1. **AE II:** Ecological Niche

2. **AE II:** Species' Traits & Structure of Ecological Space

3. **Practicals:** Mapping Functional Diversity & Philosophy of Niche

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Ecological Niche

Sam Sidders

1610s, "shallow recess in a wall," from French *niche* "recess (for a dog), kennel" (14c.), perhaps from Italian *nicchia* "niche, nook," which is said to be from *nicchio* "seashell," itself said by Klein, Barnhart, etc. to be probably from Latin *mitulus* "mussel," but the change of -m- to -n- is not explained. Watkins suggests that the word is from an Old French noun derived from *nichier* "to nestle, nest, build a nest," via Gallo-Roman *nidicare from Latin nidus "nest" (see nidus), but that, too, has difficulties. The figurative sense is recorded by 1725.

www.etymonline.com

“At its most ambitious, the theory of niche helps us understand fundamental questions of ecology.”

T. W. Schoener (1989)

“I think it is good practice to avoid the term niche whenever possible.”

M. H. Williamson (1972)

“No concept in ecology has been more variously defined or more universally confused than “niche.“

L. A. Real & S. A. Levin (1991)

“The concept of niche provides a way of characterizing important ecological attributes of species while recognizing their uniqueness.“

J. H. Brown (1955)

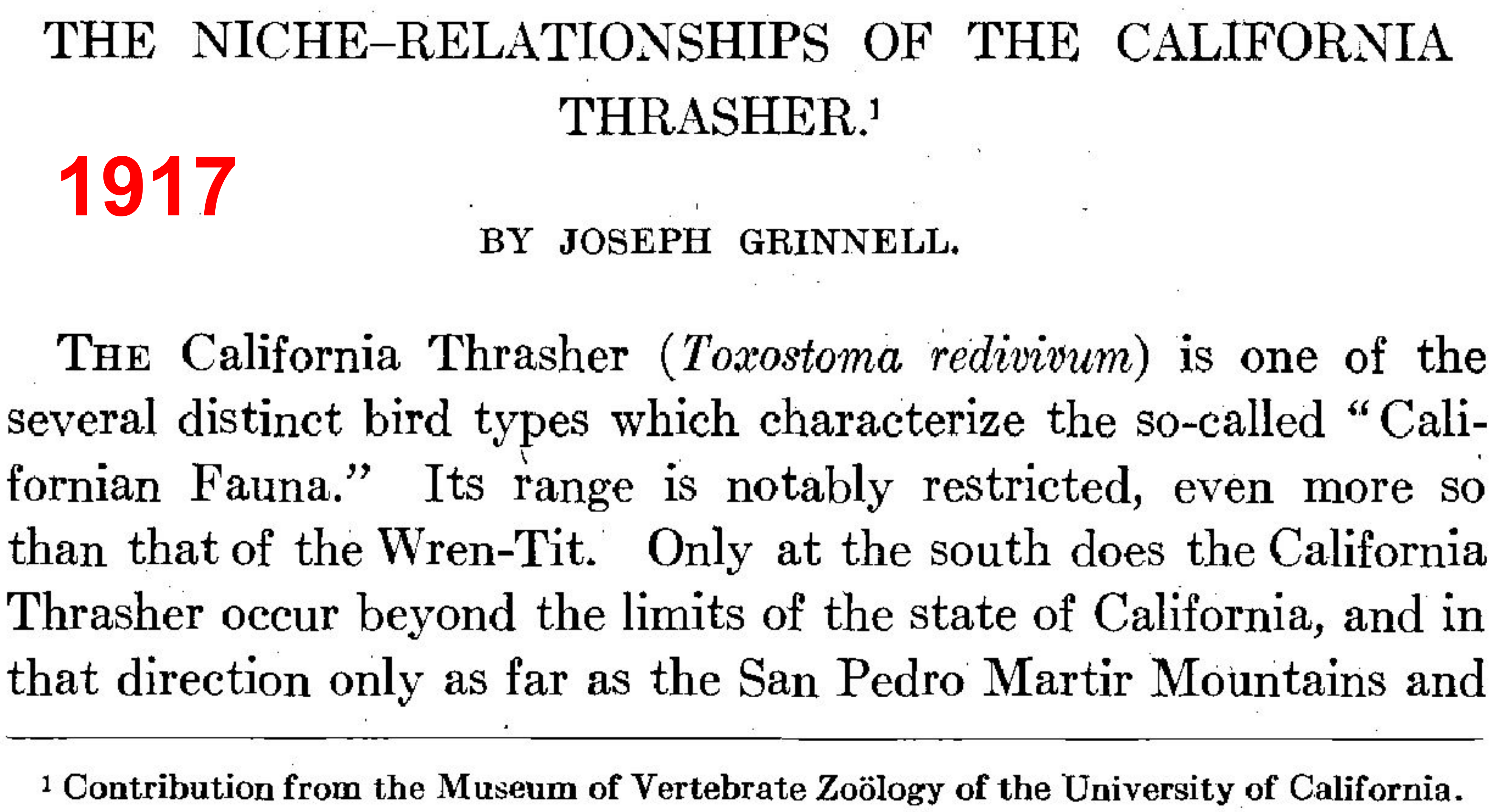
“Studies of the niche have played an important role in the development of community ecology, and are likely to do so in the future.”

B. A. Mauer (1999)

“I believe that community ecology will have to rethink completely the classical niche-assembly paradigm from the first principles.”

S. P. Hubbel (2001)

1917



THE NICHE–RELATIONSHIPS OF THE CALIFORNIA THRASHER.[1]

BY JOSEPH GRINNELL.

The California Thrasher (*Toxostoma redivivum*) is one of the several distinct bird types which characterize the so-called "Californian Fauna." Its range is notably restricted, even more so than that of the Wren-Tit. Only at the south does the California Thrasher occur beyond the limits of the state of California, and in that direction only as far as the San Pedro Martir Mountains and

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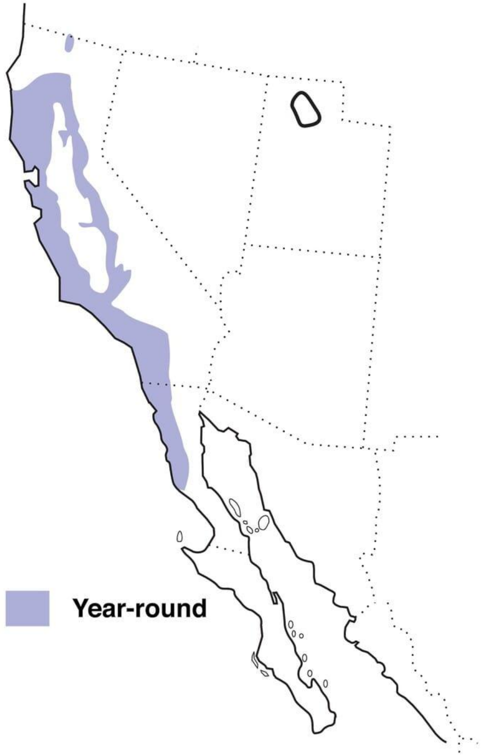
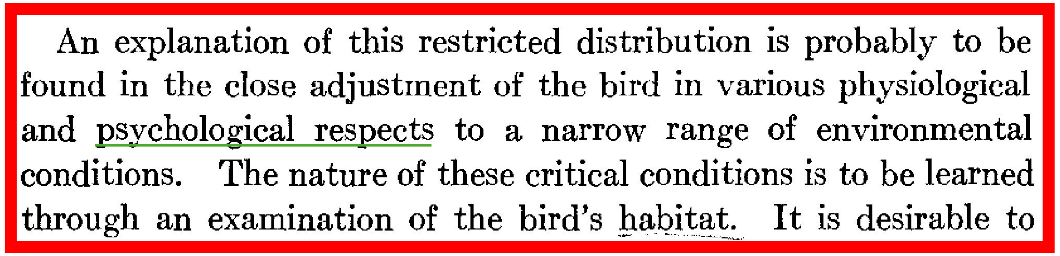
[1] Contribution from the Museum of Vertebrate Zoölogy of the University of California.




An explanation of this restricted distribution is probably to be found in the close adjustment of the bird in various physiological and psychological respects to a narrow range of environmental conditions. The nature of these critical conditions is to be learned through an examination of the bird's habitat. It is desirable to

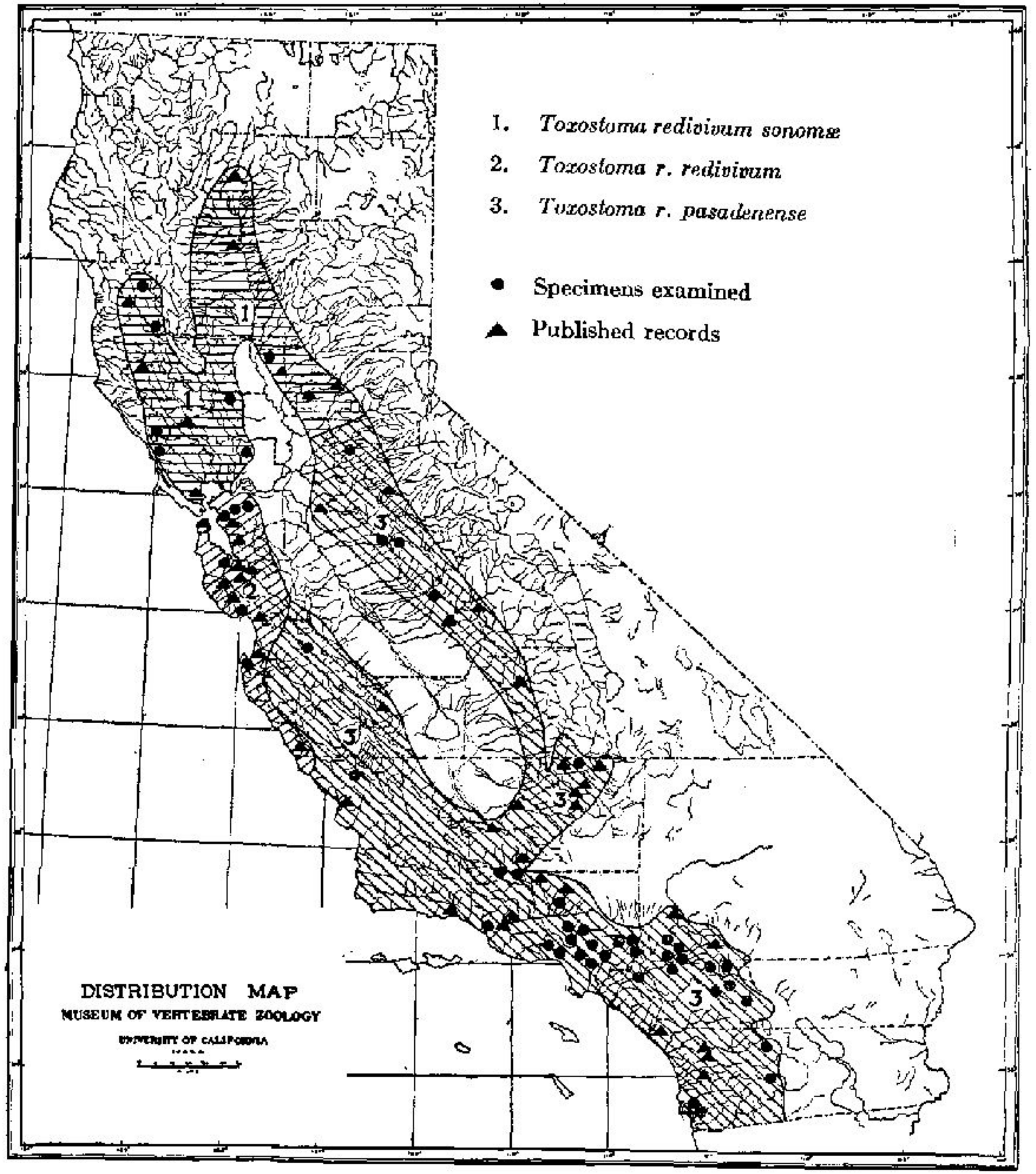


Figure 1.

These various circumstances, which emphasize dependence upon cover, and adaptation in physical structure and temperament thereto, go to demonstrate the nature of the ultimate associational niche occupied by the California Thrasher. This is one of the minor niches which with their occupants all together make up the chaparral association. It is, of course, axiomatic that no two species regularly established in a single fauna have precisely the same niche relationships.

As a final statement with regard to the California Thrasher, we may conclude, then, that its range is determined by a narrow phase of conditions obtaining in the Chaparral association, within the California fauna, and within the Upper Sonoran life-zone.

Grinnell’s niche concept (1917)

niche designate the place in an association occupied by a single species

- <u>undistinguishable from a *habitat*</u>
- a property of the environment
  x a characteristic of the species (species’s habitat)
- geographical definition
- limitation by environmental factors (= interactions overlooked!)

☐ ultimate distributional unit, within which each species is held by its structural and functional limitations...

Let us draw a niche…?

Niche position

NICHE, HABITAT, AND ECOTOPE

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Cornell University, Ithaca, New York 14850

> It is a maxim of the civil law that definitions are dangerous.
>
> [SAMUEL JOHNSON, *The Rambler*]

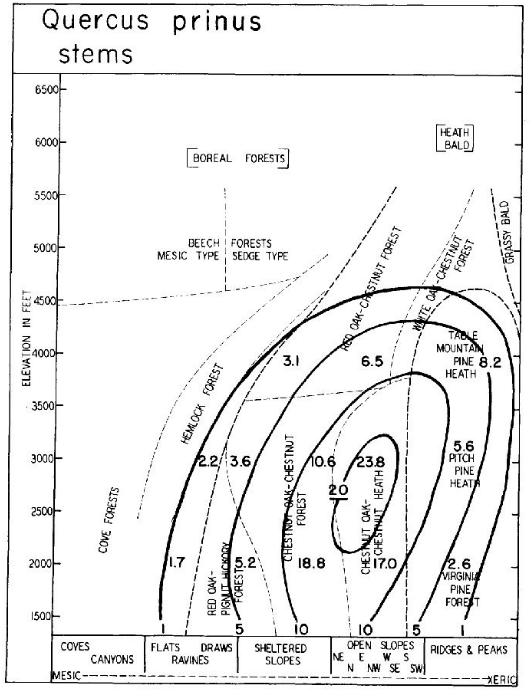


FIG. 2.—A Gaussian response surface or ''binomial solid'' for the habitat of *Quercus prinus* (chestnut oak) in the Great Smoky Mountains, Tennessee (Whittaker 1956). The population is centered in the chestnut oak heath, at the middle elevations in moderately dry sites, and decreases in all directions away from this, as indicated by the population contour lines. Data points are percentages of stems over 1 cm dbh in composite samples of approximately 1,000 stems each.

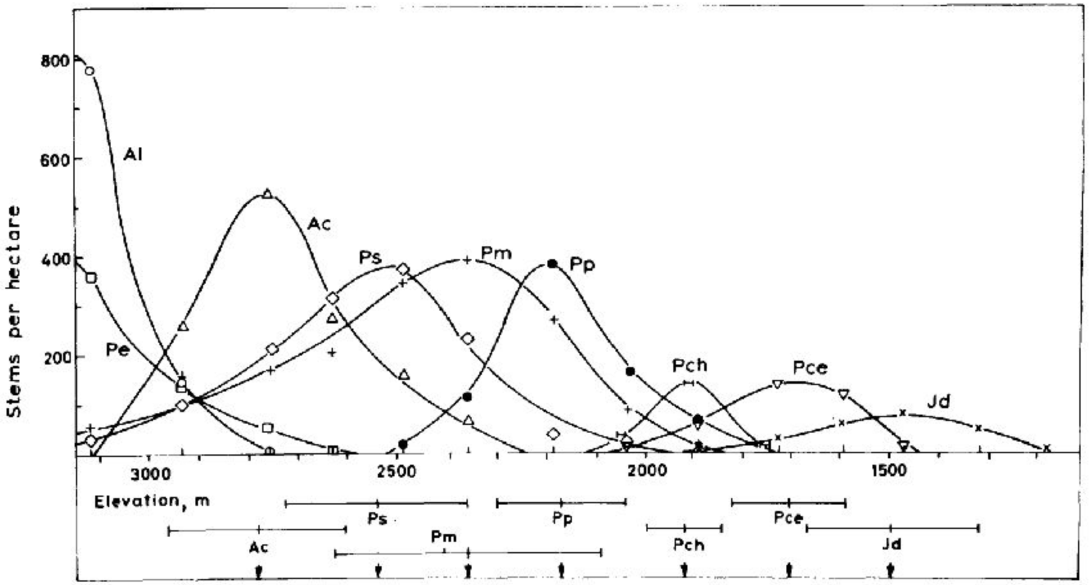
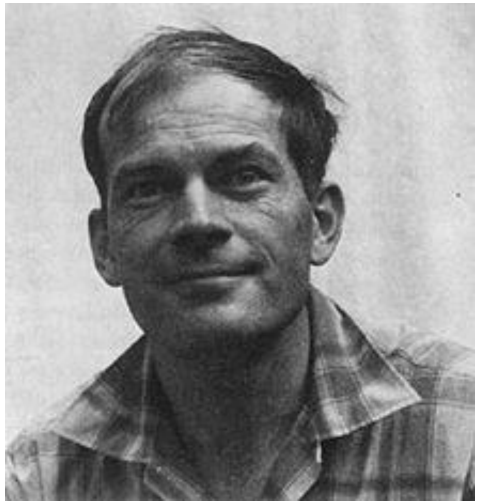


FIG. 1.—Population distributions on a habitat gradient. Coniferous tree species populations are plotted in relation to the elevation gradient on north-facing slopes in the Santa Catalina and Pinaleño Mountains, Arizona (data of Whittaker and Niering 1965). The tree species, competing as community dominants, form a replacement series along the gradient (comparable series formed by oak species along the same gradient are shown by Whittaker [1969]). Whereas the modes of species populations are apparently distributed randomly along the gradient when there are many competing species (Whittaker 1956), the distribution of modes of these competing dominants appears to be regular. Furthermore, in those cases in which the bars for habitat widths overlap, the species of an overlapping pair are differently distributed along the topographic moisture gradient. Species pairs of which the first occupies the more mesic and the second the more xeric topographic position at a given elevation are: Al and Pe, Ac and Ps, Pm and Ps, Pm and Pp, Pce and Jd. Data are numbers of tree stems over 1 cm dbh per hectare, based on sets of five 0.1-hectare samples grouped by elevation intervals and plotted at the mean elevations for the groups. The bars below the abscissa give means and habitat widths expressed as one standard deviation, except for Pm, in which the apparent mode has been used as its center rather than its mean (also indicated). Tree species are indicated by genus and species initials: *Picea engelmanni, Abies lasiocarpa, Abies concolor, Pinus strobiformis, Pseudotsuga menziesii, Pinus ponderosa, Pinus chihuahuana, Pinus cembroides,* and *Juniperus deppeana*. These species are dominants of a community gradient from subalpine forest (Pe and Al), through montane forests (Ac, Ps, Pm, and Pp) to submontane woodlands (Pch, Pce, and Jd).

