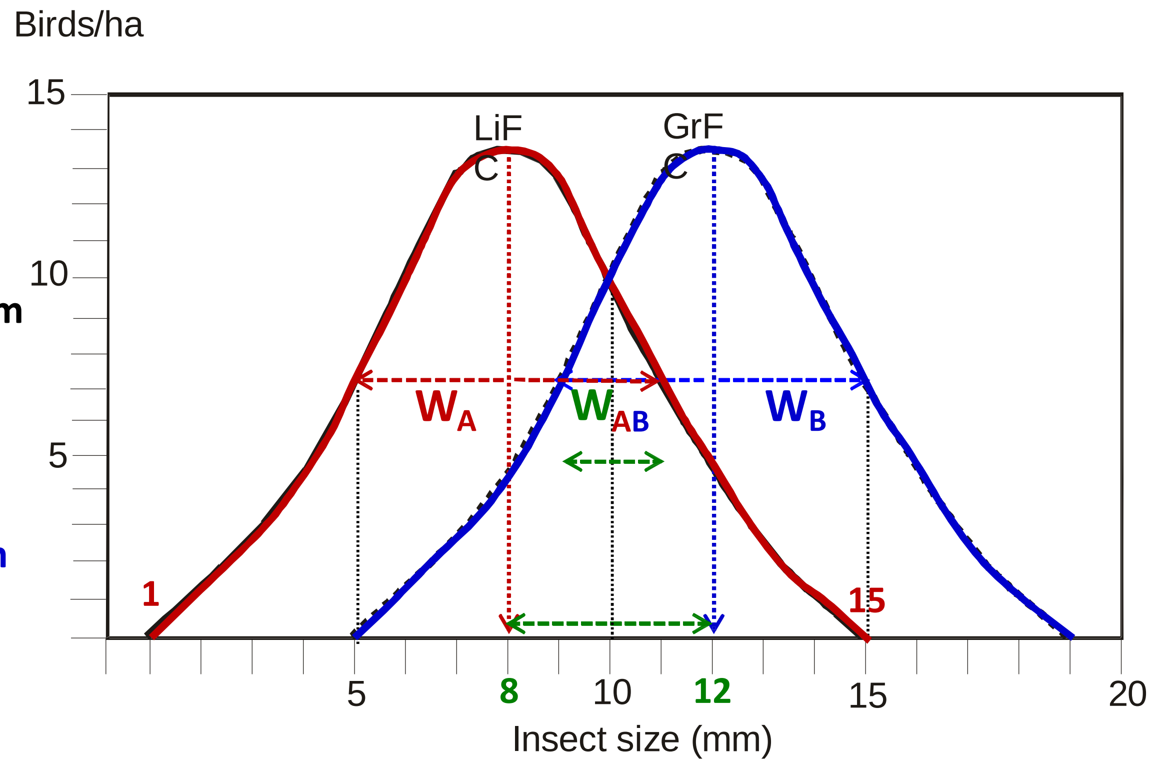
Fundamental niche = **5-19 mm**

Uncontested niche = **15-19 mm**

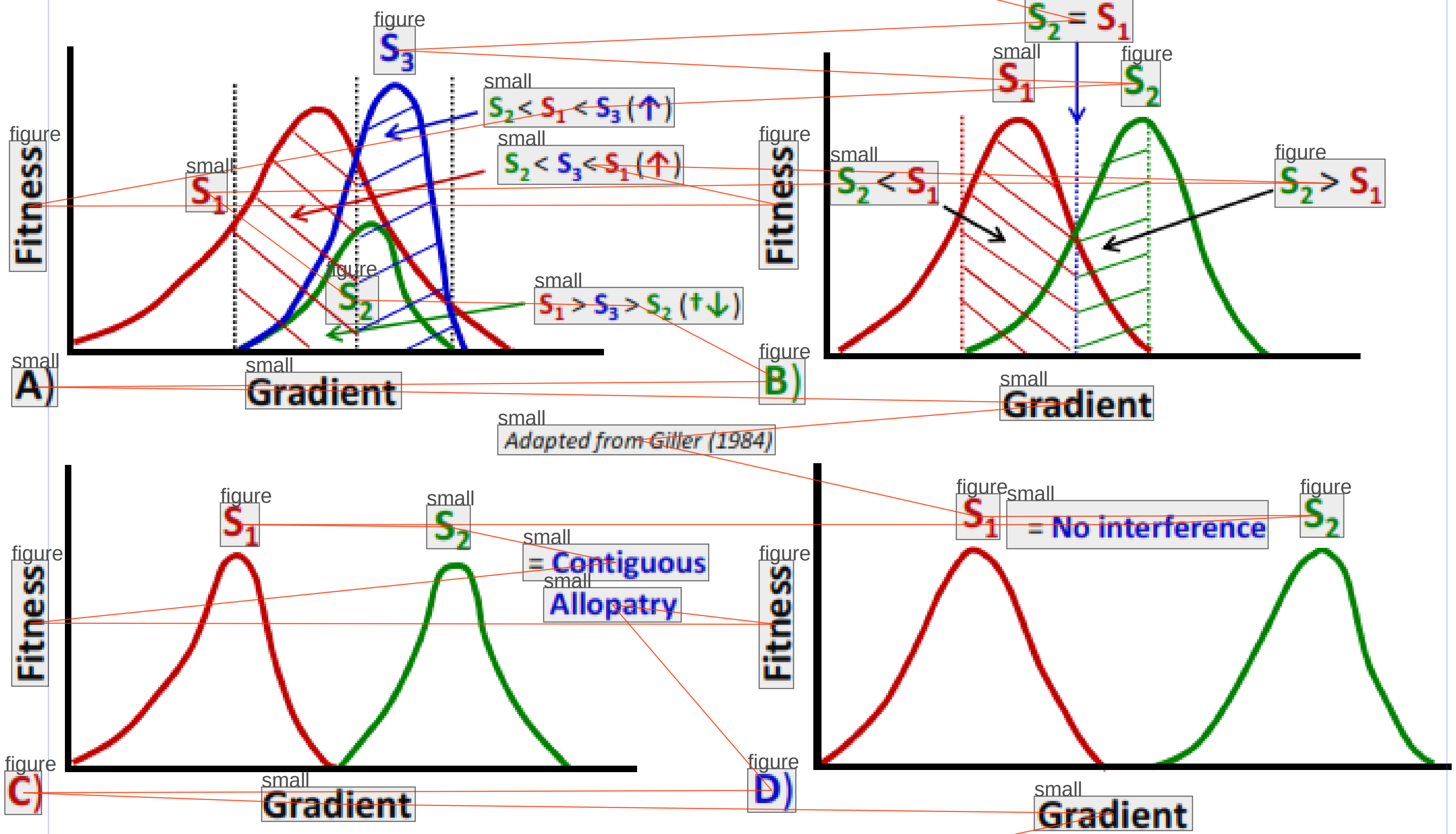
Superior niche = **10-15 mm**

Curve maximum = **12 mm**

Niche width STD (W) = **3 mm**

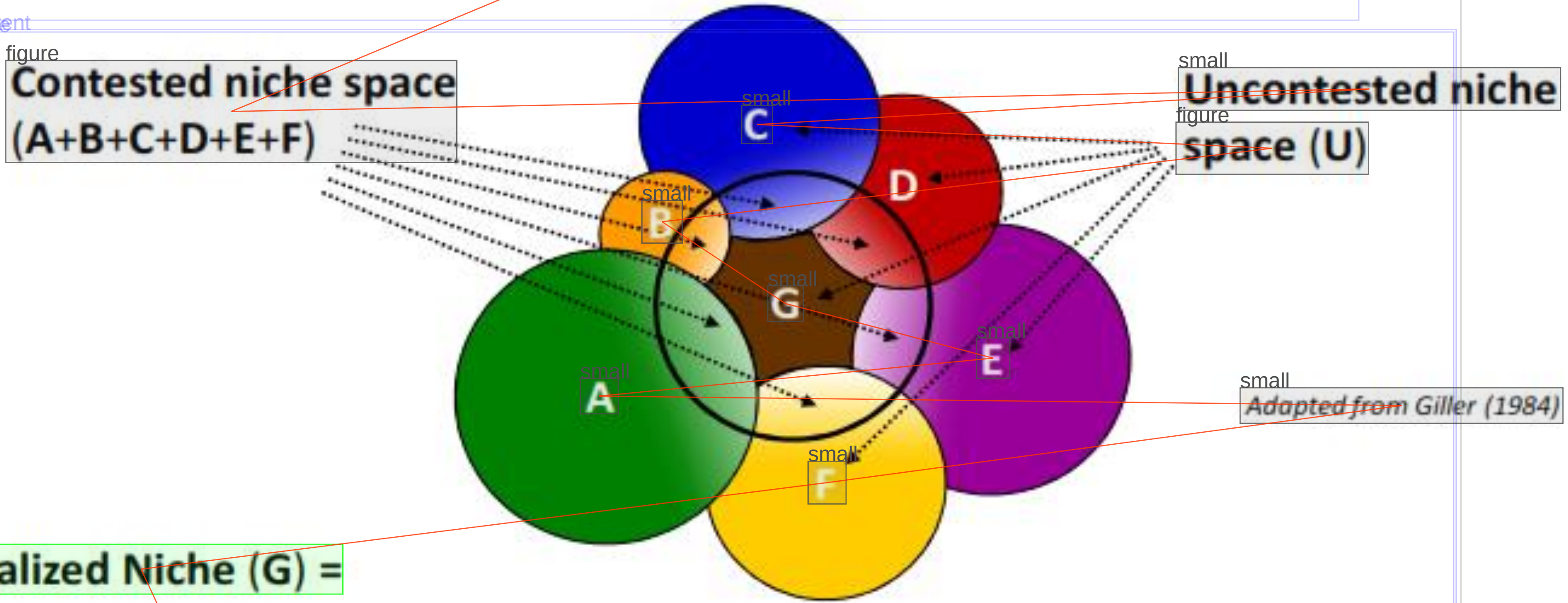


Niche Theory – Niche Width & Overlap (3)



- **Possible niche relationships of two species (S_1, $S_2$and S_3; one niche dimension):**
- A) **Included**, B) **Overlapping**, C) **Abutting**, D) **Disjunct** niches.

Niche Theory – Niche Width & Overlap (4)



Realized Niche (G) =

G - ∑[(A+B+C+D+E+F)/G]

- **Diffuse competition** of several species on a single species.
- **The fundamental niche** of species **G** is greatly reduced by subtracting the overlapping fundamental niches of species **A-F**.
- This illustrates how several species may **squeeze out** another species by this **cumulative** or **diffuse competition**.

Summary - Theory & Concept of the Ecological Niche

1. The Niche Width expressed by individual morphs in the whole population:

- **Within-phenotype component**: High - Few mono/oligo-morph **generalists**
- **Between-phenotype component**: High - Many poly-morph **specialists**.

2. The general relationship between Niche Overlap and Competition:

- **Intraspecific**: **Population density** ↑ → Degree of **generalists** ↑ → **Niche width** ↑
- **Interspecific**: **Species density** ↑ → Degree of **specialists** ↑ → **Niche width** ↓

3. There are 4 modes of interspecies niche relationship and positioning:

- **Included:** The included is **inferior** and will eventually be **excluded**
- **Disjunct**: Niches are **clearly separated** and **no competition** exist
- **Abutting**: Niches adjacent with **minimal competition** (**contiguous allopatry**).
- **Overlapping**: Niches may **overlap** more than the **maximum for coexistence**

4. Basic Rules for niche width, niche overlap and limiting similarity

- **Niche width** = **W**, **Niche distance** between two species = **d**
- **Coexistence**: **d/w** > **1**, **Exclusion**: **d/w** < **1** (**Note**: **d/w = 1** - it can go either way!)
- **No competition (disjunct)**: **d/w** > **3**, Invasion of adjacent species: **d/w** > **1.56**.

Objectives - Differential Niche overlap & Complementarity

1. An Introduction to the concept of niche overlap and interspecific competition:

- How does **spatio-temporal variation** on food availability affect **trophic niche**?
- Which mechanisms **separate species** to **limit similarity** and **segregate niches**?

2. An Overview of various modes of differential niche overlap

- How are **niche dimensions complementary** to each other?
- How does various means of **niche segregations** operate?
- What are the relationships among **trophic** and **spatio-temporal** niche division?

3. An Account of relationships between niche dimensionality and complementarity:

- What is the effect of **increasing niche dimensions** and **complementarity**?
- What are the **basic rules** for **complementarity** and **niche dimensionality**?
- How does **niche differentiation** and **complementarity** increase **coexistence**?

4. A Comparison of ways in which niches are partitioned at the community level:

- What are the **basic structures** of **community wide niche partitioning**?
- What are the **basic rules** (**Hutchinson's**) of **community wide niche partitioning**?

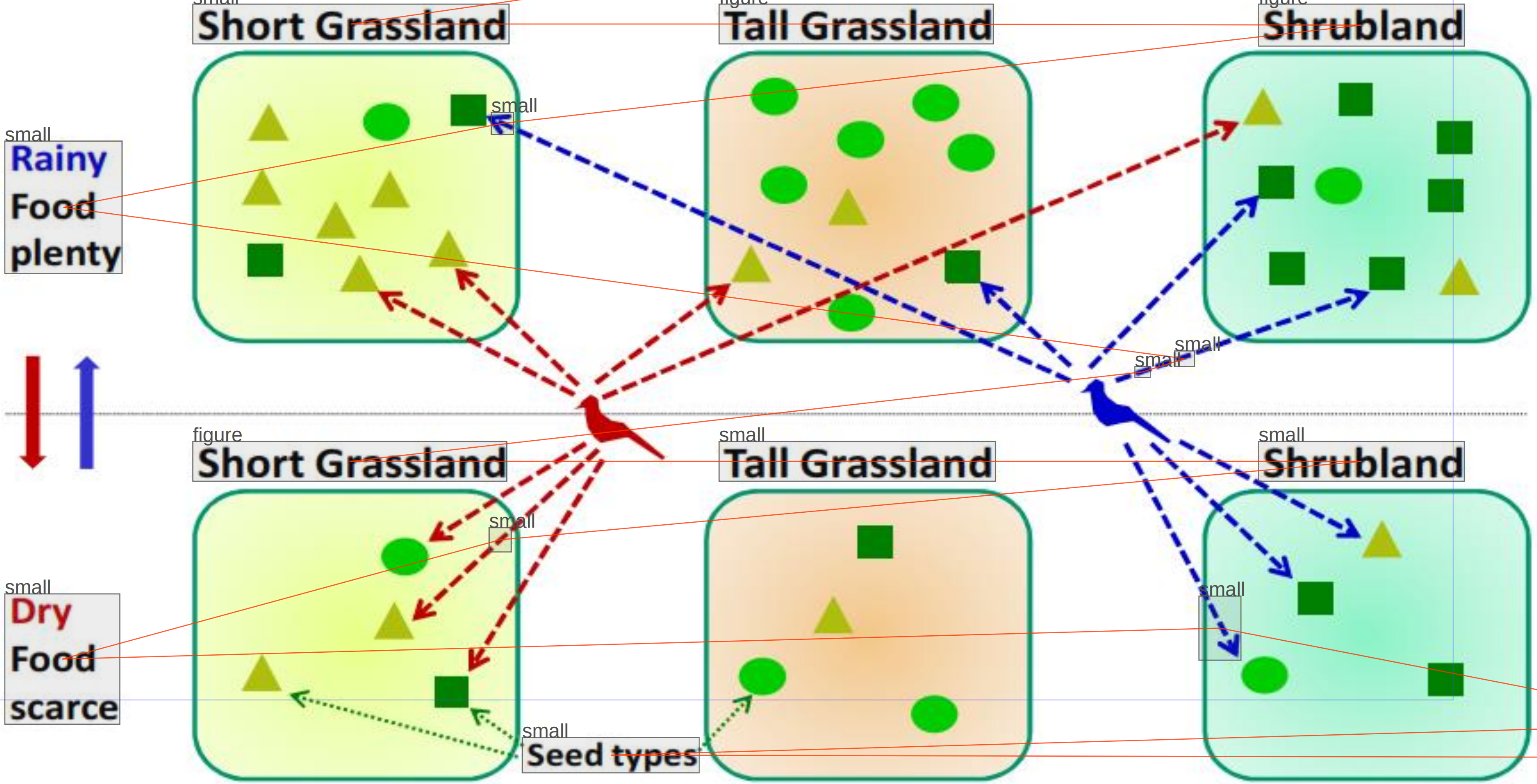
Differential Niche Overlap & Complementarity (1)

Categories of species separation along complementary resource dimensions

1. **Food type & habitat** – species showing overlap in habitat eat different foods, or vice versa
2. **Food type & time** – species use the same food at different times or different foods at the same time
3. **Habitat & time** – species uses the same habitat at different times or different habitats at the same time
4. **Habitat & habitat** – species overlapping in horizontal habitat often differ in vertical habitat or vice versa
5. **Food type and food type** – species may eat similar-sized foods but different species or types, or vice versa

Differential Niche Overlap & Complementarity (2)

- **Seasonal** (temporal)variation in habitat and dietary overlap among granivorous birds in an Arizonian grassland (= **spatio-temporal dietary niche segregation**):
- Rainy Season (**food plenty**): Birds **specialize** on a seed type across overlapping habitat types
- Dry Season (**food scarce**): Birds **specialize** on separate habitats foraging on **many** seed types



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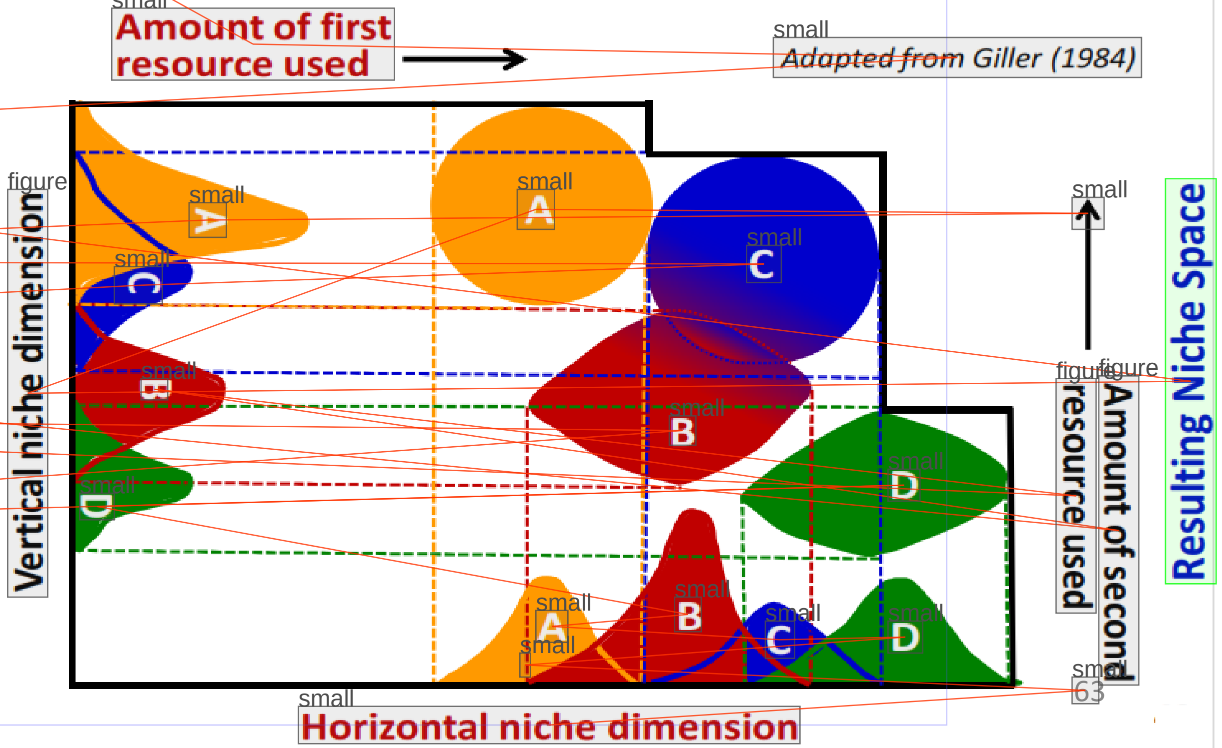
Differential Niche Overlap & Complementarity (3)

❑Differential Niche Overlap between 4 hypothetical species (A, B, C, D)

- Horizontal niche dimension considered alone: **Species C** is apparently in trouble facing **diffuse competition** from both **B** and **D** – coexistence doubtful.
- Vertical niche dimension considered alone: **Species C** subject to **heavy** niche **overlap** with **A**, and **moderate overlap** from **B** – coexistence doubtful.