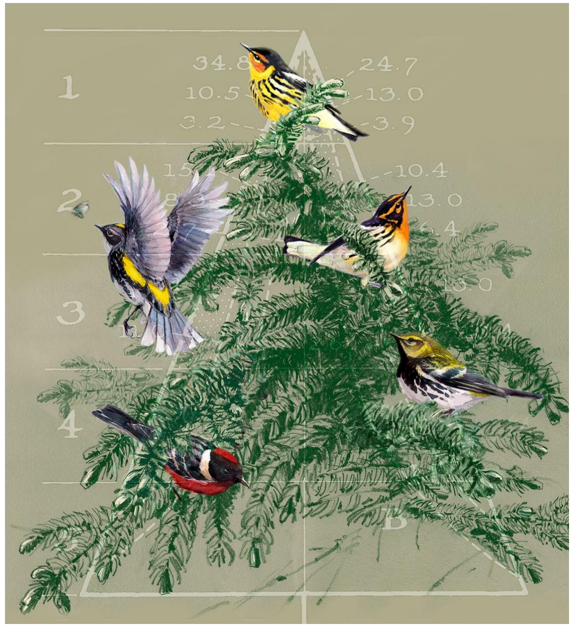
Niche position

MacArthur's warblers



POPULATION ECOLOGY OF SOME WARBLERS OF NORTHEASTERN CONIFEROUS FORESTS[1]

ROBERT H. MACARTHUR
Department of Zoology, University of Pennsylvania



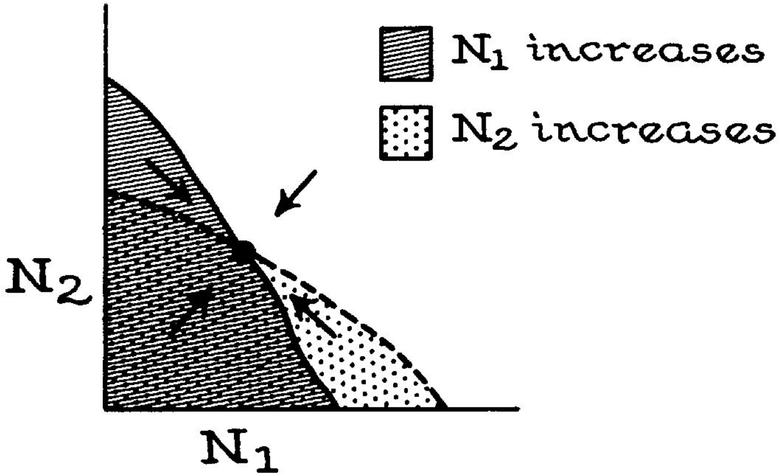


FIG. 1. The necessary conditions for a stable equilibrium of two species. The coordinate axes represent the populations of the species.

INTRODUCTION

Five species of warbler, Cape May (*Dendroica tigrina*), myrtle (*D. coronata*), black-throated green (*D. virens*), blackburnian (*D. fusca*), and bay-breasted (*D. castanea*), are sometimes found together in the breeding season in relatively homogeneous mature boreal forests. These species are congeneric, have roughly similar sizes and shapes, and all are mainly insectivorous. They are so similar in general ecological preference, at least during years of abundant food supply, that ecologists studying them have concluded that any differences in the species' requirements must be quite obscure (Kendeigh, 1947; Stewart and Aldrich, 1952). Thus it appeared that these

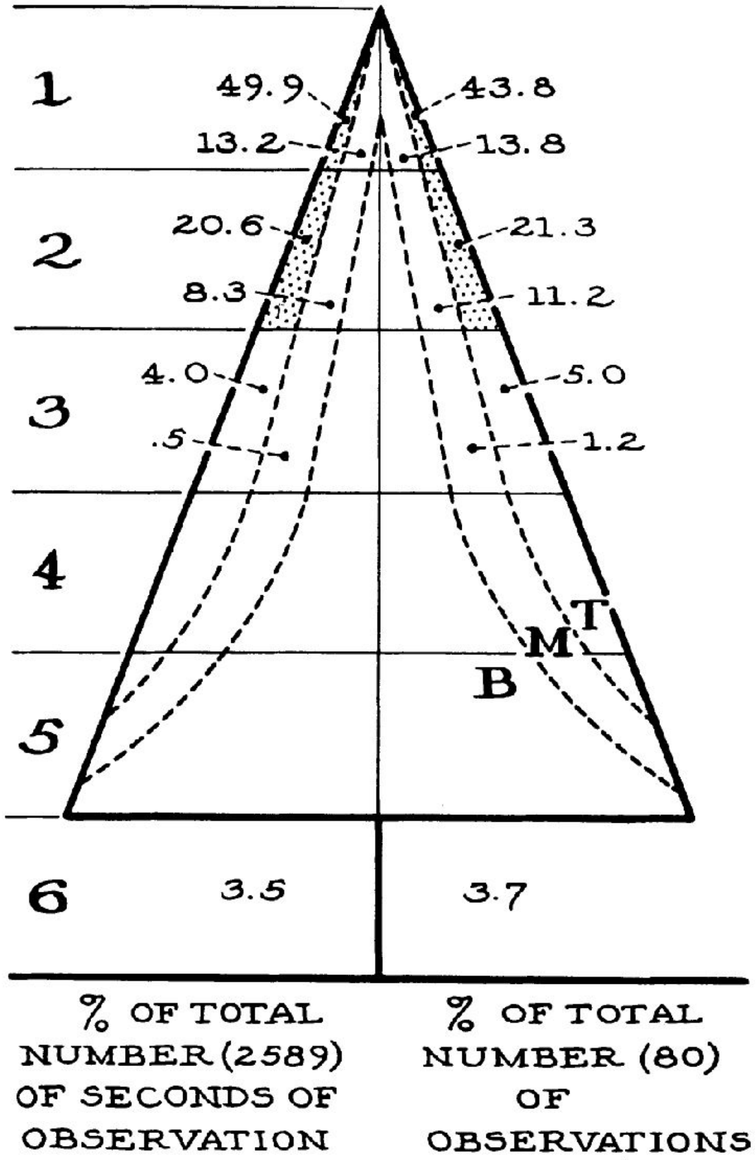


FIG. 2. Cape May warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

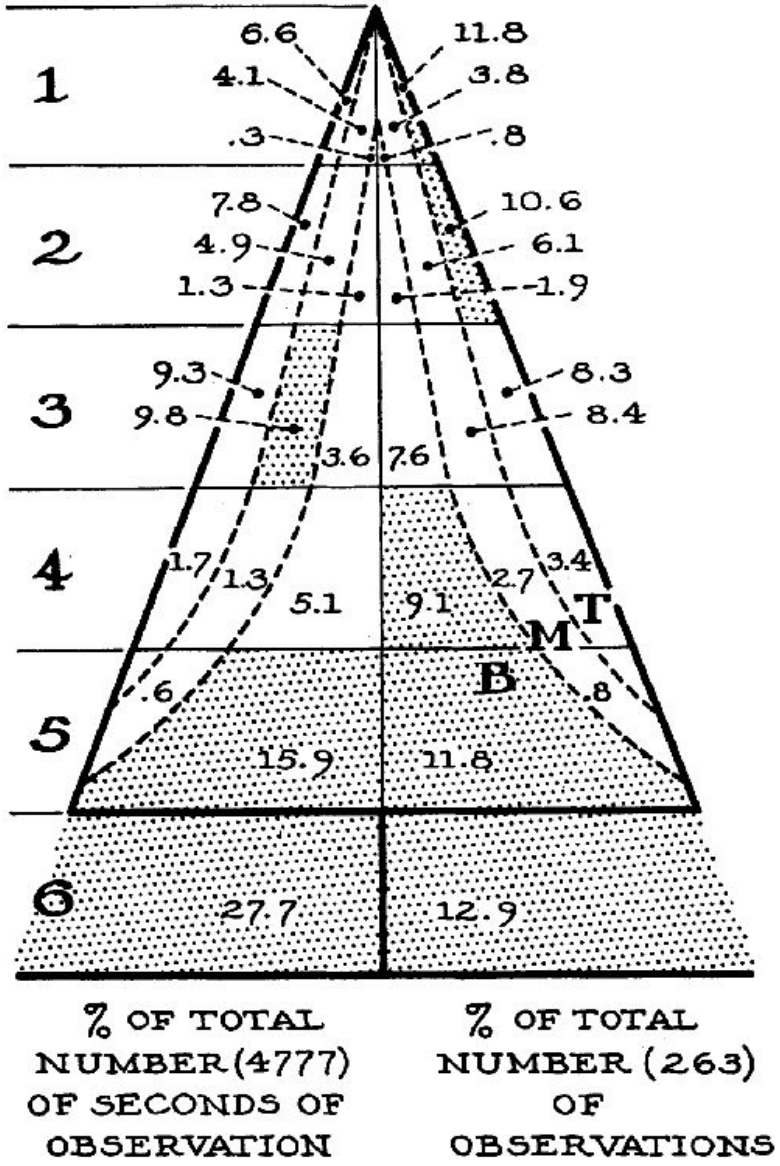


FIG. 3. Myrtle warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

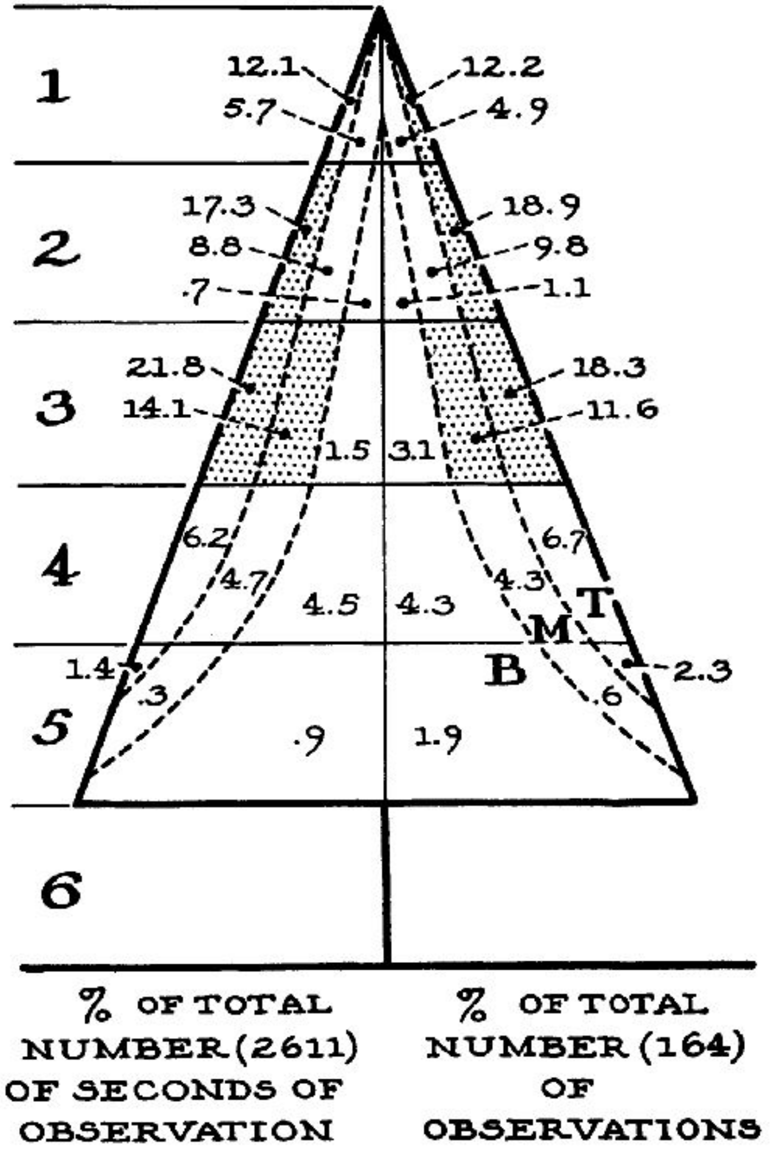


FIG. 4. Black-throated green warbler feeding position. The zones of most concentrated activity are shaded until at least 50% of the activity is in the stippled zones.

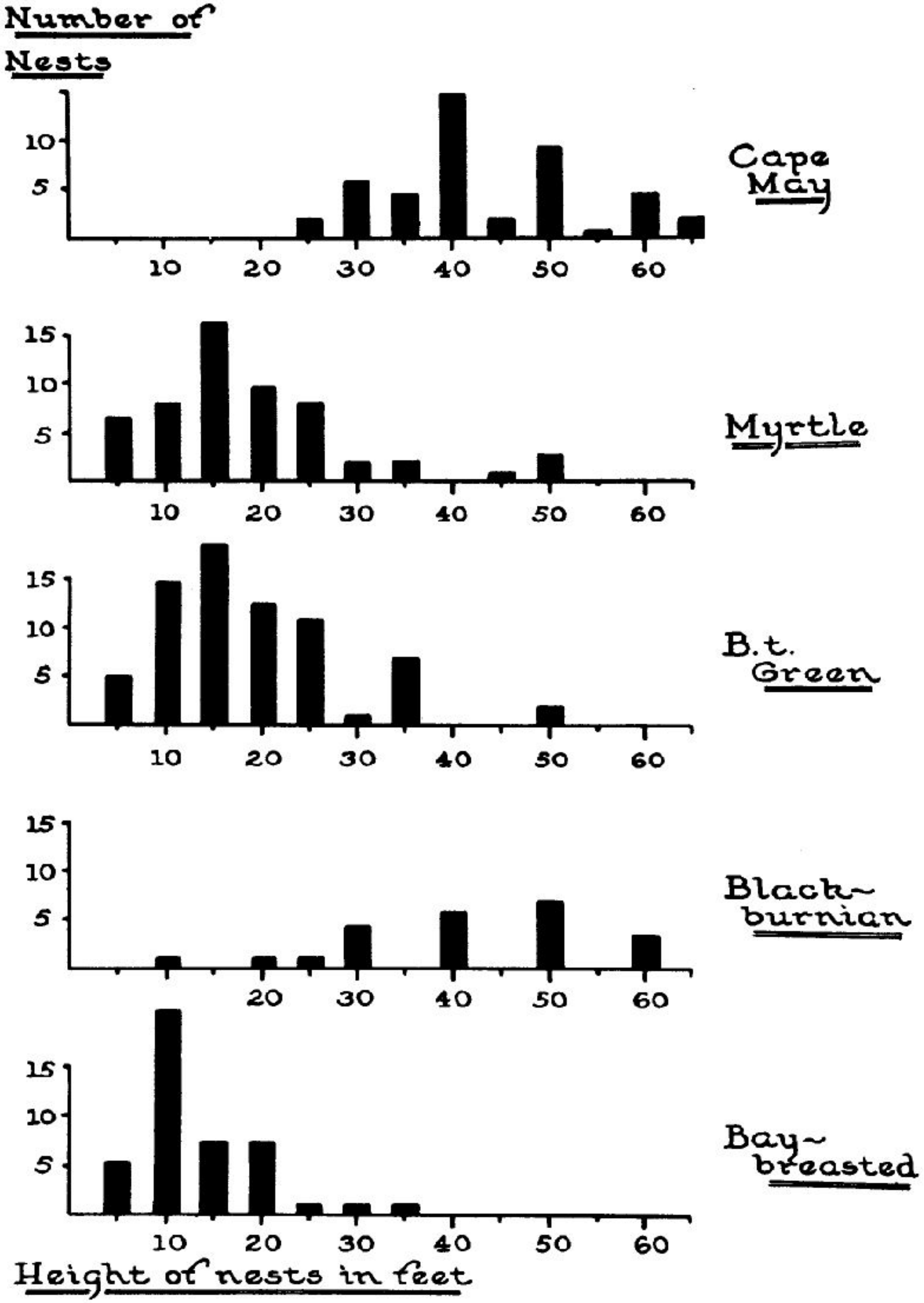


FIG. 8. Nesting heights of warblers.

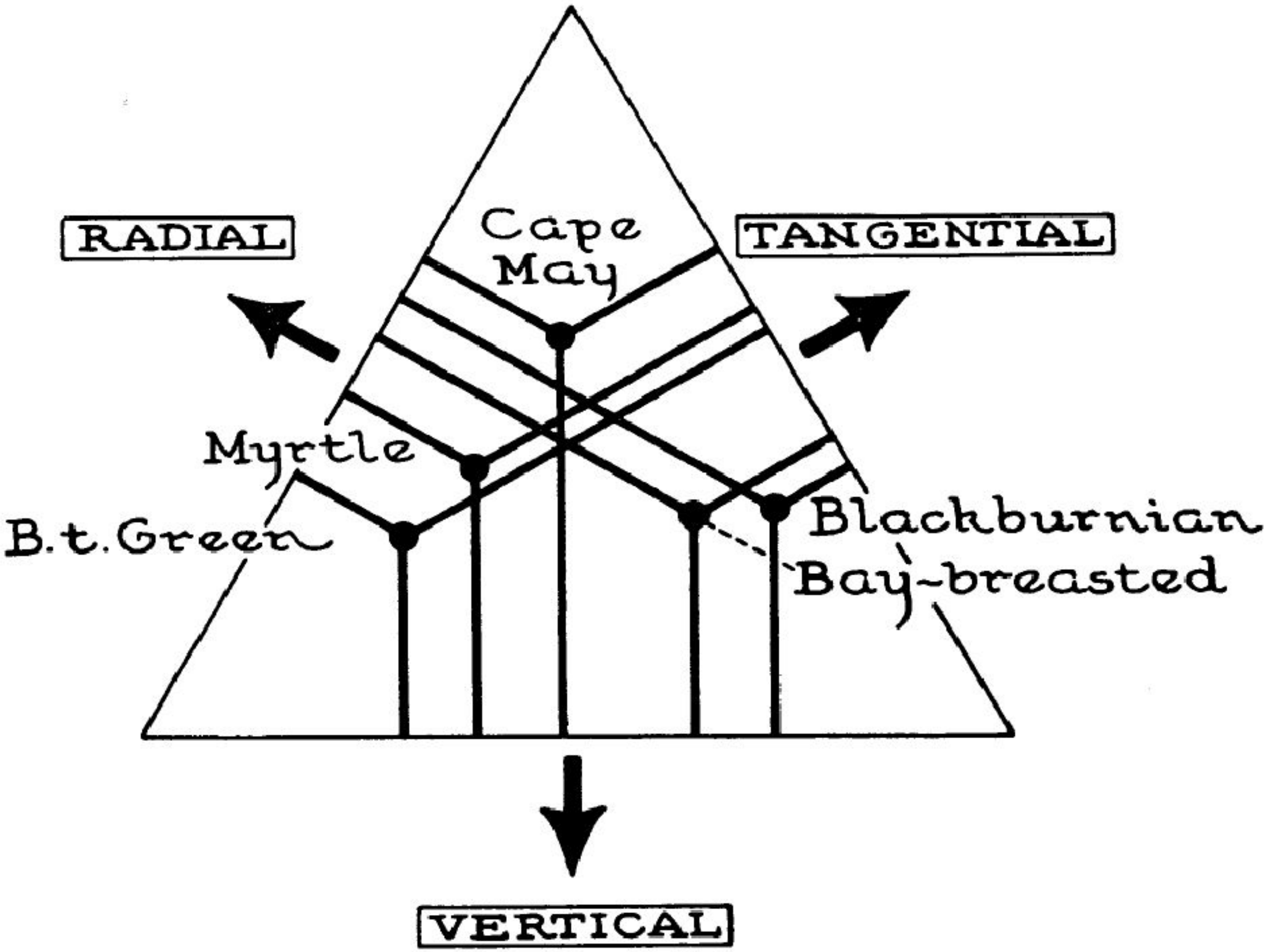


FIG. 7. Components of Motion. From the dot representing a species, lines are drawn to the sides of the triangle. The lengths of these lines are proportional to the total distance which the species moved in radial, tangential, and vertical directions, respectively.