- Both Niche dimensions considered simultaneously
- **A, B, C** versus **D disjunct**
- **A versus B disjunct**
- **A** and **C abutting**
- Only little overlap between species B and C

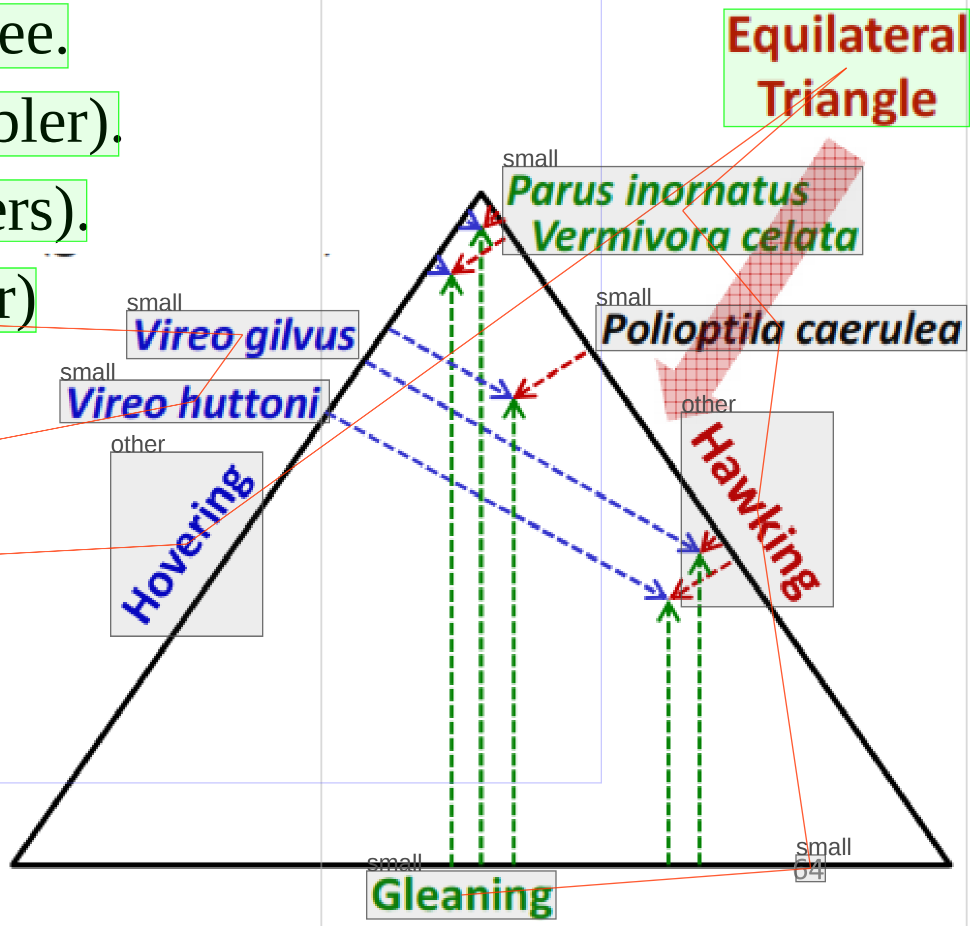


Differential Niche Overlap & Complementarity (4)

- Foraging Techniques of 5 sympatric Bird Species in Oak Forest

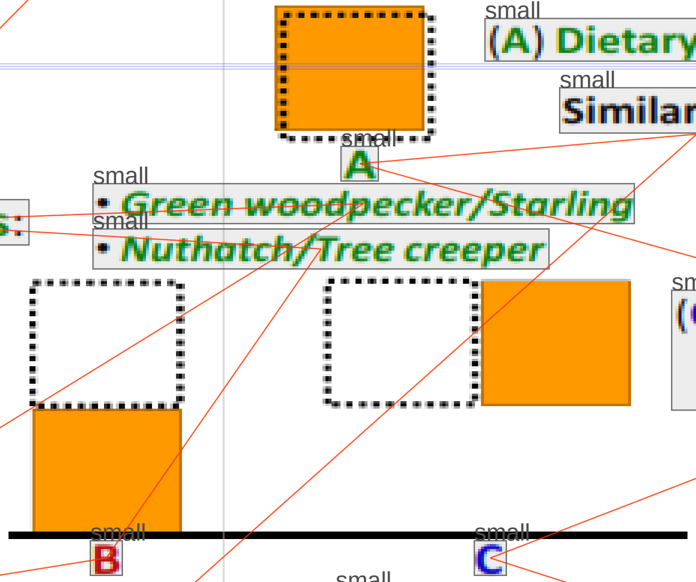
- The time spent on 3 foraging tactics for each species monitored:
  1.Hovering, 2. Gleaning, 3. Hawking
- All 5 species adopt all strategies, but to a variable degree.
- Gleaners: *Parus inornatus* (tit), *Vermivora celata* (warbler).
- Hover-Gleaners: *Vireo gilvus*, *V. huttoni* (shrike-warblers).
- Glean-Hover-Hawker: *Polioptila caerulea* (gnatcatcher)

- Differences in foraging techniques may reduce direct interference and also resource exploitation as each method is best designed for a particular prey type in a particular micro-habitat



Differential Niche Overlap & Complementarity (5)

Trophic and Spatial Niche Separation of Birds in Woodlands:



(A) Dietary Separation of Niche:

Similar Foraging Height and Habitat Type

Species pairs:

- *Green woodpecker/Starling*
- *Nuthatch/Tree creeper*

(B) Vertical Separation of Niche:

Similar Diet and Habitat Type

Species pairs:

- *Nuthatch/Tits*
- *Tree creeper/Tits*
- *Nuthatch/Pied Flycatcher*
- *Tree creeper/Pied Flycatcher*
- *Nuthatch/Redstart*
- *Tree creeper/Redstart*
- *Tits/Pied Flycatcher*
- *Tits/ Redstart*

(C) Horizontal Separation of Niche:

Similar Diet and Foraging Height

: Species pairs

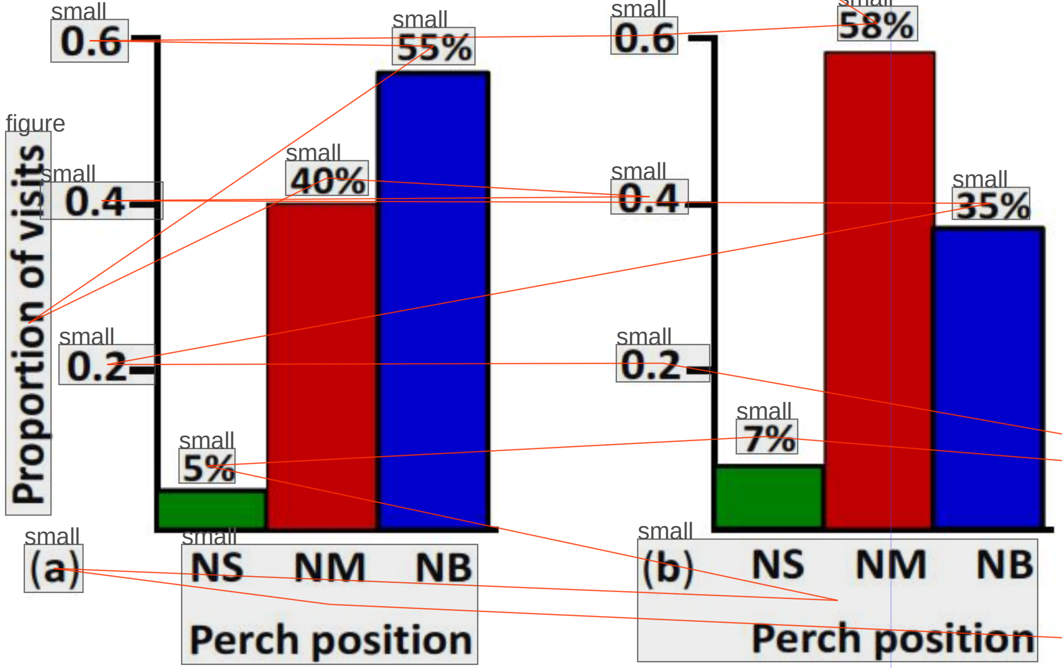
- *Wood Warbler/Willow Warbler*
- *Redstart/Pied Flycatcher*
- *Great Tit/Blue Tit/Marsh tit*
- *Green Woodpecker/All other spp.*
- *Starling/All other spp.*

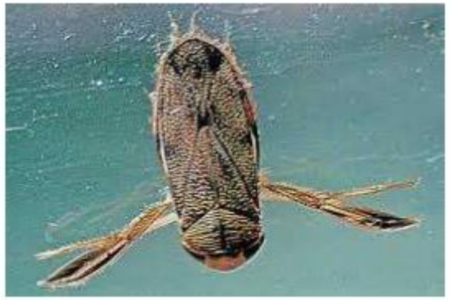
Adapted from Giller (1984)