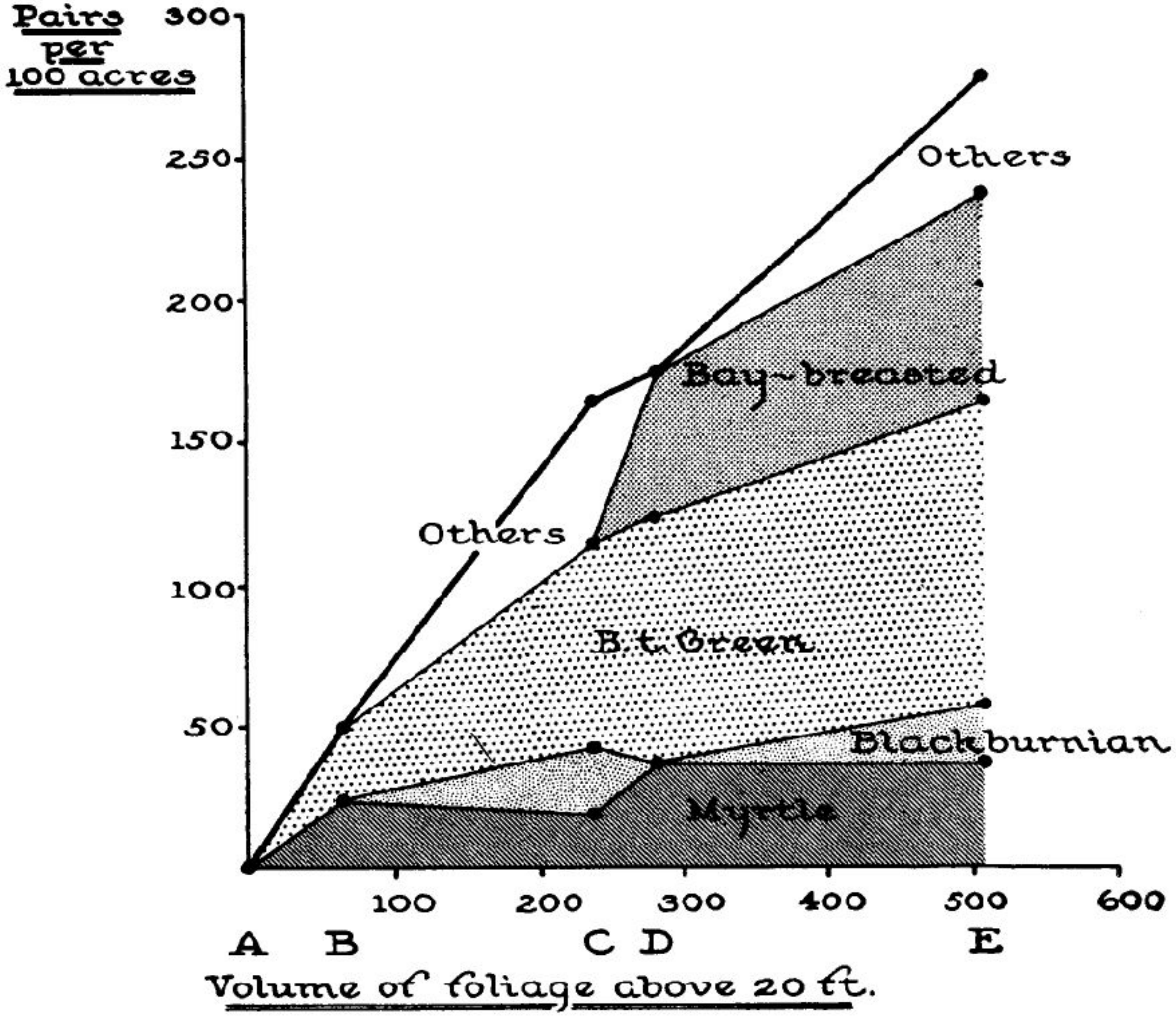
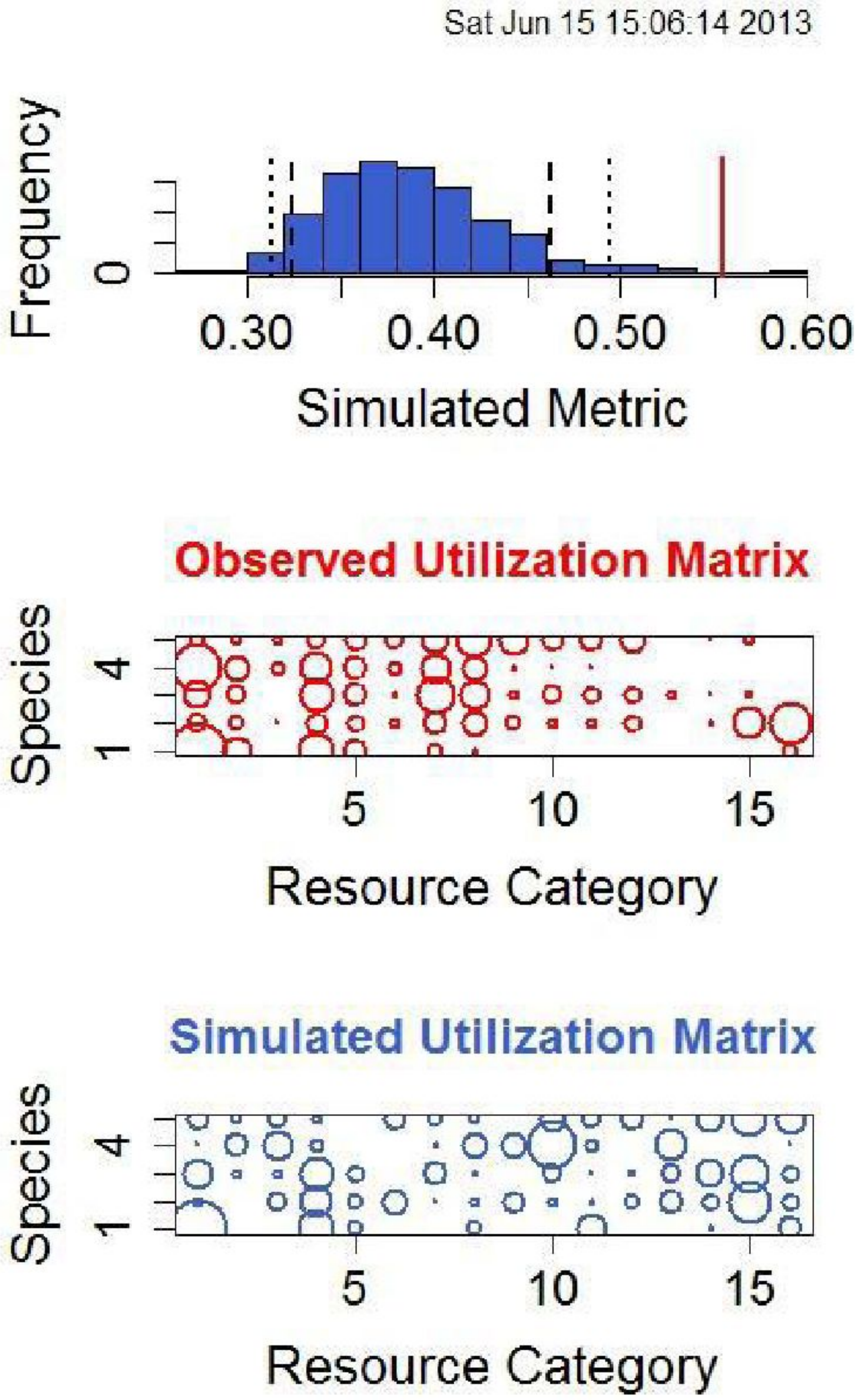


FIG. 10. Composition of the warbler population in plots A, B, C, D, and E. "Others" refers to other warbler species which feed at greater heights than 20 feet above the ground. The units of volume measurement are only proportional to the volume, but each unit roughly equals 1500 cubic feet per acre.

“There are differences of feeding position, behavior, and nesting date which reduce competition. These, combined with slight differences in habitat preferences and perhaps a tendency for territoriality to have a stronger regulating effect upon the same species than upon others, permit the coexistence of species.“

MacArthur concludes that the mechanisms keeping the five species in these forests could result from five populations limited by differing resources, the same resources in different habitats, or the same resources at different times.



“*There is more overlap than expected by chance.*“

Nicolas J. Gotelli

…so what?

ECOLOGY LETTERS

Ecology Letters, (2010) **13**: 1310–1324 doi: 10.1111/j.1461-0248.2010.01515.x

REVIEW AND SYNTHESIS

Niche conservatism as an emerging principle in ecology and conservation biology

Closely related species have similar niches…

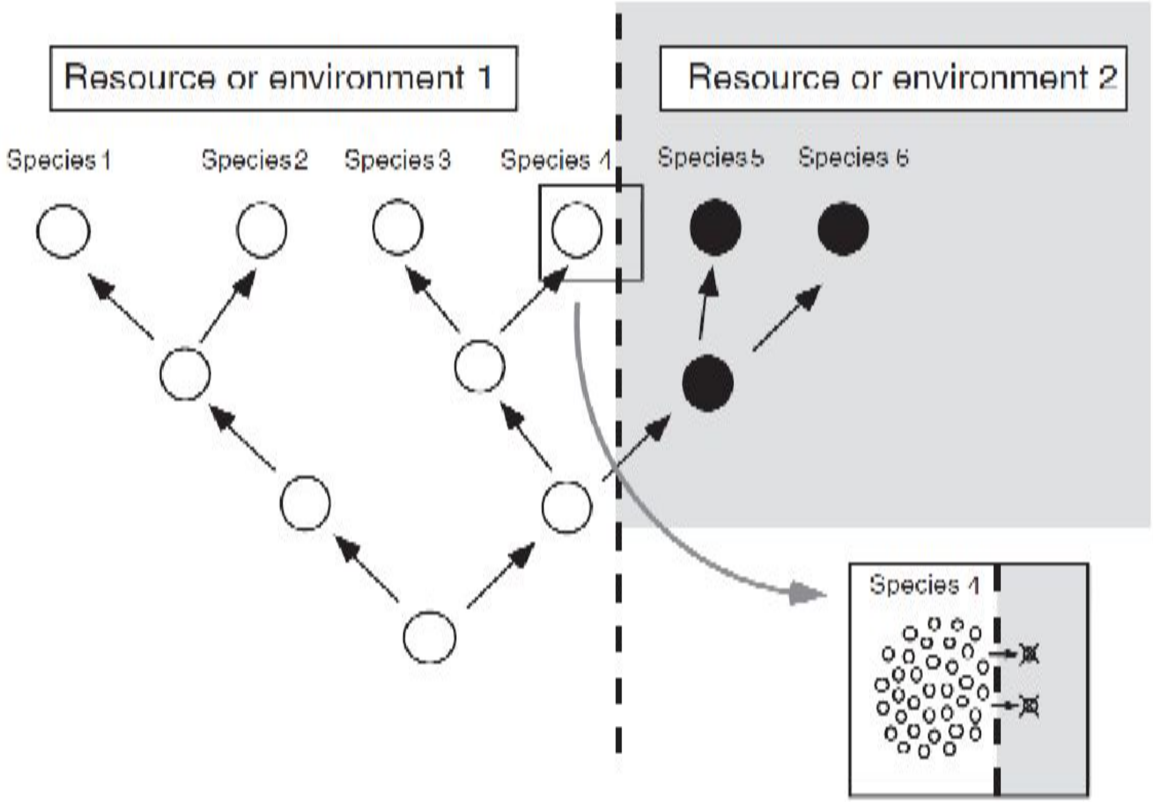
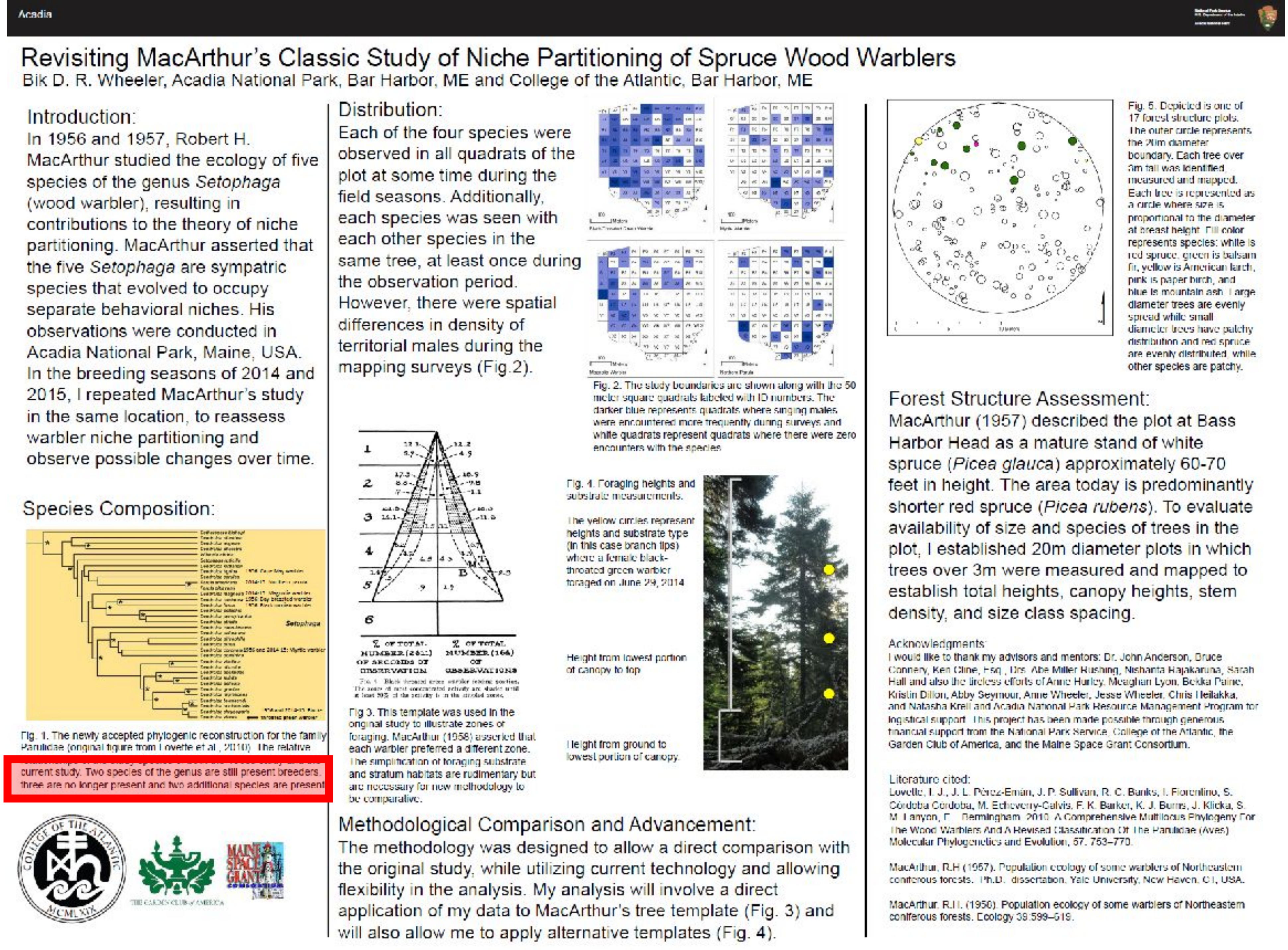


Figure 1 Niche conservatism creates phylogenetic patterns in ecological data. For a given ecological variable, the clade originates as a single ancestral species that utilizes a given environment or resource (e.g. diet, host, habitat, climatic regime). Early in the history of the group, there is a niche shift to utilize an alternate resource or environment. At the present time, there are four species utilizing resource 1 and two species utilizing resource 2, and strong phylogenetic structure in resource use among these six species. We argue that a major driver of this pattern is the process (niche conservatism) illustrated in the inset for species 4 (where circles represent individuals); the species is currently utilizing resource 1 and individuals attempting to utilize resource 2 and expand the species niche have reduced fitness. Thus, the ancestral niche is conserved in species 4. This conservatism may be maintained through a variety of population-level processes in species 4, including lack of genetic variation for necessary traits, selection favouring consistent choice of resource 1, and competition with species already utilizing resource 2. Similar processes are assumed to occur in the other species utilizing both resource 1 and resource 2, in both the past and present. This figure also illustrates the combination of niche conservatism and the time-for-speciation effect in creating patterns of species richness. The clade originates in environment 1 and a shift to environment 2 occurs more recently. Given the greater time for speciation and accumulation of diversity in region 1 (time-for-speciation effect) and infrequent dispersal between environments (due to niche conservatism), there are now more species in environment 1 than environment 2.

After 60 years…



Acadia

Revisiting MacArthur's Classic Study of Niche Partitioning of Spruce Wood Warblers

Bik D. R. Wheeler, Acadia National Park, Bar Harbor, ME and College of the Atlantic, Bar Harbor, ME

Introduction:

In 1956 and 1957, Robert H. MacArthur studied the ecology of five species of the genus *Setophaga* (wood warbler), resulting in contributions to the theory of niche partitioning. MacArthur asserted that the five *Setophaga* are sympatric species that evolved to occupy separate behavioral niches. His observations were conducted in Acadia National Park, Maine, USA. In the breeding seasons of 2014 and 2015, I repeated MacArthur's study in the same location, to reassess warbler niche partitioning and observe possible changes over time.

Species Composition:

Fig. 1. The newly accepted phylogenic reconstruction for the family Parulidae (original figure from Lovette et al., 2010). The relative [illegible] current study. Two species of the genus are still present breeders, three are no longer present and two additional species are present.

Distribution:

Each of the four species were observed in all quadrats of the plot at some time during the field seasons. Additionally, each species was seen with each other species in the same tree, at least once during the observation period. However, there were spatial differences in density of territorial males during the mapping surveys (Fig.2).

Fig. 2. The study boundaries are shown along with the 50 meter square quadrats labeled with ID numbers. The darker blue represents quadrats where singing males were encountered more frequently during surveys and white quadrats represent quadrats where there were zero encounters with the species.

% OF TOTAL NUMBER (2611) OF SECONDS OF OBSERVATION

% OF TOTAL NUMBER (164) OF OBSERVATIONS

Fig 3. This template was used in the original study to illustrate zones of foraging. MacArthur (1958) asserted that each warbler preferred a different zone. The simplification of foraging substrate and stratum habitats are rudimentary but are necessary for new methodology to be comparative.