Differential Niche Overlap & Complementarity (6)

❑Spatial Foraging Niche Separation of 2 water boatmen/bugs (Heteroptera)

- *Perch positions monitored quantitatively over time*:
- Species (**a**) prefers near bottom (55%), and least at water surface (5%)
- Species (**b**) prefers middle of water (58%), and least at water surface (7%)
- In this way they **separate foraging depth** and reduces competition





NS = water surface
NM = middle of water
NB = near bottom

From Giller (1984)

Community Wide Niche Partitioning (1)

Nine squirrel species in African rainforest:

- 3 Habitat types:
- Dense growth (1 sp.), Flooded forest (1 sp.)
- Mature & Disturbed Forest (7 sp.)
- Trophic specialization (1 sp.)
- Bark scraping on tree trunks
- Frugivores separate spatially (6 sp.):
- Ground (3 sp.) & Arboreal (3 sp.)
- In each of the two vertical guilds, the 3 species separate on fruit size and hardness both of which is related to jaw musculature which again is related to mere body size (Hutchinson's Body Size Ratio Rule)

Myosciurus pumilio

H. rufobrachium

Protoxerus stangeri

9 Squirrel Species

Sympatric in Forest (7 species)

Specialized Habitat (2 species):
Dense growth: *Funisciurus isabella*
Flooded forest: *Funisciurus anerythrus*

Specialized food/ foraging niche (1 species):
Bark scraping on trunks: *Myosciurus pumilio*

Frugivores (6 species):

Terrestrial (3 species):
Large: *Epixerus ebii*
Medium: *Funisciurus pyrrhopus*
Small: *Funisciurus lemniscatus*

Arboreal (3 species):
Large: *Protoxerus stangeri*
Medium: *Heliosciurus rufobrachium*
Small: *Aethosciurus poensis*

Segregated by Body Size:
Fruit size and Hardness
(Hutchinson's Rule)

Adapted from Giller (1984)

Community Wide Niche Partitioning (2)

Nineteen species of Coral Reef Fish at Great Barrier Reef, Australia:

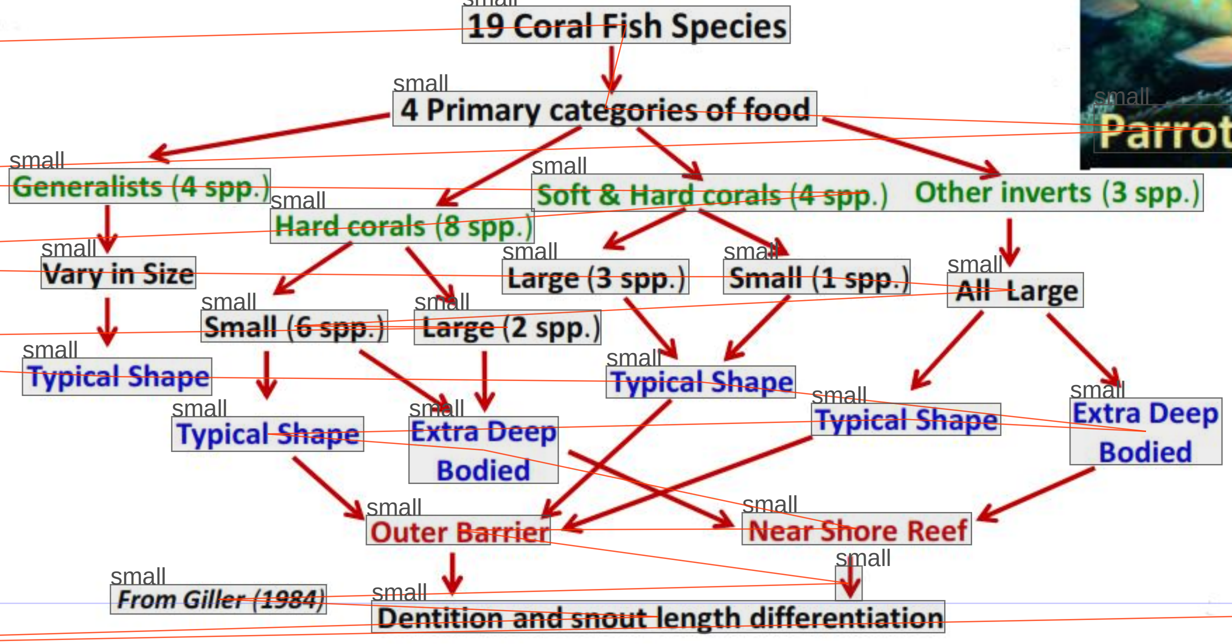
- Segregation into 4 main trophic levels (in which size/ body shape vary):
- Generalists (4 sp.): Typical fish shape, vary in size following **Hutchinson's Rule**
- Hard corals (8 sp.): 6 **Small** (typical shape/ extra deep body), 2 large (deep body)
- Soft/ Hard corals (4 sp.) 3 **Large**, 1 **Small** (all typical shape)
- Other invertebrates (3 sp.): **Large** (typical shape/ deep body)

Parrot fish

Typical shape: Adapted to outer barrier with strong current (**short snout**)

Extra deep body:
Adapted to near shore reef with timid water
(**long snout**)

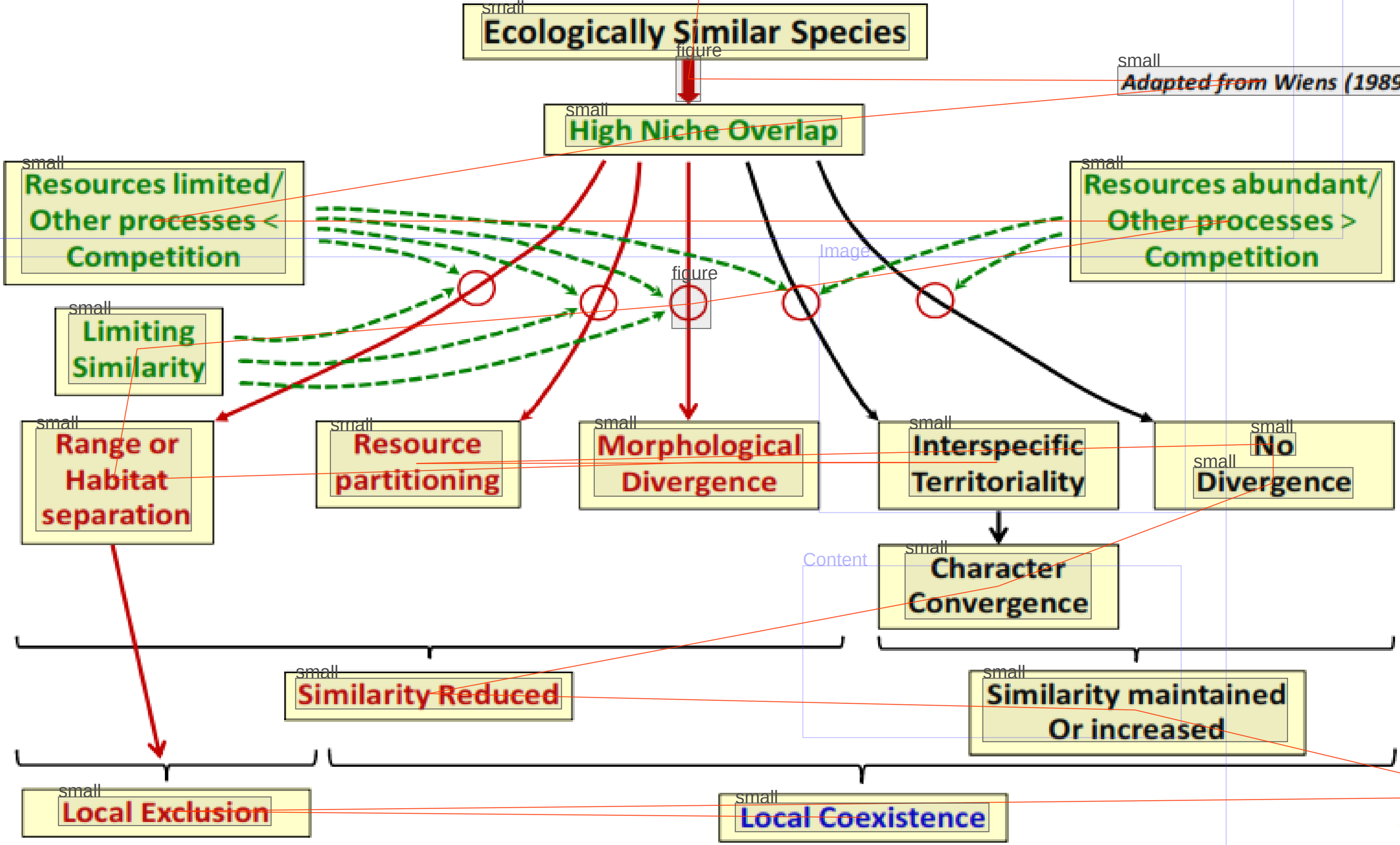
Butterfly fish



From Giller (1984)

Niche Overlap, Partitioning & Coexistence

Summarizing Flow Chart showing the various ways that ecologically similar species may segregate or differentiate the overlap of their foraging niches (Birds)



Summary: Differential Niche Overlap & Complementarity

1. Differential Niche Overlap comprises 3 major dimensions:

- **Spatial:** Horizontal (habitat types) & vertical (altitude, vegetation strata)
- **Temporal**: Time of day/night, seasonal variation (dry/wet, summer/winter)
- **Trophic**: Generalist or Specialist dietary trait, foraging techniques/ strategies

2. Niche Differentiation, Complementarity and Coexistence often interrelated:

- Niche dimensionality ↑→ Niche differentiation ↑→ Complementarity ↑
- High niche differentiation predisposes Complementarity → Coexistence
- High overlap in some niche dimensions tolerated by otherwise low overlaps

Summary: Differential Niche Overlap & Complementarity

3. Community wide niche partitioning limits similarity and increase coexistence:

- High overlap in vertical and horizontal space → low trophic overlap
- High dietary overlap → low, abutting, disjunct and spatial niches
- High dietary and spatial overlap → low overlap in temporal niche

4. Coexistence facilitated by limiting similarity and hence niche overlap:

- **Spatial separation**: vertical-horizontal habitat ranges, territoriality
- **Resource partitioning**: Diet and foraging techniques diverging
- **Morphological divergence**: Body size, feeding apparatus (teeth, claws, beaks)

ABCS 349: Objectives of Lecture 6 – Niche Partitioning & Species Richness

1. **An Introduction** to **modelling** of **species richness** using **niche partitioning**:

- What pertinent **factors** within the niche concept theory **predicts diversity**?
- How are these **factors interrelated** and what are the **dynamics among** them?

2. **An Overview** of various **models** to explain **species numbers** in **space** and **time**:

- Are they mathematical **stochastic** or **deterministic** models?
- **Graphically** explained models to **support** the **notational equations**?
- How does the **models explain** the **links** between **niche dimensionality** and **how many species** than can be '**packed**' into a natural system or community?

3. **A Comparison** of various **models** to explain **species numbers** on **islands**:

- The **species-area models** explained - **islands** and **mainland islands**
- The **island biogeography model**: immigration-emigration-speciation-extinction

4. **An Account** of the **theories** behind **speciation** and **extinction** processes:

- What drives **speciation** in relation to **niche overlap** and **competition**?
- What drives **extinction** in relation to **niche overlap** and **competition**?

Niche Partitioning & Species Richness (1)

MacArthurs simple equation of factors influencing species diversity:

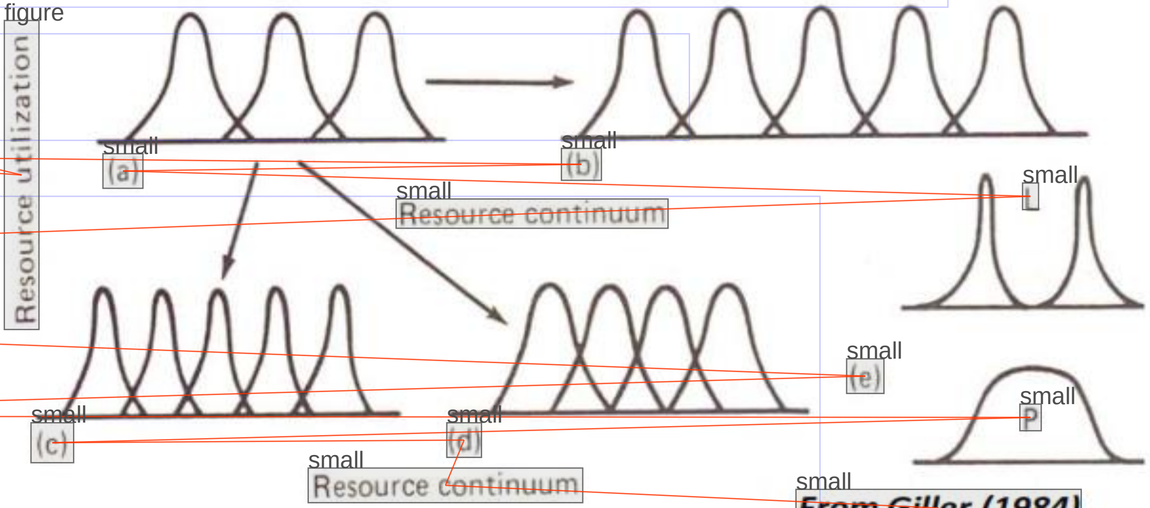
$$Ds = \frac{Dr}{Du}(1 + C\tilde{a}),\ \text{where}$$

Dr = Resource diversity of entire community

Du = Niche width of each species (assumed identical)

C = Number of potential competitors (habitat dimensionality)

$\tilde{a}$ = Mean competitive coefficient or mean niche overlap



From Giller (1984)

- Based on MacArthur's model, communities diversity is shaped in 3 potentially interacting ways:

1. Resource base: How big is **n** in the **niche hypervolume**. Areas with more available resource have larger ***Dr*** and ***C*** components (= niche space) and can therefore contain more species (**b**).
2. Niche width or degree of specialization of component species (***Du***)
   Narrow niches can be packed tighter and thus contain more species (c)
3. Niche overlap between species (***ā***). Greater species overlap (i.e. smaller exclusive niches) leads to greater diversity even if two communities are similar in both (a) and (b) areas (**d**)
4. Niche curve shape also counts, i.e. in thick-tailed (***leptokurtic***) curves (**e**) more species can be packed on the same resource gradient than thin-tailed (***platykurtic***) curves (**e**)

Niche Partitioning & Species Richness (2)

Forest Succession and Increased Bird Diversity (Species Richness):

- As **habitat heterogeneity** increases and more bird species are added, these have to separate on an increasing number of niche dimensions, particularly:

➢ Food type, Foraging techniques, Foraging height, Micro-habitat type

From Wiens (1989)

Forest Successions:

A = Herbaceous

B = Herb-Shrubs

C = Young forest

D = Old forest

Attribute	A	B	C	D
	Successional stage[a]			
Number of guilds	2.3	6.8	6.6	8.8
Species/guild	2.3	2.3	1.9	2.7
Percent total density				
Omnivore	0	5.3	4.1	5.0
Granivore/insectivore	80.5	44.8	16.1	4.3
Frugivore/insectivore	0	6.4	0.6	0.9
Ground insectivore	8.5	2.7	26.3	13.9
Undergrowth insectivore	3.1	13.7	5.2	6.9
High foliage insectivore	0	19.5	35.7	38.5
Twig/branch insectivore	0	0.5	3.4	5.9
Trunk surface insectivore	0	0	2.6	7.6
Sallying flycatcher	0	3.4	3.6	15.4
Number of species				
Omnivore	0	1.2	0.8	1.6
Granivore/insectivore	3.7	4.3	1.6	1.9
Frugivore/insectivore	0	1.4	0.2	0.4
Ground insectivore	0.9	0.7	2.1	3.0
Undergrowth insectivore	0.5	2.1	0.7	1.9
High foliage insectivore	0	2.9	4.4	6.2
Twig/branch insectivore	0	0.1	0.7	1.7
Trunk surface insectivore	0	0	0.7	3.3
Sallying flycatcher	0	1.3	0.8	2.6

Biogeography – The Species-Area Model (1)

- When increasing the **area (A)** from which one samples various species populations, the **total species number (S)** increase in a positive way according to the following logarithmic deterministic model: $S = C.A^{z}$ (Areas = **Oceanic islands** or **Habitat islands** on mainlands)

- Factors that specifically contribute to the **S-Area relationship** are:

1. Large islands are also subject to larger **sampling sizes** of individuals (N) from species populations thereby increasing the **probability of encountering new species**; hence a mere **sampling phenomenon** or artefact of more effective species sampling as N increases

2. As the island size increases, the **probability of encountering different habitat types** also increases: High **landscape heterogeneity**: Lakes, mountains, valleys, swamps, oases etc., and such features contain more **potential niches** that can be filled by species

Biogeography – The Species-Area Model (2)

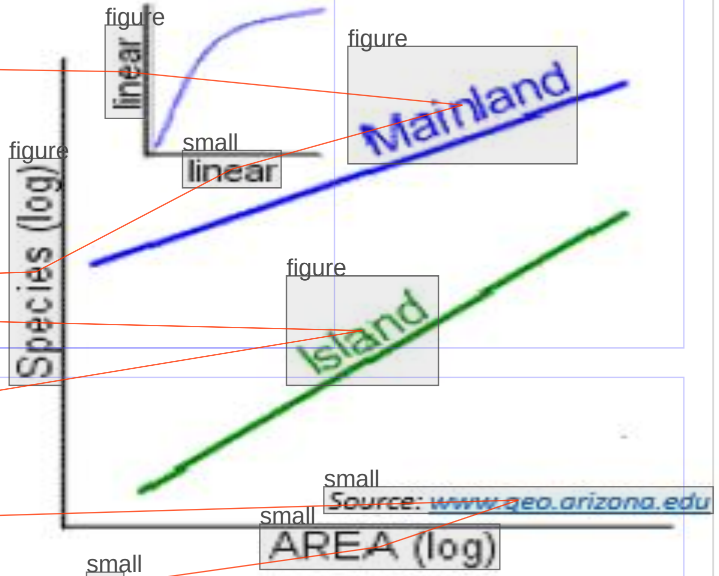
3. Large islands inevitably also contain large populations, and large populations are less **vulnerable to local extinction phenomena** (e.g. predation, parasites, pathogens)

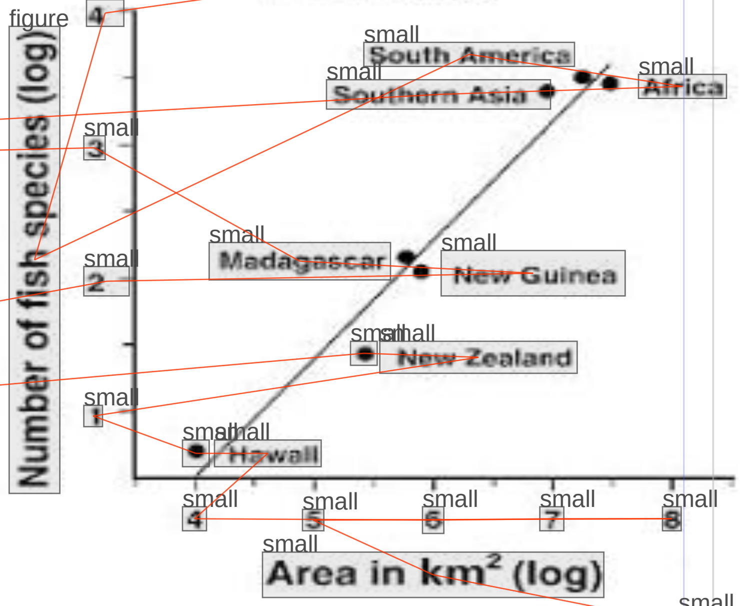
4. Large island populations also have **higher speciation potentials** due to higher **population variability** contained herein (high **polymorphism** and **resource use diversity**)