Fig. 4. Foraging heights and substrate measurements.

The yellow circles represent heights and substrate type (in this case branch tips) where a female black-throated green warbler foraged on June 29, 2014.

Height from lowest portion of canopy to top

Height from ground to lowest portion of canopy.

Methodological Comparison and Advancement:

The methodology was designed to allow a direct comparison with the original study, while utilizing current technology and allowing flexibility in the analysis. My analysis will involve a direct application of my data to MacArthur's tree template (Fig. 3) and will also allow me to apply alternative templates (Fig. 4).

Fig. 5. Depicted is one of 17 forest structure plots. The outer circle represents the 20m diameter boundary. Each tree over 3m tall was identified, measured and mapped. Each tree is represented as a circle where size is proportional to the diameter at breast height. Fill color represents species: white is red spruce, green is balsam fir, yellow is American larch, pink is paper birch, and blue is mountain ash. Large diameter trees are evenly spread while small diameter trees have patchy distribution and red spruce are evenly distributed, while other species are patchy.

Forest Structure Assessment:

MacArthur (1957) described the plot at Bass Harbor Head as a mature stand of white spruce (*Picea glauca*) approximately 60-70 feet in height. The area today is predominantly shorter red spruce (*Picea rubens*). To evaluate availability of size and species of trees in the plot, I established 20m diameter plots in which trees over 3m were measured and mapped to establish total heights, canopy heights, stem density, and size class spacing.

Acknowledgments:
I would like to thank my advisors and mentors: Dr. John Anderson, Bruce Connery, Ken Cline, Esq., Drs. Abe Miller Rushing, Nishanta Rajakaruna, Sarah Hall and also the tireless efforts of Anne Hurley, Meaghan Lyon, Bekka Paine, Kristin Dillon, Abby Seymour, Anne Wheeler, Jesse Wheeler, Chris Heilakka, and Natasha Krell and Acadia National Park Resource Management Program for logistical support. This project has been made possible through generous financial support from the National Park Service, College of the Atlantic, the Garden Club of America, and the Maine Space Grant Consortium.

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MacArthur, R.H. (1958). Population ecology of some warblers of Northeastern coniferous forests. Ecology 39:599–619.

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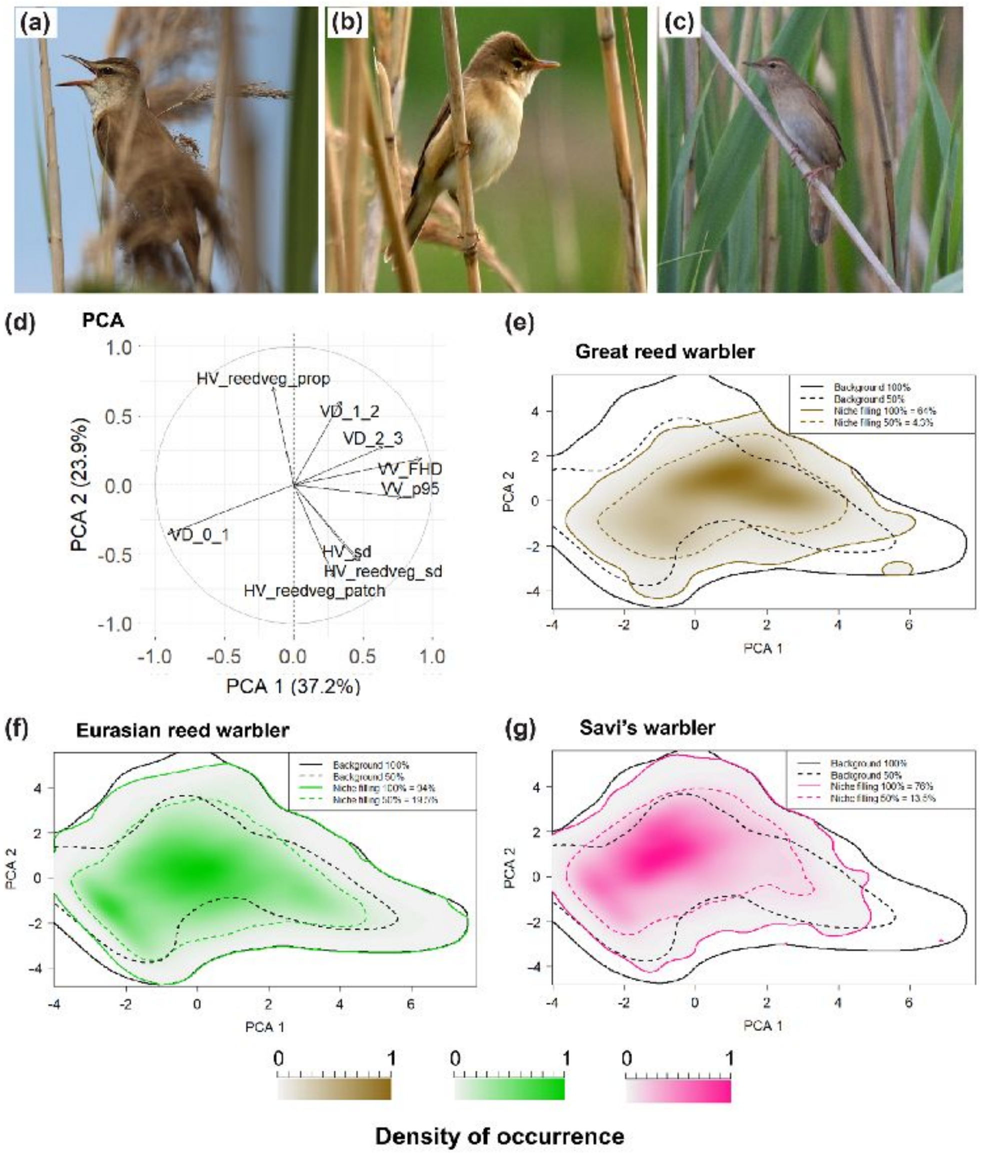


Figure 2. Habitat niches of three reed warbler species in the Netherlands. (a) Great reed warbler *Acrocephalus arundinaceus* (photo credit: Michele Lamberti, source: Flickr). (b) Eurasian reed warbler *Acrocephalus scirpaceus* (photo credit: Martien Brand, source: Wikipedia). (c) Savi's warbler *Locustella luscinioides* (photo credit: Ron Knight, source: Wikipedia). (d) First two axes of a principal component analysis (PCA) based on nine LiDAR metrics capturing vertical vegetation structure and horizontal heterogeneity of vegetation in Dutch wetlands (see metric abbreviations and definitions in Table 1, and variable loadings in the Supporting information). (e–g) Niche filling of the three reed warbler species illustrated with a 50% and 100% kernel density estimation (dashed lines and straight lines, respectively). Niche filling for each species is shown relative to the available background environment (i.e. presence and absence records intersected with LiDAR metrics within wetland-related land cover types).

Niche breadth

1. Survival experiments such as those of Tantawy's in Figure 3.1. Since fitness requires not only survival but also successful reproduction, this is clearly not a complete fitness measure but is an important component. In the figure it is seen that *D. simulans* has a narrower, higher, more specialized temperature niche than *D. melanogaster*. Any measure of spread could be used to quantify niche breadth.

2. Habitat or food selectivity in multiple choice experiments. For example, Martinez et al. (1965) set out several different kinds of bait (banana, tomato, potato, and oranges) in *Drosophila* traps less than ten feet apart. Thus any fly caught on any bait could have reached any of the others.

THE THEORY OF THE NICHE

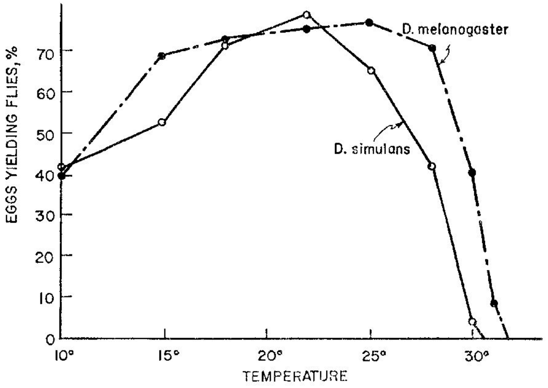


Figure 3.1. The temperature/emergence relation for two species of *Drosophila*. Clearly *D. melanogaster* has a broader temperature niche than *D. simulans*. (After Tantawy and Mallah, 1961.)

THE THEORY OF THE NICHE

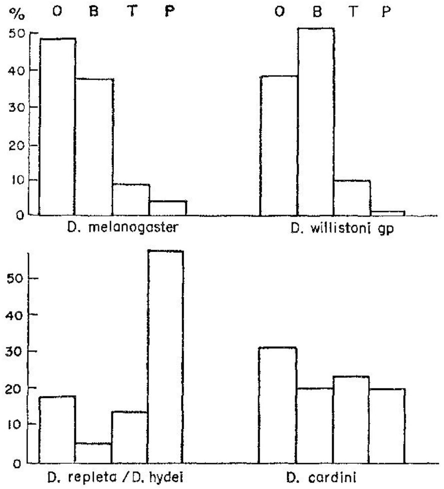


Figure 3.2. Food preference histograms for four species of *Drosophila*. O, orange; B, banana; T, tomato; P, potato. (From Martinez Pico et al., 1965.)

Levins, R. (1968). *Evolution in changing environments: some theoretical explorations*. Princeton University Press.

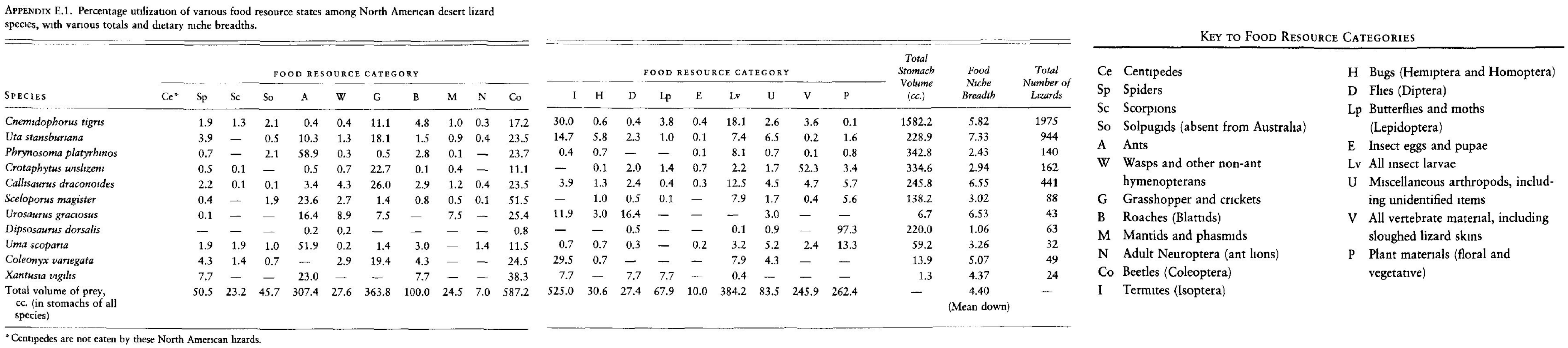
Niche breadth

$$\log B = -\sum p_i \log p_i$$

Shannon index

$$1/B = \sum p_i^2$$

p_i is the proportion of the species which is found in environment *i*, which selects environment *i*



APPENDIX E.1. Percentage utilization of various food resource states among North American desert lizard species, with various totals and dietary niche breadths.

SPECIES	FOOD RESOURCE CATEGORY																				Total Stomach Volume (cc.)	Food Niche Breadth	Total Number of Lizards
	Ce*	Sp	Sc	So	A	W	G	B	M	N	Co	I	H	D	Lp	E	Lv	U	V	P			
Cnemidophorus tigris		1.9	1.3	2.1	0.4	0.4	11.1	4.8	1.0	0.3	17.2	30.0	0.6	0.4	3.8	0.4	18.1	2.6	3.6	0.1	1582.2	5.82	1975
Uta stansburiana		3.9	—	0.5	10.3	1.3	18.1	1.5	0.9	0.4	23.5	14.7	5.8	2.3	1.0	0.1	7.4	6.5	0.2	1.6	228.9	7.33	944
Phrynosoma platyrhinos		0.7	—	2.1	58.9	0.3	0.5	2.8	0.1	—	23.7	0.4	0.7	—	—	0.1	8.1	0.7	0.1	0.8	342.8	2.43	140
Crotaphytus wislizeni		0.5	0.1	—	0.5	0.7	22.7	0.1	0.4	—	11.1	—	0.1	2.0	1.4	0.7	2.2	1.7	52.3	3.4	334.6	2.94	162
Callisaurus draconoides		2.2	0.1	0.1	3.4	4.3	26.0	2.9	1.2	0.4	23.5	3.9	1.3	2.4	0.4	0.3	12.5	4.5	4.7	5.7	245.8	6.55	441
Sceloporus magister		0.4	—	1.9	23.6	2.7	1.4	0.8	0.5	0.1	51.5	—	1.0	0.5	0.1	—	7.9	1.7	0.4	5.6	138.2	3.02	88
Urosaurus graciosus		0.1	—	—	16.4	8.9	7.5	—	7.5	—	25.4	11.9	3.0	16.4	—	—	—	3.0	—	—	6.7	6.53	43
Dipsosaurus dorsalis		—	—	—	0.2	0.2	—	—	—	—	0.8	—	—	0.5	—	—	0.1	0.9	—	97.3	220.0	1.06	63
Uma scoparia		1.9	1.9	1.0	51.9	0.2	1.4	3.0	—	1.4	11.5	0.7	0.7	0.3	—	0.2	3.2	5.2	2.4	13.3	59.2	3.26	32
Coleonyx variegata		4.3	1.4	0.7	—	2.9	19.4	4.3	—	—	24.5	29.5	0.7	—	—	—	7.9	4.3	—	—	13.9	5.07	49
Xantusia vigilis		7.7	—	—	23.0	—	—	7.7	—	—	38.3	7.7	—	7.7	7.7	—	0.4	—	—	—	1.3	4.37	24
Total volume of prey, cc. (in stomachs of all species)		50.5	23.2	45.7	307.4	27.6	363.8	100.0	24.5	7.0	587.2	525.0	30.6	27.4	67.9	10.0	384.2	83.5	245.9	262.4	—	4.40 (Mean down)	—

* Centipedes are not eaten by these North American lizards.

KEY TO FOOD RESOURCE CATEGORIES

Ce	Centipedes
Sp	Spiders
Sc	Scorpions
So	Solpugids (absent from Australia)
A	Ants
W	Wasps and other non-ant hymenopterans
G	Grasshopper and crickets
B	Roaches (Blattids)
M	Mantids and phasmids
N	Adult Neuroptera (ant lions)
Co	Beetles (Coleoptera)
I	Termites (Isoptera)
H	Bugs (Hemiptera and Homoptera)
D	Flies (Diptera)
Lp	Butterflies and moths (Lepidoptera)
E	Insect eggs and pupae
Lv	All insect larvae
U	Miscellaneous arthropods, including unidentified items
V	All vertebrate material, including sloughed lizard skins
P	Plant materials (floral and vegetative)

Levins, R. (1968). *Evolution in changing environments: some theoretical explorations*. Princeton University Press.
Pianka, E. R. (2017). *Ecology and natural history of desert lizards: analyses of the ecological niche and community structure*. Princeton University Press.

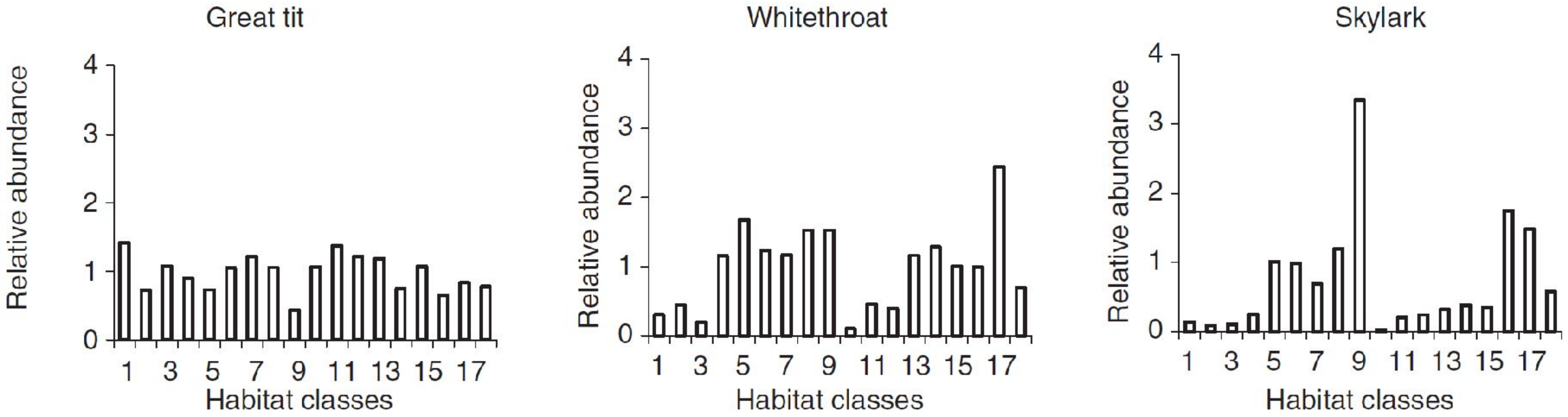
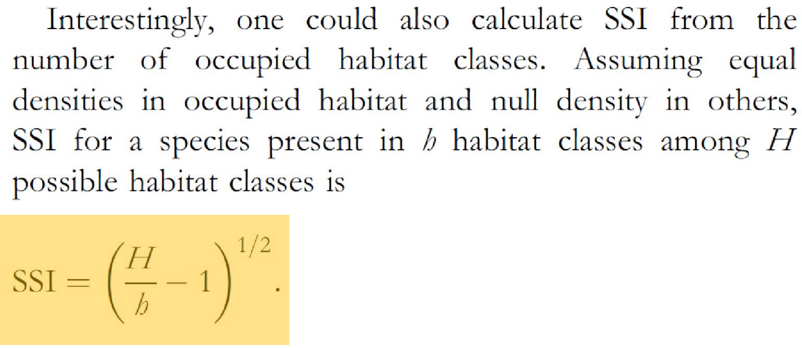


Figure 1 (a) Relative abundance (abundance/mean) variation among the 18 habitat classes for three species. Habitats are ranked as in Table 1. Left, the great tit, *Parus major* L., a generalist species (species specialization index, SSI = 0.29; mean abundance: 0.73 individuals per point count); centre: the whitethroat, *Sylvia communis* L., an intermediate species (SSI = 0.65; mean abundance: 0.23 individuals per point count); right, the skylark *Alauda arvensis* L., a specialist species (SSI = 1.16; mean abundance: 0.61 individuals per point count). (b) The



Interestingly, one could also calculate SSI from the number of occupied habitat classes. Assuming equal densities in occupied habitat and null density in others, SSI for a species present in h habitat classes among H possible habitat classes is

$$\mathrm{SSI} = \left(\frac{H}{h} - 1\right)^{1/2}.$$

Species Specialization Index

Julliard, R., Clavel, J., Devictor, V., Jiguet, F., & Couvet, D. (2006). Spatial segregation of specialists and generalists in bird communities. Ecology letters, 9(11), 1237-1244.