5. Large islands inevitably represent **larger targets** for **colonizing species** (immigration) as the probability of encountering the area increases with size

Biogeography – The Species-Area Model (3)

- The normal range of Z is 0.20 – 0.40 for true (oceanic) islands and often around 0.25.
- Z is only 0.1 – 0.25 for recently isolated habitat islands (e.g. forest surrounded by farms, a lake, a gap in the forest, or an oasis).
- Z > 0.26 for long-term isolated habitats on the mainland or very large islands such as Australia.
- As **habitat connectivity** increases, the S-Area relationship is reduced => Low z-value
- Habitat connectivity is related to habitat diversity and as oceanic islands are more isolated than mainland habitat islands, they display stronger S-Area relationship (high z-value)



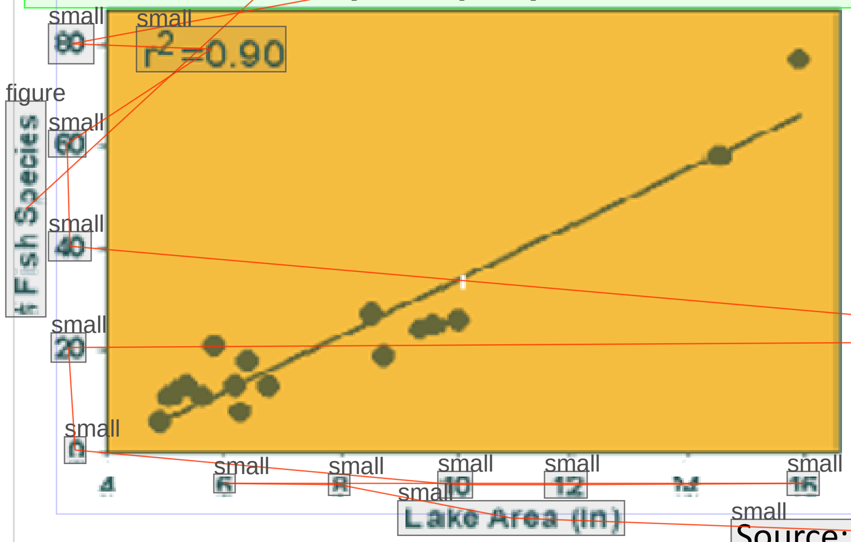


Biogeography – The Species-Area Model (4)

- Logging both sides of the S-Area power function:

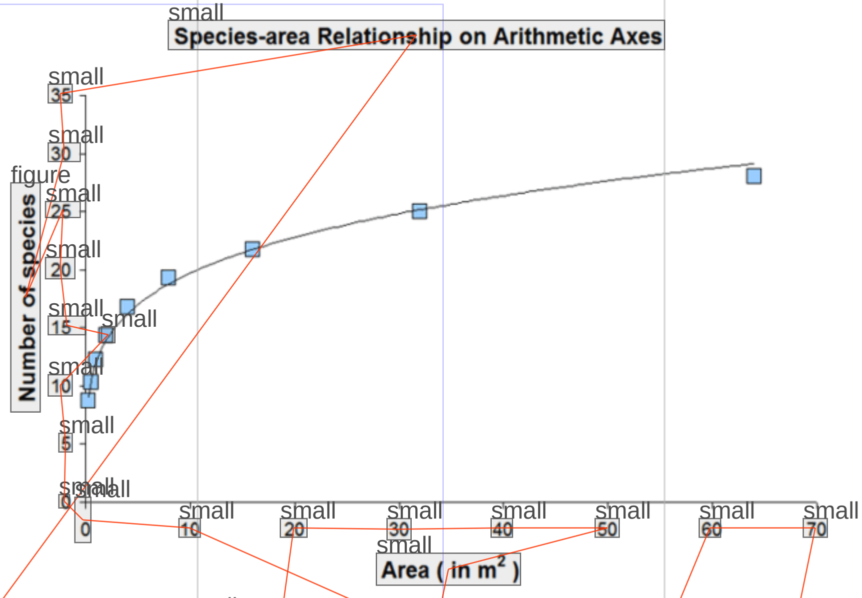
$$\log S = \log C + z \log A$$

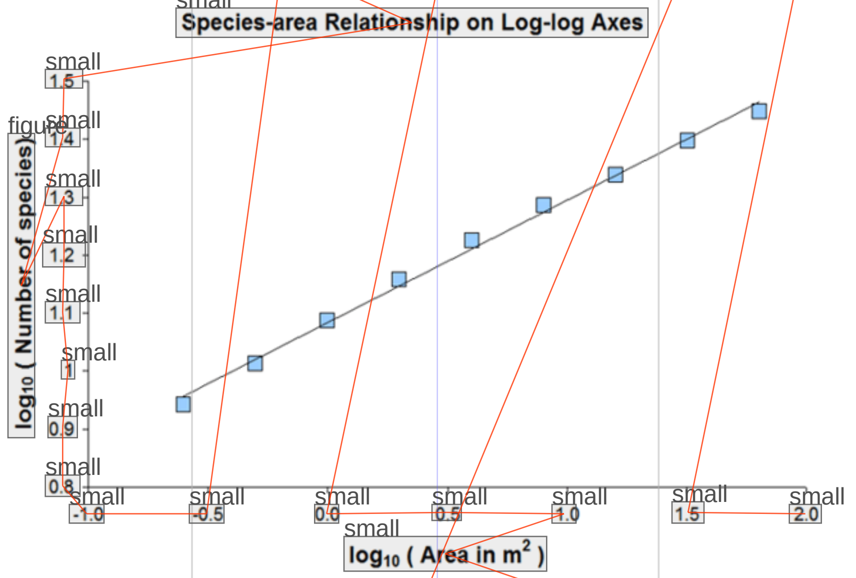
- **C** and Z are constants depending on both **habitat type, animal community** and is specific to variability in dispersability and mobility of the species herein.
- In a **x-y logarithmic plot**, log C is the intercept on the y-axis, and z denotes the graph slope.
- The **z-value** denotes how strong the S and A relationship is (= positive correlation).



Species area relationship for fish in selected Quebec and Ontario lakes. Unpublished data from Jake Vender Zenden

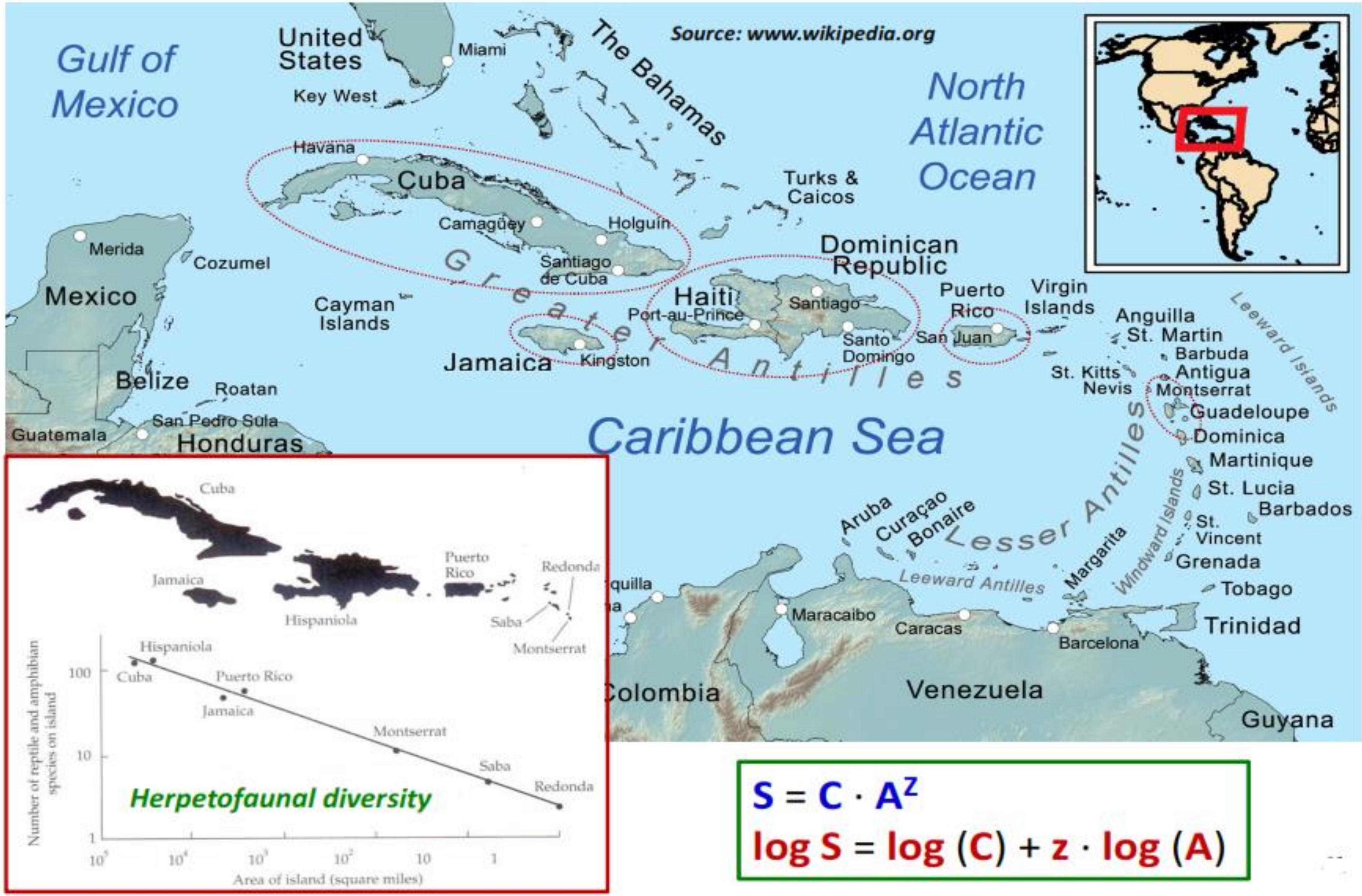
Source: www.redpath – museum.mcgill.ca





Source: www.en.wikepedia.org

Biogeography – The Species-Area Model (5)