Research

Oikos 117: 507–514, 2008
doi: 10.1111/j.2008.0030-1299.16215.x,

Subject Editor: Tadashi Fukami, Accepted 5 December 2007

Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation

Vincent Devictor, Romain Julliard and Frédéric Jiguet

V. Devictor (devictor@mnhn.fr), R. Julliard and F. Jiguet, MNHN-CNRS-UPMC, UMR-5173 'Conservation des espèces, restauration et suivi des populations', Mus. Natl d'Histoire Naturelle, 55 rue Buffon, CP 51, FR-75005 Paris, France.

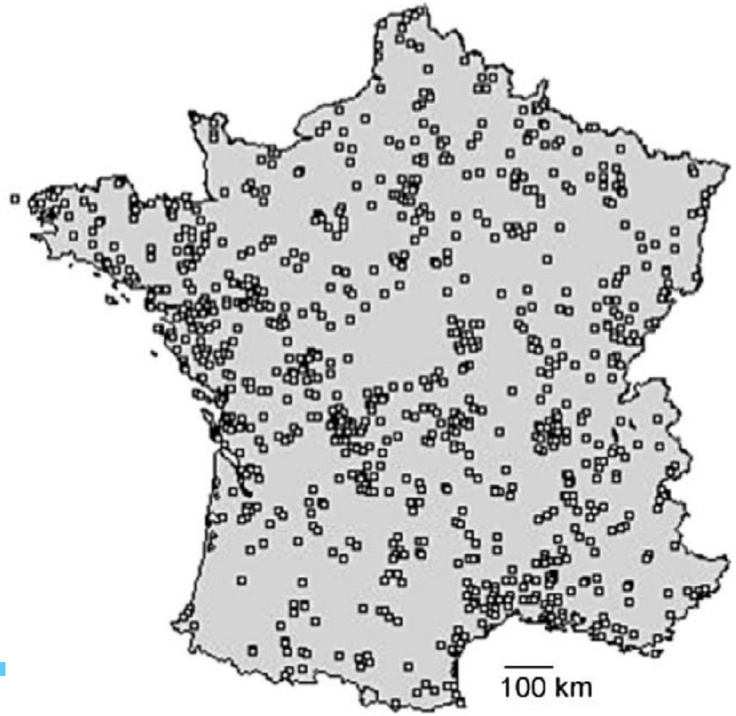


Fig. 1. Spatial distribution of the French Breeding Bird Survey plots. Each square (n = 891), is a 2 × 2 km landscape sampling replicate in which 10 point counts, evenly distributed in the square were monitored at least 2 years between 2001 and 2005.

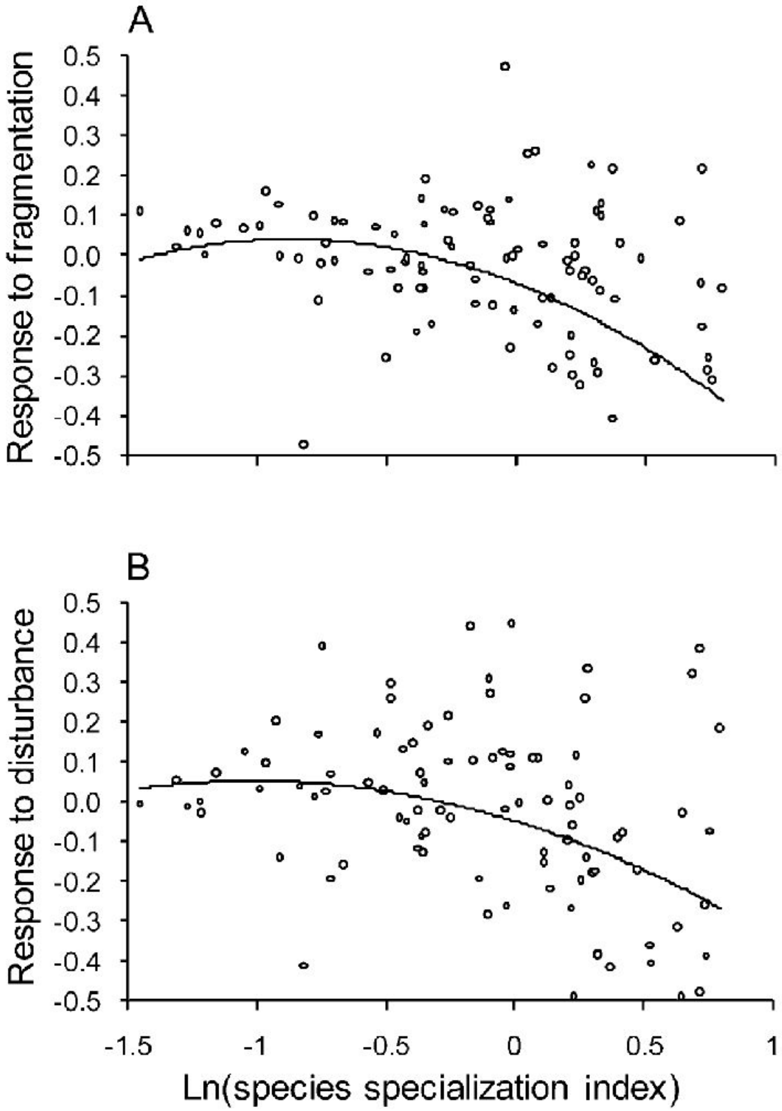


Fig. 2. (A) Spatial distribution of more or less specialized species, along a habitat fragmentation gradient, (B) Spatial distribution of more or less specialized species, along a habitat disturbance gradient. Each species distribution was previously estimated by a GLM model controlling for a second order polynomial spatial trend and its preferred habitat classes (among all monitored point counts, n = 8910). Smoothed plots were obtained using GAM models with 3 DF.

Niche breadth within the assemblage

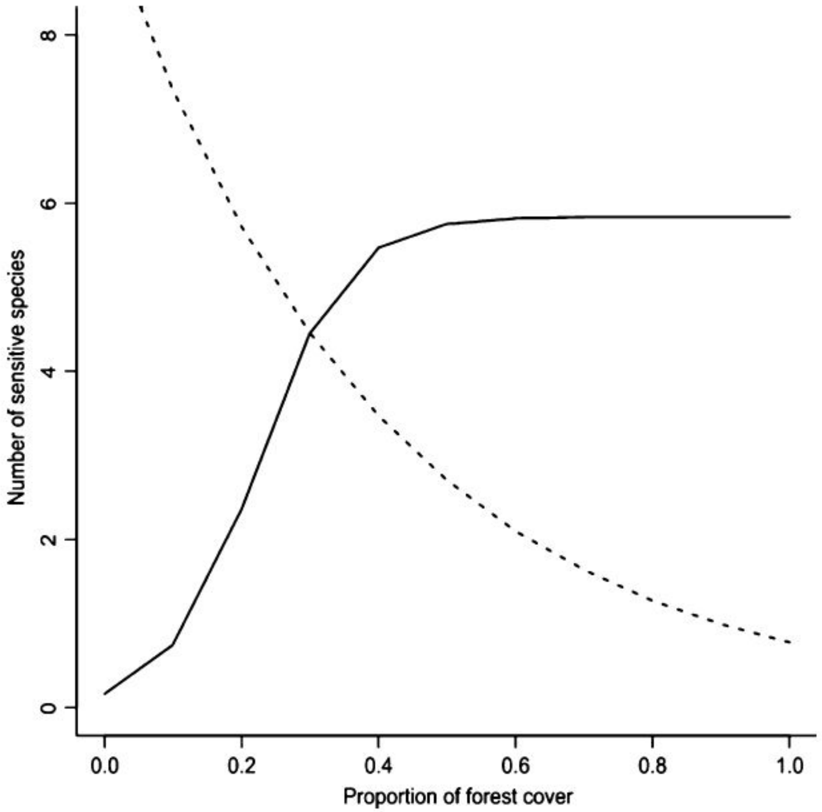
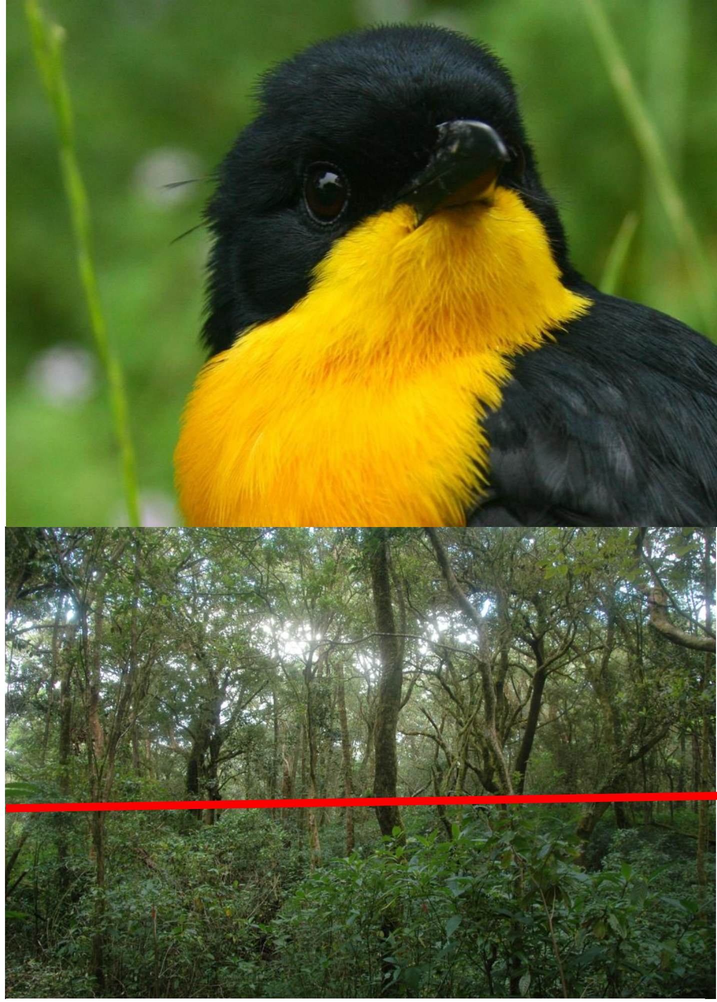


Fig 1 The threshold values of the forest specialists (birds showing a significant positive response to change in the proportion of forest cover, solid line) and savanna specialists (birds showing a significant negative response to change in the proportion of forest cover, dashed line) plotted as a function of the forest cover

- species differ in sensitivity to the gradients
- their response to environmental changes depends also on specializations within the biotope, a forest specialist living in the forest undergrowth (e.g. *Laniarius atroflavus*) remains abundant even after the trees are removed…



When savannah encroaches on the forest: thresholds in bird–habitat associations in the Bamenda Highlands, Cameroon

David Hořák[1]*, Ondřej Sedláček[1], Jiří Reif[2], Jan Riegert[3] and Michal Pešata[4]

African Journal of Ecology

Worldwide decline of specialist species: toward a global functional homogenization?

Joanne Clavel*, Romain Julliard, and Vincent Devictor

Panel 1. Community specialization index: an indicator of functional homogenization

Julliard *et al.* (2006) have quantified the specialization of species as the coefficient of variation (standard deviation/average) of their densities among habitat classes. The species specialization index (SSI) may be useful in building a sensitive (yet simple) index of biotic homogenization at the community level. The community specialization index (CSI) could, in turn, be used to test the role played by human-induced disturbances, such as habitat fragmentation, in functional biotic homogenization.

We used data from the French Breeding Bird Survey and considered 100 common species. We investigated the response of the CSI to habitat fragmentation and quantified these pressures using a land-cover survey (CORINE Land Cover database; Figure 3). The CSI was then calculated as the weighted average of the SSI in the site *j* (weighted by the number of individuals at the *j* site).

$$CSI_j = \frac{\sum_{i=1}^{N} a_{ij}(SSI_i)}{\sum_{i=1}^{N} a_{ij}},$$

Where N was the total number of species recorded, a_{ij} the abundance of individuals of species i in plot j, and SSI_i its specialization index.

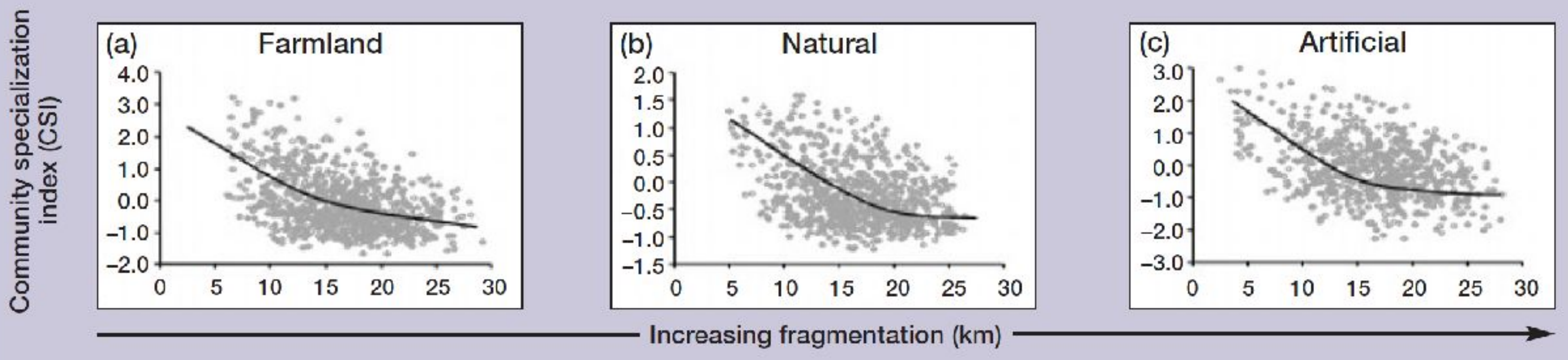
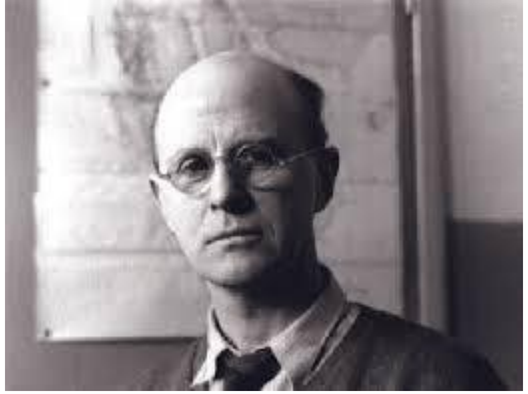


Figure 3. *Relationship between the community specialization index (CSI) and landscape fragmentation within each habitat type. We tested the relationships between the CSI and fragmentation (in kilometers) or disturbance using point counts monitored in (a) farmland (n = 5087), (b) natural (n = 3210), or (c) artificial (n = 1544) habitats. Smoothed curves were obtained with generalized additive mixed models, taking into account spatial dependence between samples.*

Elton's niche concept (1927)



niche is the status of an animal in its community / *a place in a biotic environment*

Clark (1954) niche stresses the ***function*** *of the species in the community rather than a physical place in the habitat*
(note that habitat harbours more than one species)

- it is NOT a habitat
- a property of the species (frequently estimated by traits)
- much more abstract
- interactions play a crucial role

Journal of Applied Ecology

British Ecological Society

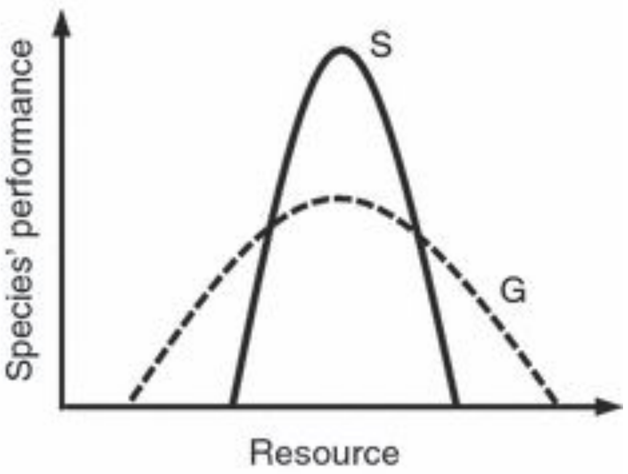
Journal of Applied Ecology 2010, **47**, 15–25 doi: 10.1111/j.1365-2664.2009.01744.x

REVIEW

Defining and measuring ecological specialization

Vincent Devictor*[1,2,3], Joanne Clavel[4], Romain Julliard[4], Sébastien Lavergne[5], David Mouillot[6], Wilfried Thuiller[5], Patrick Venail[3], Sébastien Villéger[6] and Nicolas Mouquet[3]

(a) Grinnellian specialization



(b) Eltonian specialization

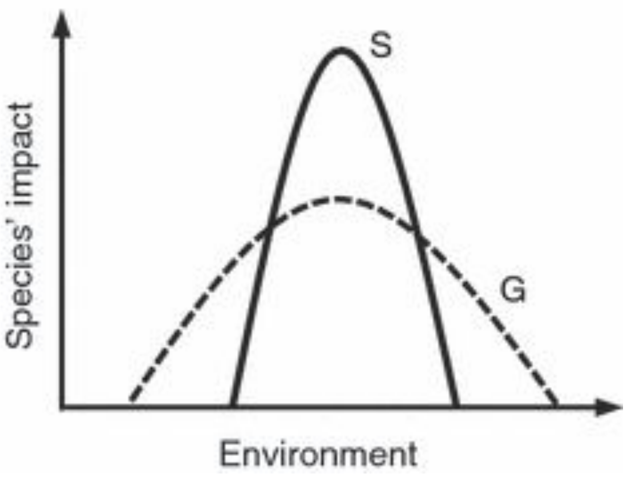


Fig. 1. Definition of Grinnellian vs. Eltonian specialization. (a) The Grinnellian specialization of a given species can be described by its variance in performance across a given range of resources. For a given mean performance, the dashed line describes the performance of a generalist species (generalist, G) and the solid line of a more specialist species (specialist, S). (b) Eltonian specialization is defined as the variance in the species' impact (instead of performance) on the environment. For a given mean impact, the species' impact can be distributed through a large part of the environment (G) or be more restricted (S).

Different types of variables!

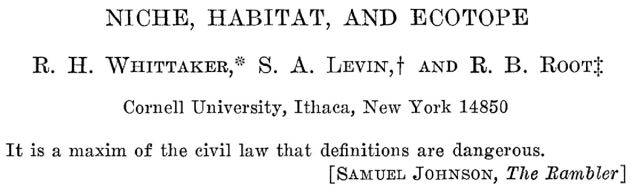
Whittaker et al. 1973: amalgam of Grinnell’s and Elton’s ideas defined by **(i) *intra*-community and (ii) *inter*-community variables**

(i) height above ground, relation to intra-community pattern (?), seasonal time, diurnal time, prey size, animal/plant food ratio etc. (**NICHE**)

(ii) elevation, slope exposure, soil moisture, from valley bottom to open south slope, soil fertility etc. (**HABITAT**)

(iii) population response variables: density, frequency of utilization, coverage, reproductive success, fitness etc.