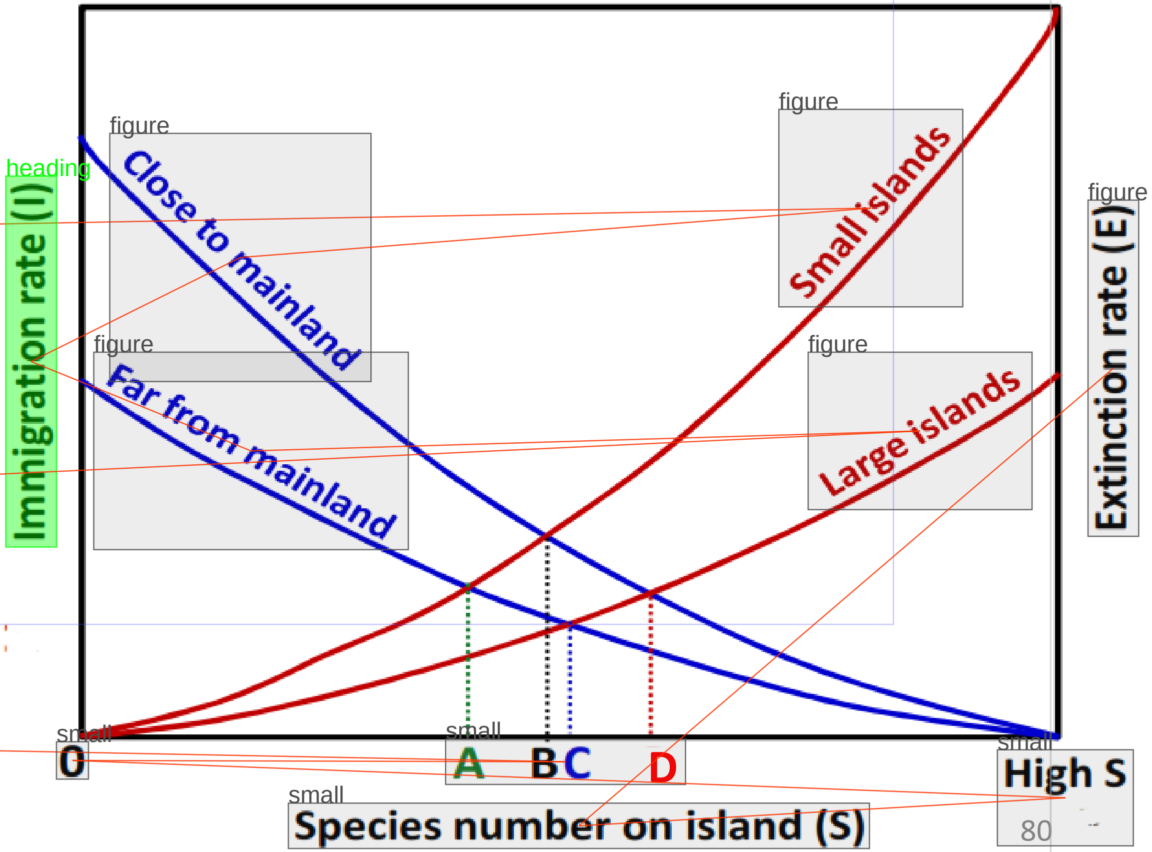
$$S = C \cdot A^{z}$$

$$\log S = \log(C) + z \cdot \log(A)$$

MacArthur-Wilson's Equilibrium Theory (1)

- Modelling species number (S) on true islands: S depends on two independent variables:
    1. Immigration rate (I)   2. Extinction rate (E)
- S is determined when an **equilibrium** between **I** and **E** rates is obtained
- As **S** ↑, **I** rate is lowered (↓) as potential niche space is occupied (saturation ↑)
- In contrast when **S** ↑ then **E** rate ↑ due to increased **interspecific competition**

- Small islands have **high E** and **low I** rates: They are small **targets** and have **small vulnerable populations**; the opposite is the case for **large** islands; **high I** and **low E**
- Distance to mainland also a factor for I rate: **Distance islands** have **low I** and **close islands** have **higher I.**
- Thus, S is highest on large islands nearby mainland (D), and smallest on small islands far from the mainland (A)



MacArthur-Wilson's Equilibrium Theory (2)

- Extinction Rate: Depends on 1) Island Size, 2) Distance to mainland (isolation degree)

- Island Size: Large islands have larger populations, hence genetic population variability is high and populations therefore more resilient towards predators, diseases, and stochastic detrimental events: e.g. storms, tsunamis, floods, drought etc.)

- Distance to mainland: If close to mainland, extinctions may be delayed by regular immigration, thus compensating for the species loss over time

MacArthur-Wilson's Equilibrium Theory (3)

- Immigration Rate: Depends on 1) Island Size, 2) Distance to mainland
- **Island Size**: A large island represents a greater target for colonisers => higher probability of colonization.
- **Distance to mainland**: If the distance is short, the likeliness of species colonizing from the mainland is higher than for more remote islands, to which many species may have difficulties in reaching successfully (depends on mobility and dispersability of animals).
- In effect species number is highest on large islands close to the mainland (CL) and smallest on small islands far away (**remote/ isolated**) from the mainland (DS)

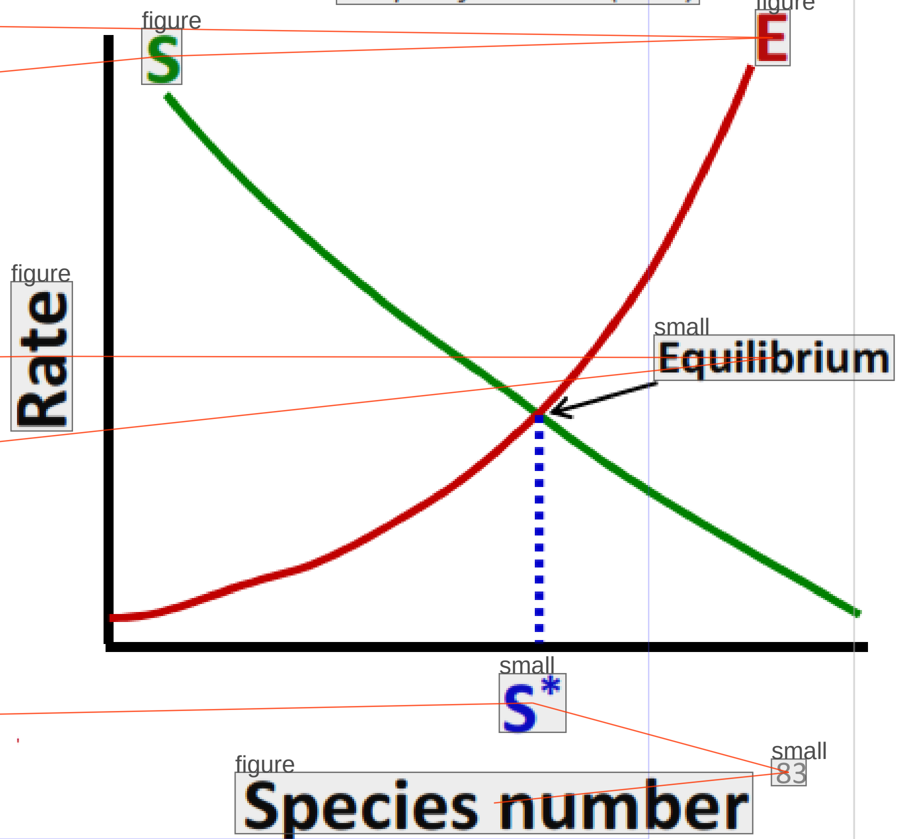
Modelling Species Number on Habitat Islands

- On habitat islands, species numbers depend on: 1) Speciation rate and 2) Extinction rate
- Immigration plays a minor role on the large scale and is replaced by speciation processes.
- However, if habitat connectivity is high between islands, immigration from species rich areas is important in ecological time frame; speciation only evolutionary time frame

Speciation Rate

- As speciation saturation increases, the probability of **speciation decreases** as the potential niche space is reduced
- Fewer empty niches reduce the chances of adaptive radiation by virtue of reducing character displacement processes

Adapted from Giller (1984)



Extinction Rate

- As species **saturation increases interspecific competition** increases extinction rate through the competitive exclusion principle (similarly to true islands)

Summary - Niche Partitioning & Species Richness (1)

1. Species richness and the niche concept are interrelated and determined by:

- **Niche dimensionality** and **differentiation**: Related to habitat heterogeneity
- **Niche width** and **shape**: Narrow and leptokurtic niches increase diversity
- **Niche overlap** and **competitive coefficient**: Complementarity increase S

2. Species richness and niches also interrelated with the habitat

- **Habitat complexity**: Both vertical and horizontal heterogeneity increase S
- **Habitat area**: Large and interconnected habitat areas increase richness

Summary - Niche Partitioning & Species Richness (2)

3. The species-area model explains the number of species on islands ($S = CA^z$):

- **True islands**: z-value higher than on mainland islands ($z = 0.20 - 0.40$, $z \approx 0.25$)
- **Mainland islands**: Lower than for true islands ($z = 0.10 - 0.25$, $z > 0.26$, if $t \uparrow$)
- **Lakes**: Similar to mainland islands but largely depends on connecting rivers.

4. The theory of island biogeography and species richness depend on

- **Area size**: Large size has larger populations and higher habitat heterogeneity
- **Distance to mainland**: Nearness → Higher colonization rate → S ↑
- **Habitat connectivity**: Low connectivity means lower colonization rate
- **Speciation-extinction dynamics**: Related to time and population size/ area

Lecture 7 – Foraging Theory

❑**Objectives of the lecture**

➢**Optimal Foraging Theory**

- Definition of the Optimal foraging Theory
- Assumptions of the theory
- Parameterizing the Optimal Foraging Theory

➢**Predator-Prey Relationships**

- Evolutionary-Behavioural-Population-Community-Macro-Ecology

➢**Predator Avoidance Strategies**

- **Species**: Genetics (Phenotype/ genotype), niches, habitat requirements
- **Populations**: Growth, structure, regulation and interactions

What is Optimal Foraging Theory, OPT?

- It is a behavioral ecology model that helps predict how an animal behaves when searching for food

Aim of the Optimal Foraging Theory

- To predict the foraging strategy of a forager/predator to be expected under specified condition

Important terminologies

- **Ideal Free Distribution theory** – theory which makes a case of uniform distribution of food for predators such that there is no need for foragers to switch foraging patches.
- **Functional response** – deals with a predator's intake rate in response to variation in prey distribution and densities
- **Aggregate response** – explains how predators are distributed in response to prey availability
- **Total response** = Functional response + Aggregate response

Assumptions inherent in Optimal Foraging Theory

1. The foraging behaviour that is exhibited by present-day animals is the one that has been favoured by natural selection in the past but almost enhances an animal's fitness at present
2. High fitness is achieved by a high net rate of energy intake (i.e. gross energy intake minus the energetic costs of obtaining that energy)
3. Experimental animals are observed in an environment to which their foraging behaviour is suited

Scenarios which unjustify the OFT

1. Other aspects of the organism's behaviour may influence fitness more than optimal foraging does. E.g. premium on avoidance of predators coercing animals to forage at places and at times associated with lower predation risk trading off efficiency in food gathering.

2. Variation in the efficiencies of energy gathering process exploiting different dietary constituents (e.g. nitrogen) by many consumers (herbivores and omnivores) creating the need for consumers to forage on a mixed and balanced diet.

Theoreticians & Mathematicians

- OFT makes predictions about foraging behaviour based on mathematical models

• Important Question

- ***Is it necessary for a real forager to be equally omniscient and mathematical, if it is to adopt the appropriate , optimal strategy?***

Theoreticians are omniscient mathematicians – the foragers need not be

- The answer is **NO**, because
- Theory says that if a forager that in some way manages to do the right thing in the right circumstances, then this forager

1. Will be favoured by natural selection
2. Possible inheritance of newly acquired abilities by future generations
3. Abilities spread, in evolutionary time, throughout the population

Parameterizing the OFT 1

- Foraging entails predators expending time and energy in obtaining food (MacArthur & Pianka, 1966)
- Intake rates of a predator is dependent on the searching (encounter rate) and handling (i.e. pursuing, subduing and consuming it) times of prey
- Generalists pursue (and may then subdue and consume) a large proportion of the prey types they encounter
- Specialists continue searching except when they encounter prey of their specifically preferred type

Parameterizing the OFT 2

- Specialists will only pursue profitable prey items, but may expend a great deal of time and energy searching for them
- Generalists will spend relatively little time searching but they will pursue both more or less profitable types of prey
- An optimal forager should therefore balance the pros and cons so as to maximise its overall rate of energy intake

Parameterizing the OFT 3

- Given that a predator already includes a certain number of profitable items in its diet, should it expand its diet (and thereby decrease its search time) by including the next most profitable item as well?
- The next most profitable prey item for an optimal forager

$$Profitability = \frac{Ei}{hi}$$

where E_i is the energy content of the next most profitable i^{th} prey item and h_i its handling time

- In addition, $\bar{E}$ / $\bar{h}$ is the average profitability of the 'present' diet (i.e. one that includes all prey types that are more profitable that $\boldsymbol{i}$, but does not include prey type $\boldsymbol{i}$ itself), and
- $\bar{s}$ is the average search time for the present diet

Parameterizing the OFT 4

- If a predator does pursue a prey item of type *i*, then its expected rate of energy intake is

$$E_i/h_i$$

- If it ignores this prey item, whilst pursuing all those that are more profitable, then it can expect to search further. The total expected rate of energy intake

$$\frac{\bar{E}}{(\bar{s}+\bar{h})}$$

where $\bar{E}$ is the average energy content, $\bar{s}$ is the average search time and $\bar{h}$ is the average handling time for the present diet

Parameterizing the OFT 4

- The most profitable, optimal strategy for a predator will be to pursue the ith item if, and only if

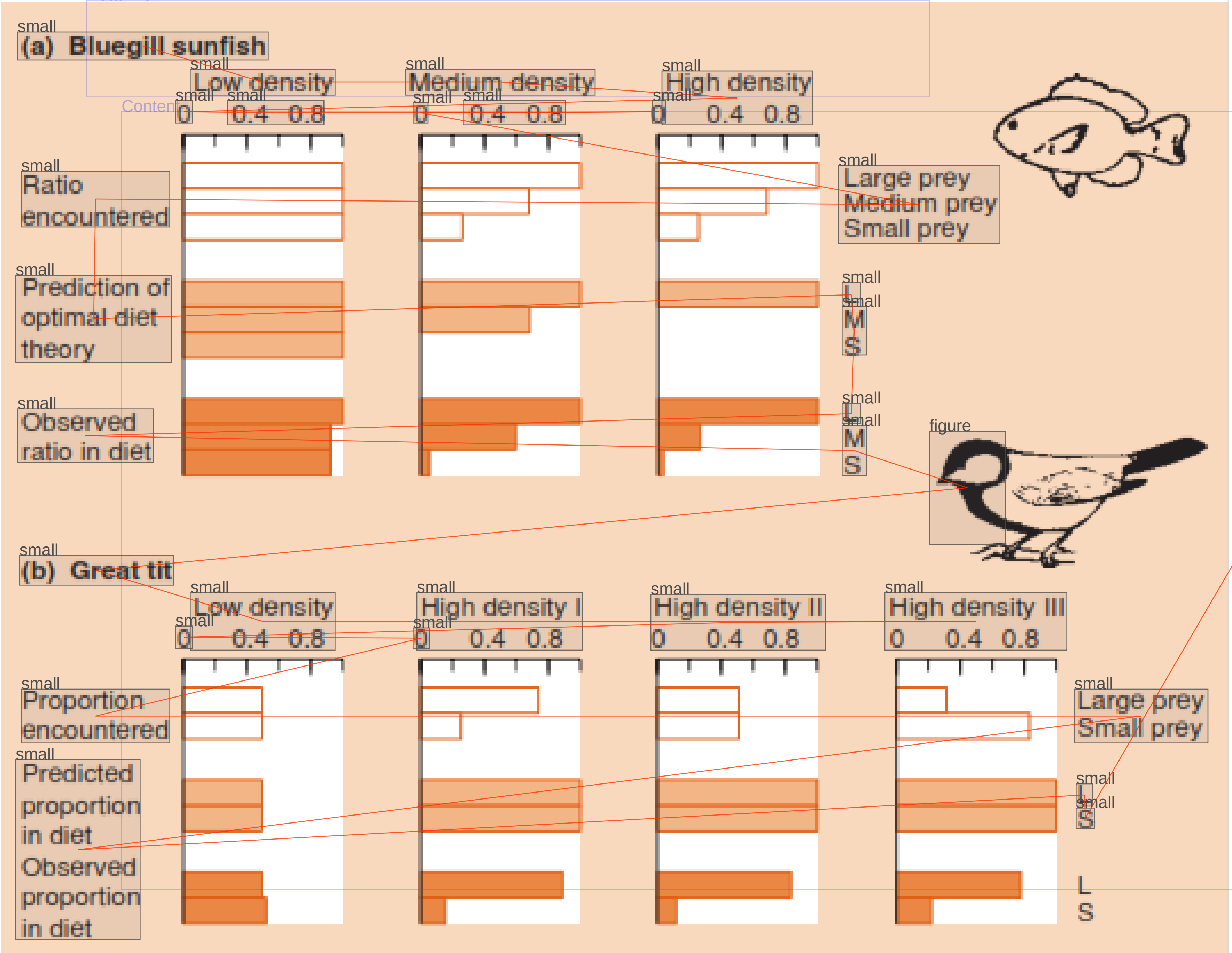
$$E_i / h_i \geq \bar{E} / (\bar{s} + \bar{h})$$

- The optimal diet model leads to a number of predictions

1. Predators with shorter handling times than search times should be generalists, because the short times taken to handle prey items already found would allow them to commence searching for another prey.
2. Predators with longer handling times than search times should be specialists because once a prey has been seen and began to be handled (include pursuit), the predator cannot go in for another food. Therefore, such predators should go in for the most profitable prey.

Parameterizing the OFT 5

3. Predators should have broader diets in unproductive environments (where prey items are relatively rare and $\bar{s}$ is relatively large) than in a productive environment (where $\bar{s}$ is smaller)
4. Predators should ignore insufficiently profitable food types irrespective of their abundance
5. Provides a context for understanding the narrow specialization of predators that live in intimate association with their prey. Since their whole lifestyle and life cycle are finely tuned to those of their prey, handling time is low.



- Two studies of optimal diet choice that show a clear but limited correspondence with the predictions of the optimal diet model. Diets are more specialised at high prey densities; but more low profitability items are included than predicted by the theory

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