Depending on employed variables,
the studies differ in or mix the niche concepts!



NICHE, HABITAT, AND ECOTOPE

R. H. WHITTAKER,* S. A. LEVIN,† AND R. B. ROOT‡

Cornell University, Ithaca, New York 14850

It is a maxim of the civil law that definitions are dangerous.
[SAMUEL JOHNSON, *The Rambler*]

Whittaker et al. (1973) suggested

(i) **NICHE** – intra-community role of the species
(ii) **HABITAT** – inter-community species’ response to environmental variables
(iii) HABITAT + NICHE = **ECOTOPE**, it is not well established

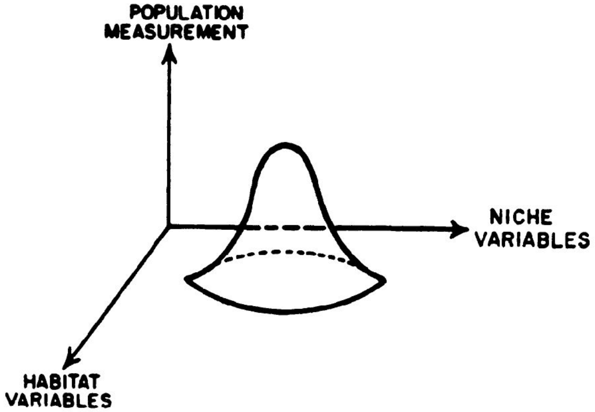


FIG. 5.—A diagrammatic representation of the relations to one another of a system of concepts including niche, habitat, and ecotope. See text.

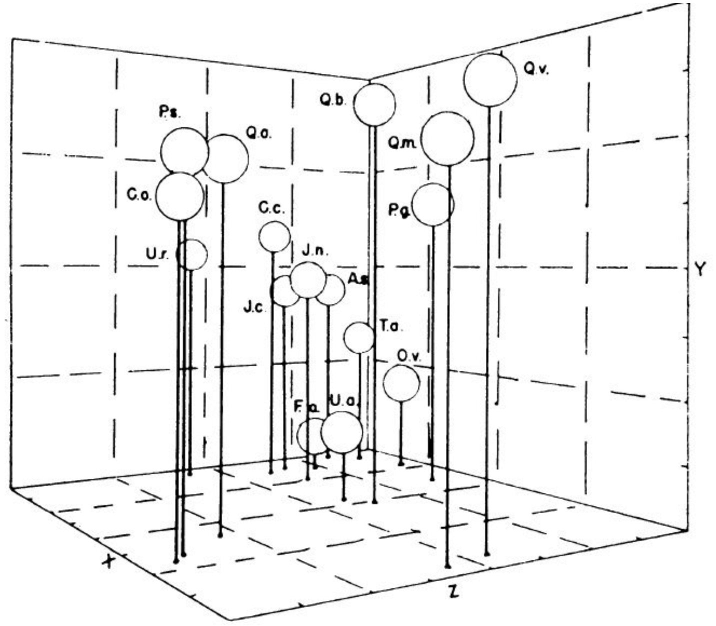


FIG. 3.—A habitat ordination of tree species by the centers of their distributions in a three-dimensional hyperspace (Bray and Curtis 1957). Tree species are indicated by genus and species initials: *Acer saccharum, Carya cordiformis, C. ovata, Fraxinus americana, Juglans cinerea, J. nigra, Ostrya virginiana, Populus grandidentata, Prunus serotina, Quercus alba, Q. borealis, Q. macrocarpa, Q. velutina, Tilia americana, Ulmus americana,* and *U. rubra.* Successional relations toward increasing mesophytism are significant along the *X* axis, soil drainage conditions along the *Y* axis, and disturbance effects along the *Z* axis.

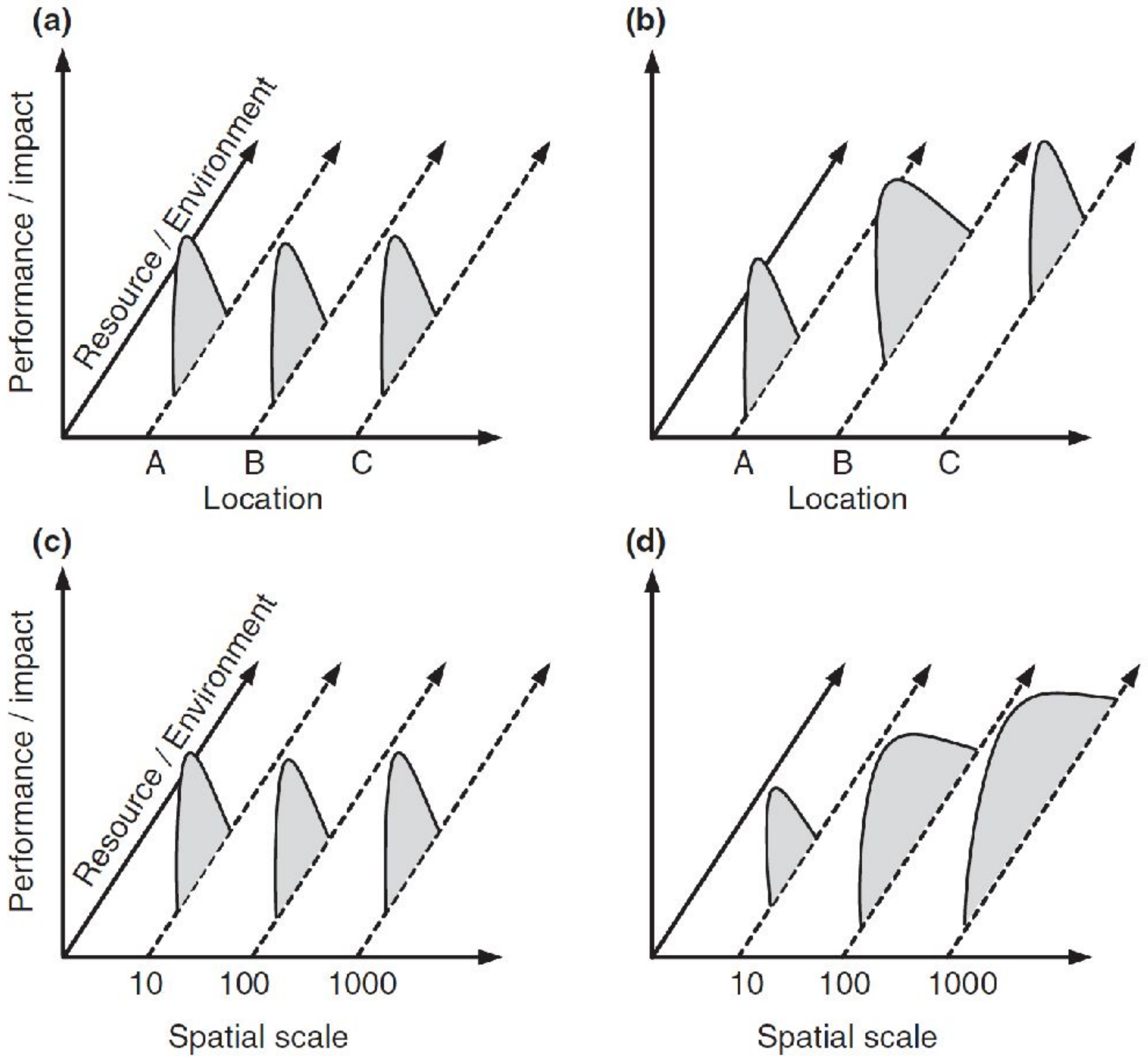


Fig. 2. Spatial dependence of specialization. (a) Specialization is often considered as an invariant species-property that is consistent across locations. (b) Alternatively, species may have different levels of specialization in varying locations. This spatial dependence of niche breadth can be induced by true shift in specialization across locations, or by variable resource availability. A spatial dependence can also be observed when the scale at which specialization is measured increases (c, d).

Journal of Animal Ecology 1997,
66, 579–601

Interspecific abundance–range size relationships: an appraisal of mechanisms

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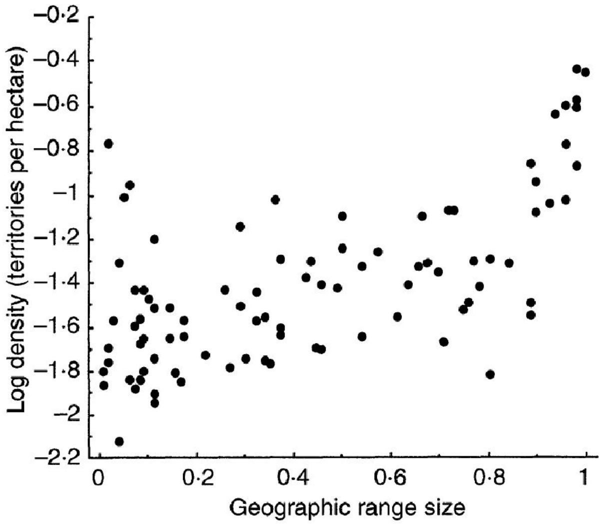


Fig. 1. The relationship between local density ($\log_{10}$ territories ha^{-1}) and the proportion of sites occupied for bird species on farmland Common Bird Census plots in Britain in 1975. For further details see Blackburn *et al.* (unpublished)

- local x regional scale
- an empirical relationship
- many possible mechanisms
- including *ecological specialization*

more specialized locally, more specialized regionally

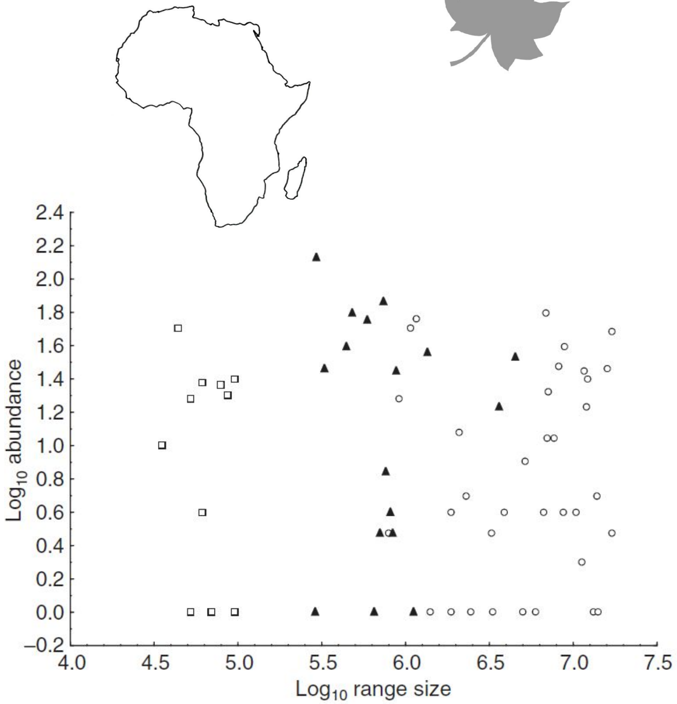
Exceptions:

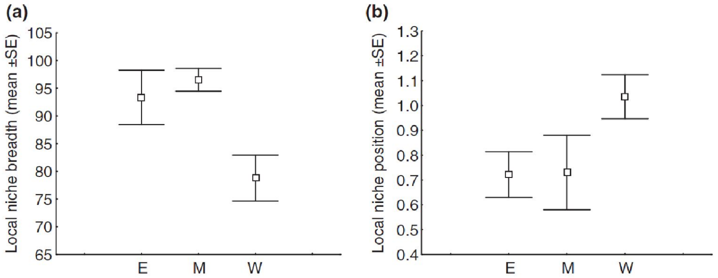
Journal of Biogeography (J. Biogeogr.) (2006) **33**, 1959–1968

ORIGINAL ARTICLE

Unusual abundance–range size relationship in an Afromontane bird community: the effect of geographical isolation?

Jiří Reif[1,2,3]*, David Hořák[2,3], Ondřej Sedláček[3], Jan Riegert[4], Michal Pešata[5], Záboj Hrázský[6,7], Štěpán Janeček[8] and David Storch[1,3]





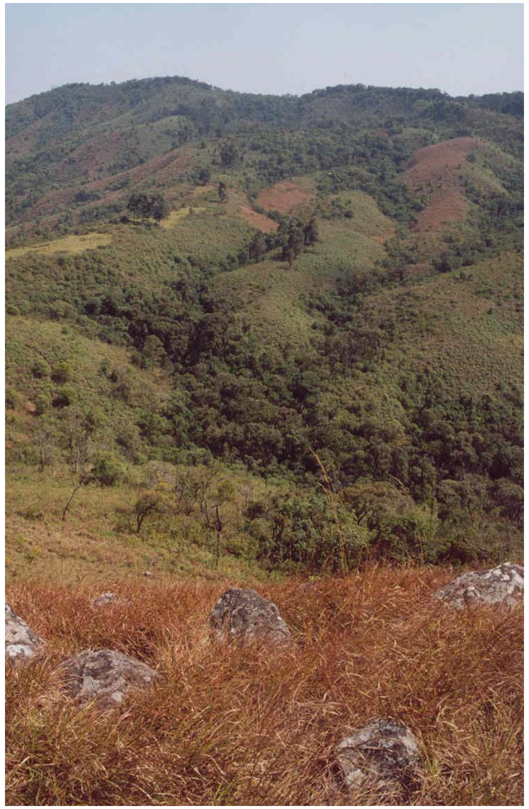
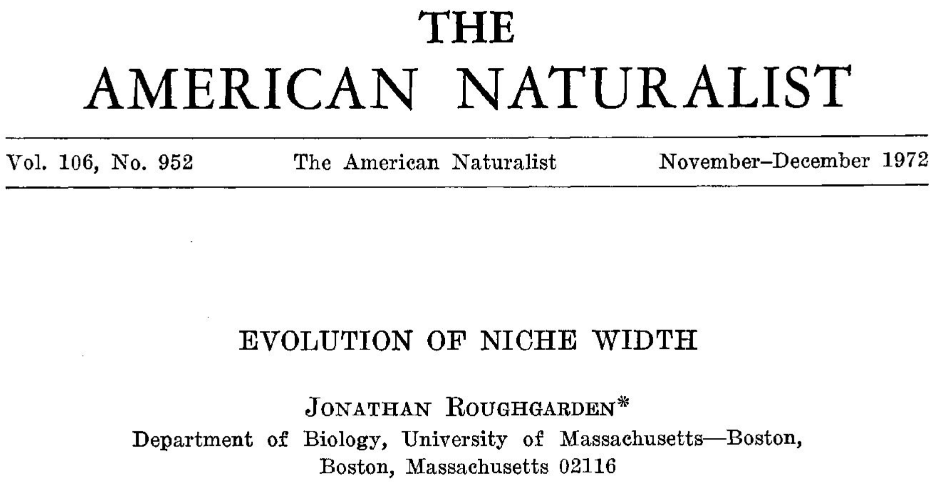


Figure 3 Differences in local niche breadth (a) and local niche position (b) between three species groups within a bird community in the My Ogade area, Bamenda Highlands, Cameroon. Both variables were calculated using canonical correspondence analysis (CCA, ter Braak & Šmilauer, 2002). Niche breadth reflects species tolerance to changes in habitat structure among census points in the study plot. Widespread species (W) have significantly narrower local habitat niches than endemic species of the Cameroon Mountains (E) and non-endemic montane species (M): ANOVA, d.f. = 2,46; $F = 6.23$, $P < 0.01$. Niche breadth is expressed as variance of CCA scores corrected by the effective number of counts. Niche position quantifies extremeness of species' local habitat requirements with respect to the community as a whole. Widespread species use slightly more extreme habitats than endemic species and non-endemic montane species: ANOVA, d.f. = 2,46; $F = 2.53$, $P = 0.09$. Niche position is expressed in CCA scores.

Specialization witihn species



THE
AMERICAN NATURALIST

Vol. 106, No. 952 The American Naturalist November–December 1972

EVOLUTION OF NICHE WIDTH

Jonathan Roughgarden*
Department of Biology, University of Massachusetts—Boston,
Boston, Massachusetts 02116

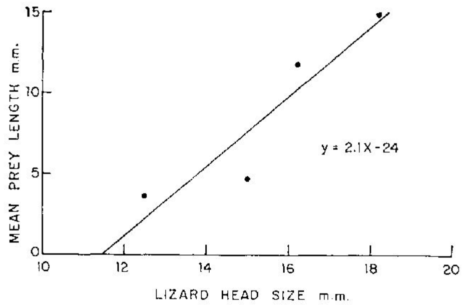
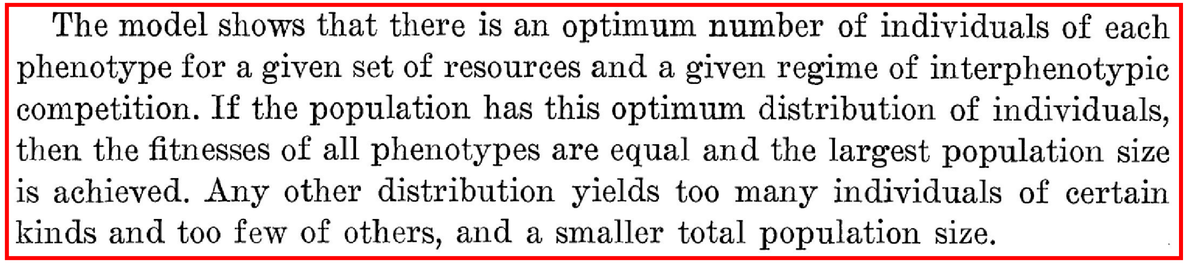


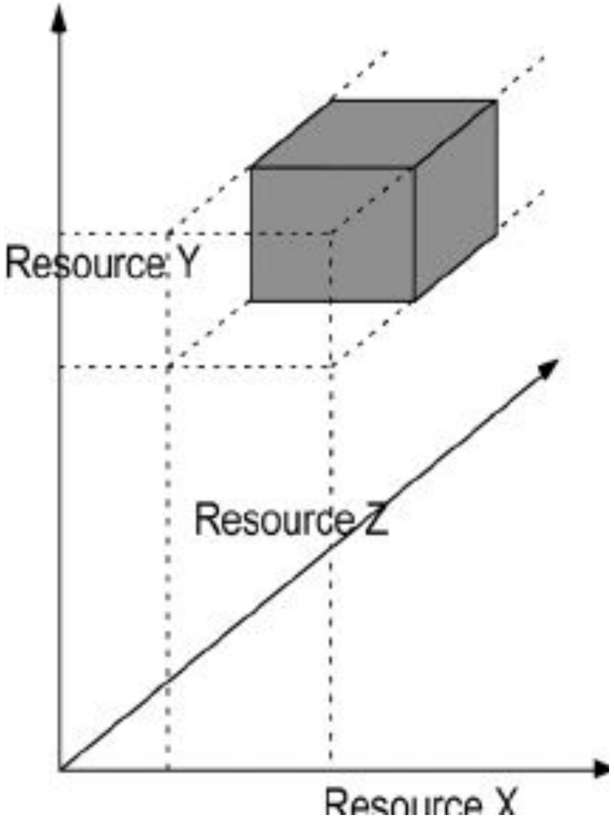
FIG. 2.—Regression of mean prey size against lizard head size for *Anolis roquet*. Lizard head size is a good predictor of mean prey size.



The model shows that there is an optimum number of individuals of each phenotype for a given set of resources and a given regime of interphenotypic competition. If the population has this optimum distribution of individuals, then the fitnesses of all phenotypes are equal and the largest population size is achieved. Any other distribution yields too many individuals of certain kinds and too few of others, and a smaller total population size.

Hutchinson’s “complication” (1958)

environmental variables affecting a species may be conceived as a **set of *n* coordinates...**



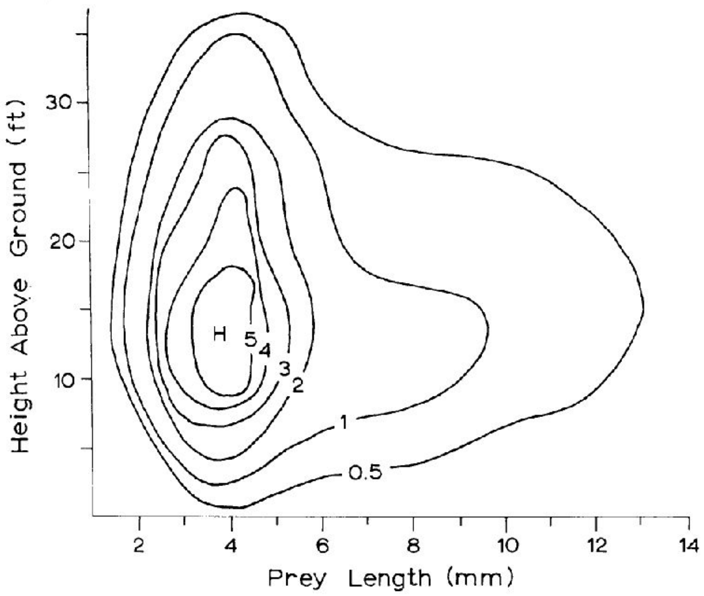
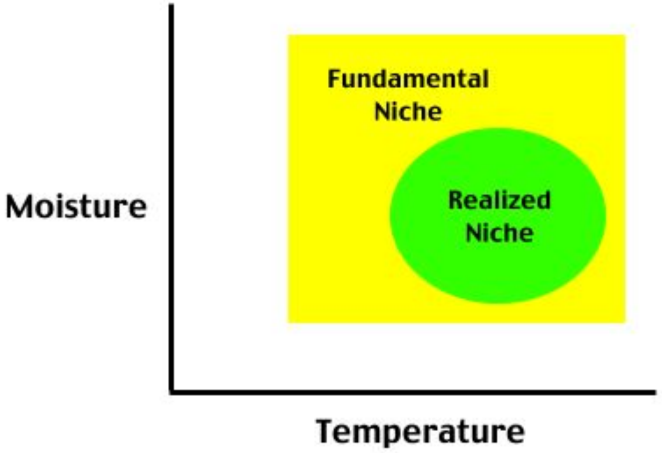


FIG. 4.—A niche response surface, representing capture of prey of different sizes taken at different heights above the ground by the blue gray gnatcatcher (*Polioptila caerulea*). The contour lines map the feeding frequencies (in terms of percentage of total diet) to these two niche axes for adult gnatcatchers during the incubation period in July and August, in oak woodlands in California (data of Root [1967]).



THE INFLUENCE OF INTERSPECIFIC COMPETITION AND OTHER FACTORS ON THE DISTRIBUTION OF THE BARNACLE *CHTHAMALUS STELLATUS*

Joseph H. Connell

Department of Biology, University of California, Santa Barbara, Goleta, California

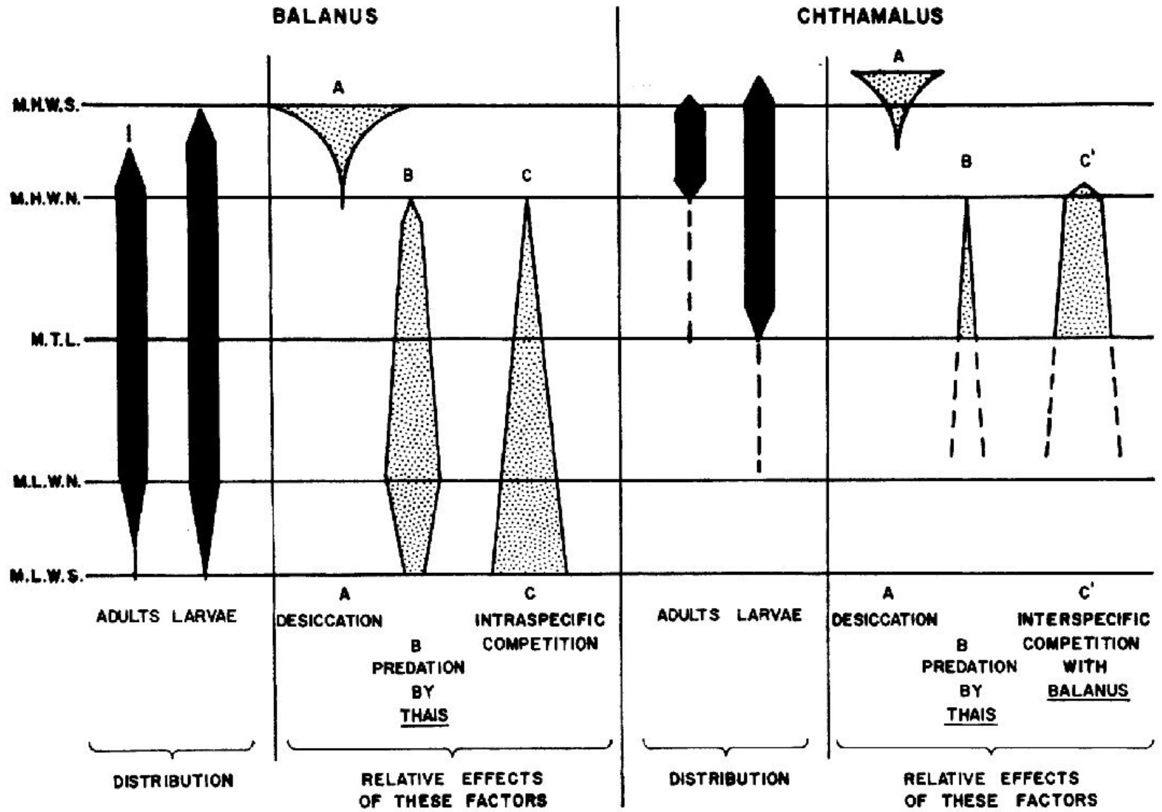


FIG. 5. The intertidal distribution of adults and newly settled larvae of *Balanus balanoides* and *Chthamalus stellatus* at Millport, with a diagrammatic representation of the relative effects of the principal limiting factors.

removal => competition release

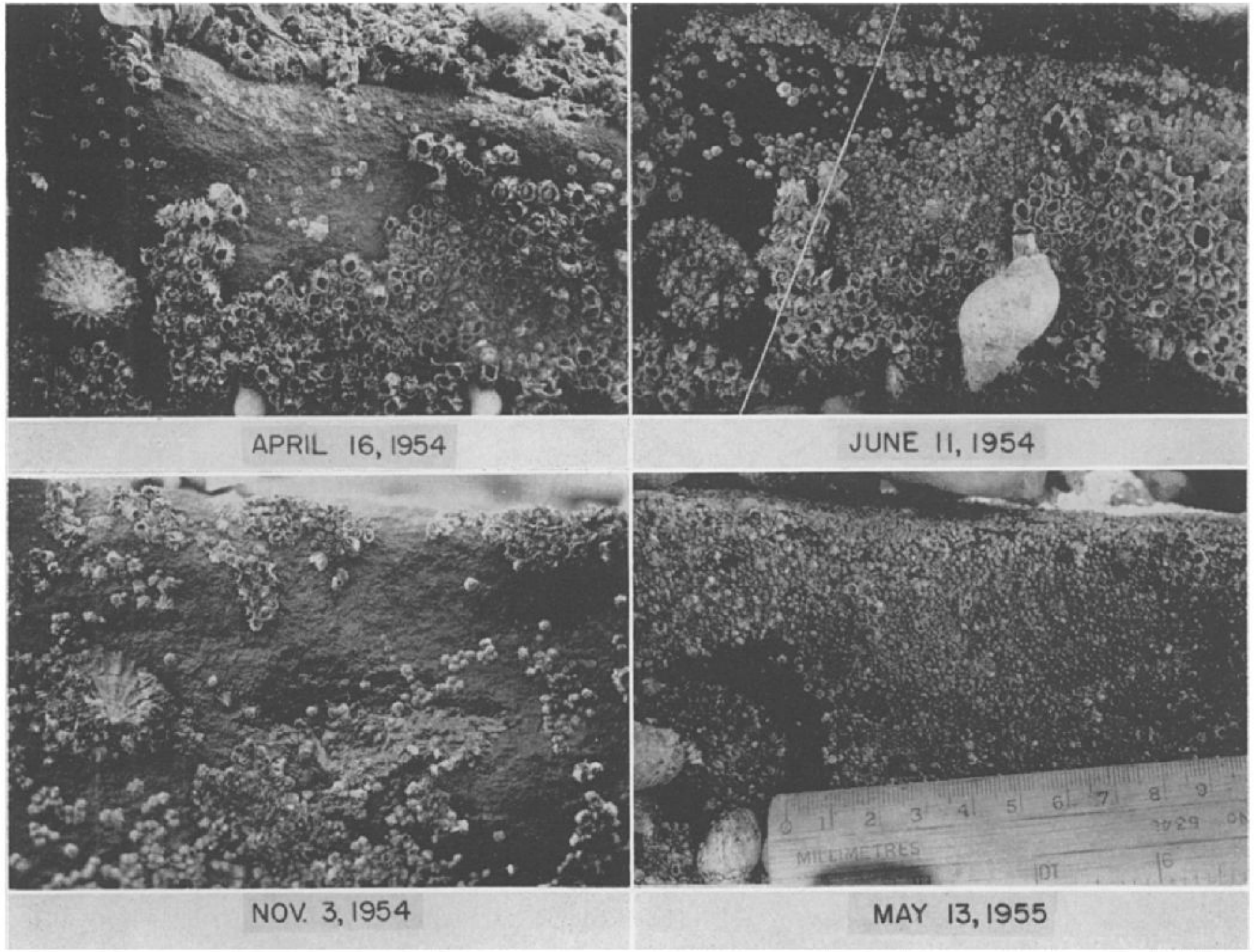


FIG. 1. Area 7b. In the first photograph the large barnacles are *Balanus*, the small ones scattered in the bare patch, *Chthamalus*. The white line on the second photograph divides the undisturbed portion (right) from the portion from which *Balanus* were removed (left). A limpet, *Patella vulgata*, occurs on the left, and predatory snails, *Thais lapillus*, are visible.

* summary in slide notes

How to measure niche?

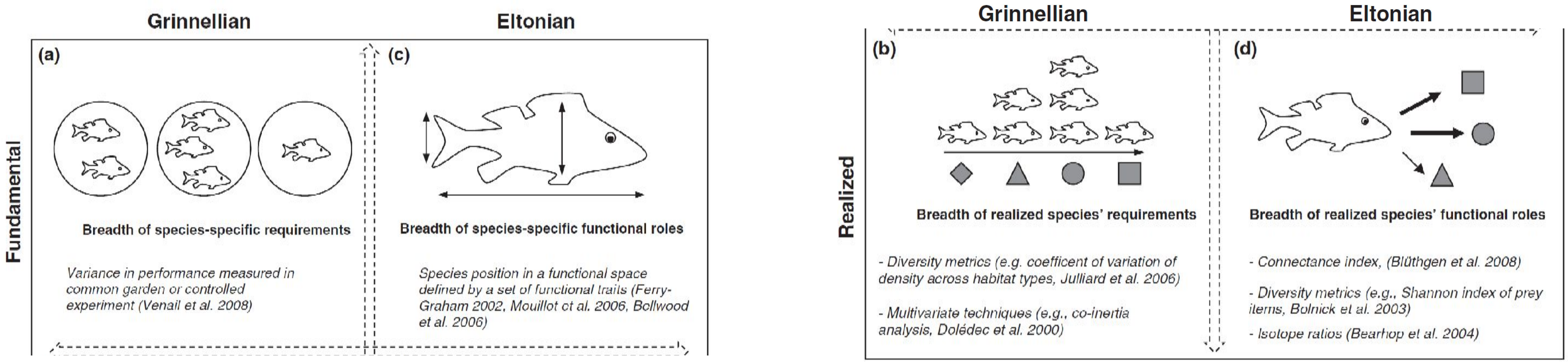
Journal of Applied Ecology

Journal of Applied Ecology 2010, 47, 15–25 doi: 10.1111/j.1365-2664.2009.01744.x

REVIEW

Defining and measuring ecological specialization

Vincent Devictor*[1,2,3], Joanne Clavel[4], Romain Julliard[4], Sébastien Lavergne[5], David Mouillot[6], Wilfried Thuiller[5], Patrick Venail[3], Sébastien Villéger[6] and Nicolas Mouquet[3]



(a) *Variance in performance measured in common garden or controlled experiment (Venail et al. 2008)*

(c) *Species position in a functional space defined by a set of functional traits (Ferry-Graham 2002, Mouillot et al. 2006, Bollwood et al. 2006)*

(b)
- *Diversity metrics (e.g. coefficent of variation of density across habitat types, Julliard et al. 2006)*
- *Multivariate techniques (e.g., co-inertia analysis, Dolédec et al. 2000)*

(d)
- *Connectance index, (Blüthgen et al. 2008)*
- *Diversity metrics (e.g., Shannon index of prey items, Bolnick et al. 2003)*
- *Isotope ratios (Bearhop et al. 2004)*

Fig. 4. A toolbox for widely used metrics of ecological specialization. Most commonly used metrics of specialization can be positioned in this box according to the type of niche considered (Grinnellian vs. Eltonian) and whether the fundamental or the realized specialization is measured. Note that this typology is flexible (i.e. the dashed arrows underline that specialization metrics are often not belonging to a unique class but rather delineate a continuum). The figure represents a fish for which specialization is measured using different metrics: (a) the variation in species' performance in a controlled experiment (three different conditions are represented by three circles) will reflect its fundamental Grinnellian specialization; (b) the variation in performance along different resource categories (symbolized by geometrical items) using field data will reflect the realized Grinnellian specialization; (c) the fundamental Eltonian specialization would be derived from metrics based on the species-specific functional traits. (d) Finally, the realized Eltonian specialization will be quantified using the diversity and strength of impact of the species on others (symbolized by geometrical items).

There is a yet more profound assumption having to do with the perfectability of tools. In human affairs we express it by saying **“ a jack of all trades is a master of none.”** It tells us that a harvester cannot be simultaneously perfect at several jobs; perfection in one involves reduced efficiency in another, and if an organism must try to harvest in various ways, it must compromise its efficiency in each. But since competition often puts a premium on efficiency, this assumption implies a division of labor among specialists. It is the ultimate reason we have so many species.

MacArthur (1972)

Character Displacement

W. L. BROWN, JR. and E. O. WILSON

Vol. 101, No. 921 The American Naturalist September–October, 1967

THE LIMITING SIMILARITY, CONVERGENCE, AND DIVERGENCE OF COEXISTING SPECIES

ROBERT MACARTHUR AND RICHARD LEVINS*

Department of Biology, Princeton University, Princeton, New Jersey, and
Department of Biology, University of Puerto Rico,
Rio Piedras, Puerto Rico

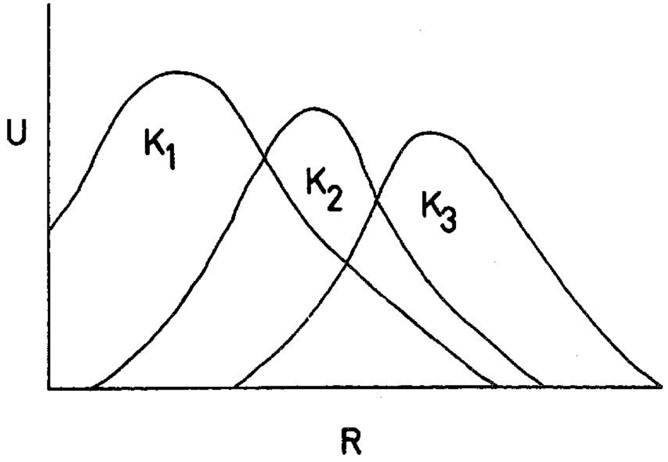


FIG. 1. The form of the niche. For each resource *r*, *U* is the probability of its utilization in a unit time by an individual. The area under each curve, therefore, is the total resource utilization K_i for species *i*.

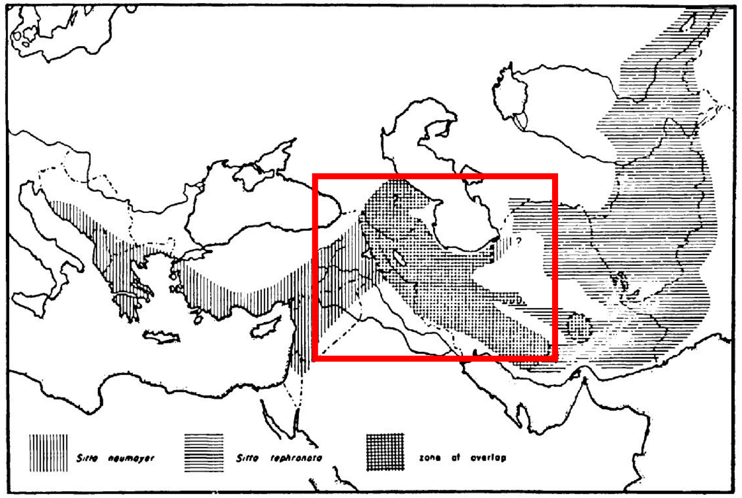


FIG. 1. Distribution of *Sitta neumayer* and *S. tephronota*. (After Vaurie.)

Hutchinson's ratio

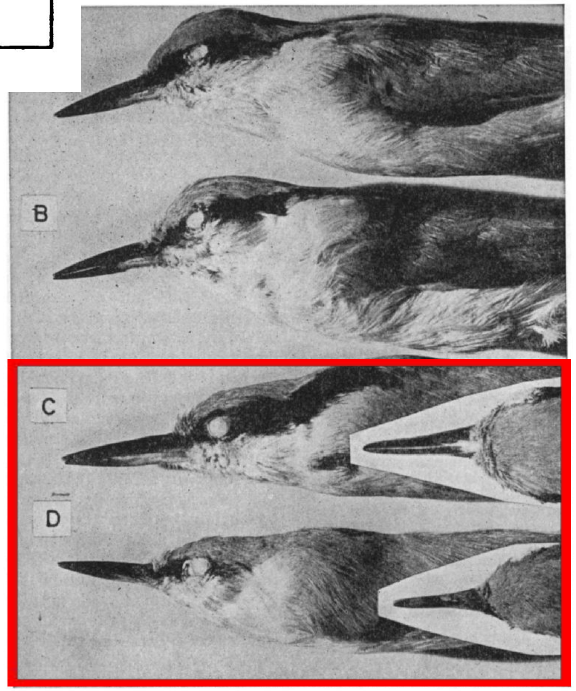


FIG. 2. Size and shape of the bill and facial stripe in *Sitta neumayer* and *S. tephronota*: ***A***, *S. neumayer* from Dalmatia; ***B***, *S. tephronota* from Ferghana; ***C***, *S. tephronota* and ***D***, *S. neumayer*, both from Durud, Luristan, in western Iran. (After Vaurie.)

Niche packing

Proc. Nat. Acad. Sci. USA
Vol. 69, No. 5, pp. 1109–1113, May 1972

Niche Overlap as a Function of Environmental Variability

(food size/birds/ecology/exclusion/model)

ROBERT M. MAY* AND ROBERT H. MAC ARTHUR

mean food size and its variance. The dynamics of this situation may be plausibly modeled by a system of first-order differential equations, with competition coefficients that depend on how closely species are packed; that is, on the degree of niche overlap (on the ratio of *d* to *w* in Fig. 1).

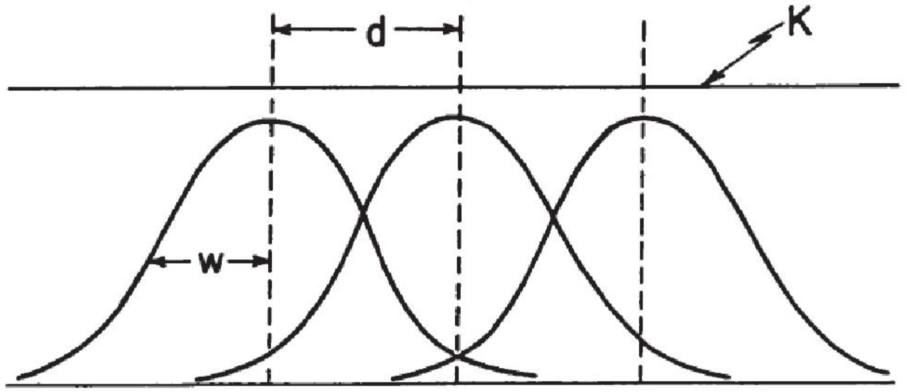
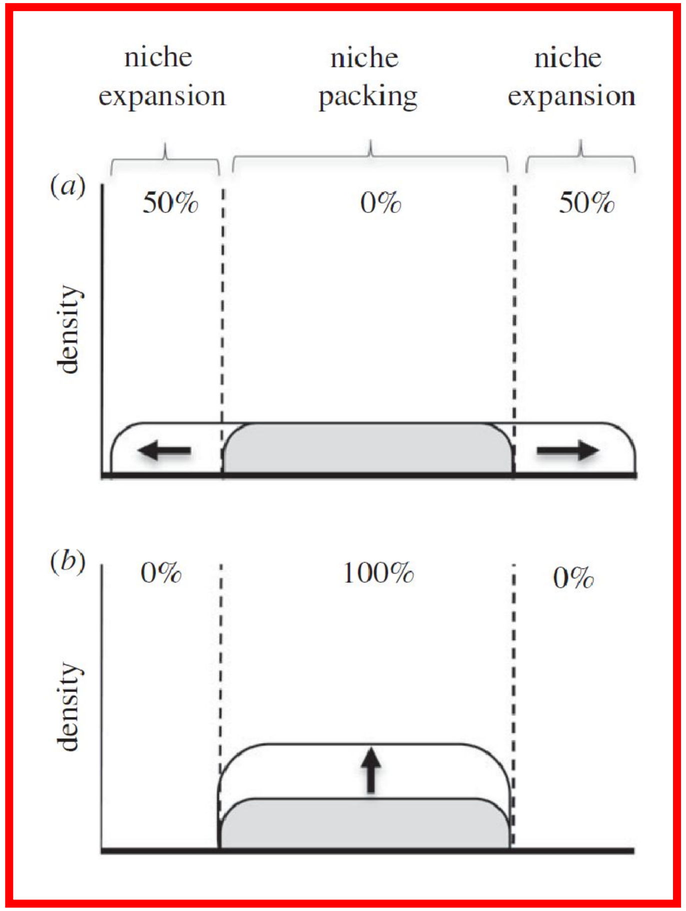


FIG. 1. The curve labeled *K* represents some resource continuum, say amount of food as a function of food size, that sustains various species whose utilization functions (characterized by a standard deviation *w* and a separation *d*) are as shown.

Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds

Alex L. Pigot[1,2], Christopher H. Trisos[2,3] and Joseph A. Tobias[2,4]



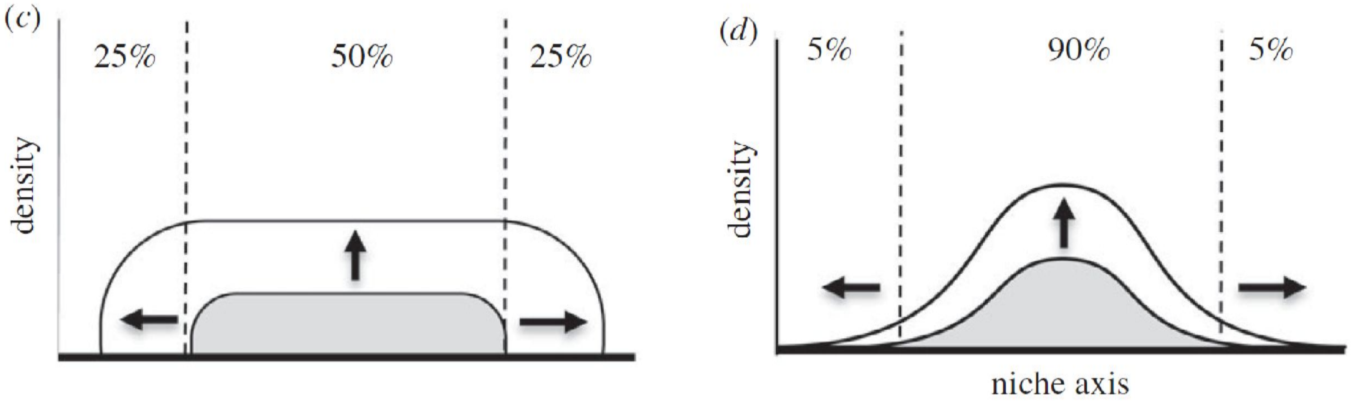
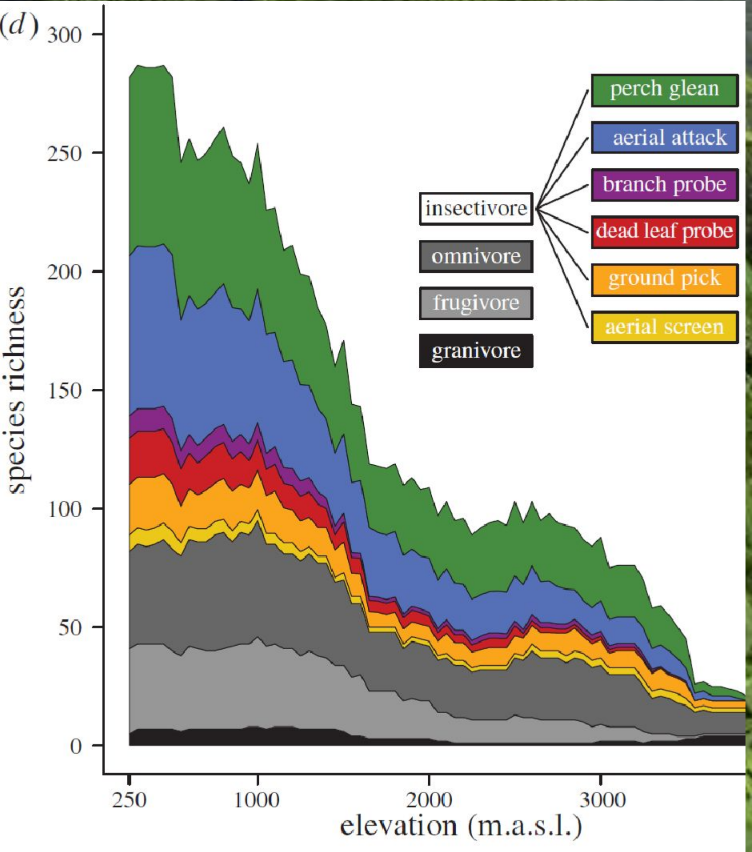
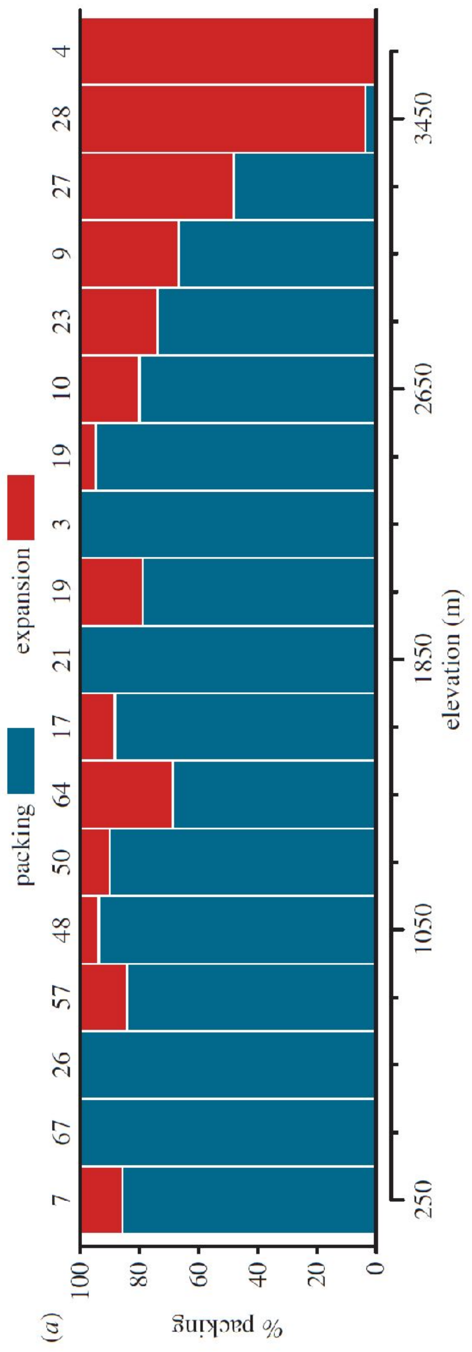


Figure 1. Three conceptual models of increasing niche density and volume, comparing assemblages of low (shaded) and high (white) species richness. The niche expansion model (*a*) predicts that increases in richness are associated with an expanding niche space (increasing volume), whereas the niche packing model (*b*) predicts that increasing richness is associated with greater niche packing (increasing density) arising though either greater specialization or overlap in resource use. In a combined model, whereby increases in assemblage richness are accommodated through both niche expansion and packing, their relative contribution depends on the distribution of species within trait space (*c*,*d*).

Manu NP Park, Peru





…and, *where* is the niche?

Hutchinson’s duality: The once and future niche

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niche space x biotope space

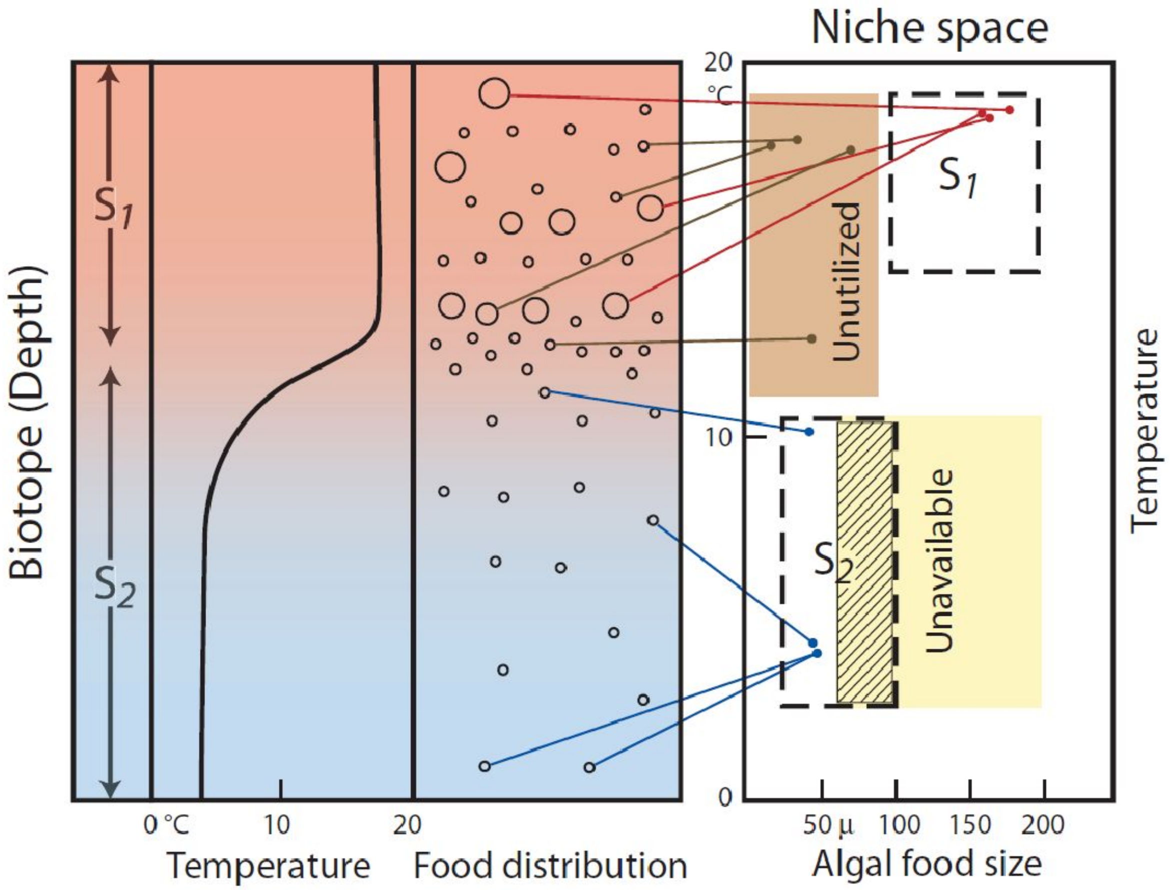
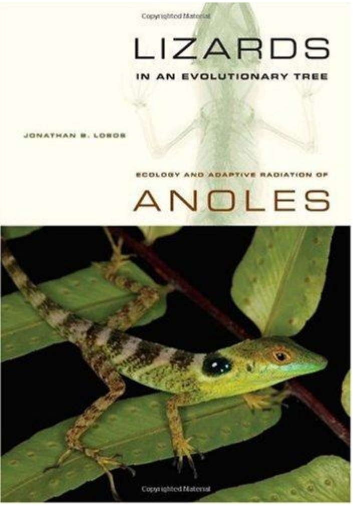


Fig. 1. Hutchinson’s illustration of the niche-biotope duality for a temperate lake with algae and two consumers of algae (species S_1 and S_2). The 1D biotope (red and blue rectangle) is a stratified water column with a strong summer thermocline. The two environmental factors characterizing the biotope (water temperature and food size, both as a function of depth) correspond to niche axes in niche space shown on the right. Red (S_1) and blue (S_2) lines connect representative algal cells of different sizes and at different depths with their corresponding points in the niches of the two consumers. The distribution of species S_1 and S_2 in the water column is the projection of their niches on the biotope. Brown lines show algae that map onto an unutilized region of niche space (small algae in warm water). The yellow region of niche space (large algae living in cold water) is unavailable (not represented in this biotope). The cross-hatched portion of the niche of consumer S_2, which overlaps unavailable niche space, is unexpressed in the biotope. Based on Hutchinson’s figure 101 in ref. 6.


LIZARDS
IN AN EVOLUTIONARY TREE
JONATHAN B. LOSOS
ECOLOGY AND ADAPTIVE RADIATION OF
ANOLES

Predictability of the niches

Is a niche property of the species or environment?

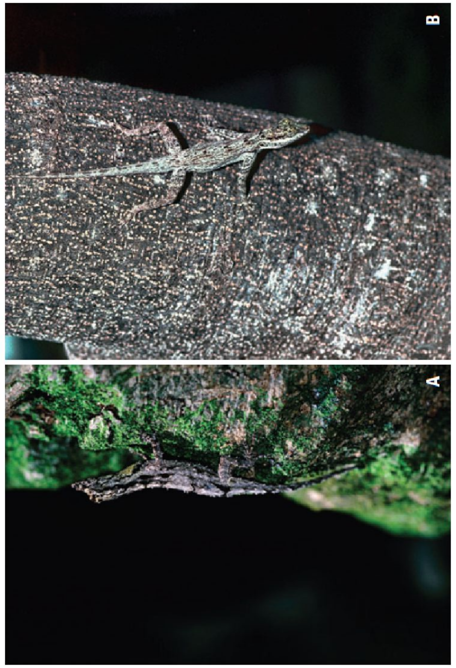


FIGURE 3.6
Trunk anoles. (a) *A. loysianus*, Cuba; (b) *A. distichus*, Hispaniola.

FIGURE 3.4
Trunk-ground anoles. (a) *A. rubribarbus*, Cuba. Photo courtesy of Richard Glor. (b) *A. cybotes*, Hispaniola; (c) *A. cristatellus*, Puerto Rico; (d) *A. lineatopus*, Jamaica.

FIGURE 3.5
Trunk-crown anoles. (a) *A. allisoni*, Cuba; (b) *A. chlorocyanus*, Hispaniola; (c) *A. evermanni*, Puerto Rico; though usually found high in the trees, in the Luquillo Mountains, *A. evermanni* forages on sunny boulders in the middle of streams; (d) *A. grahami*, Jamaica.

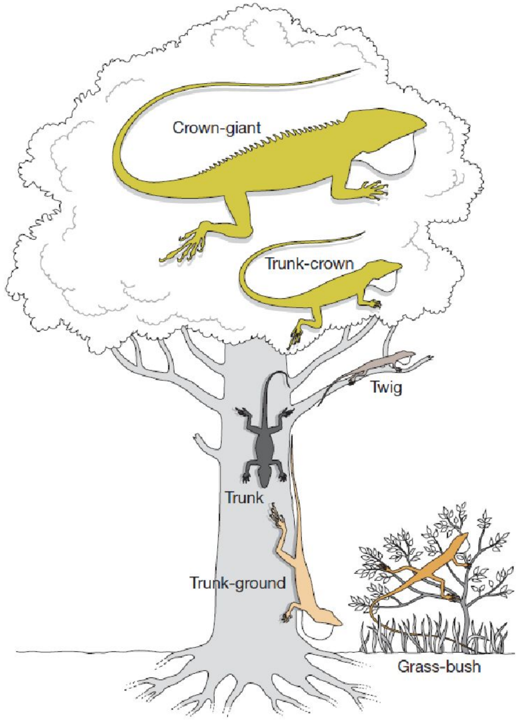


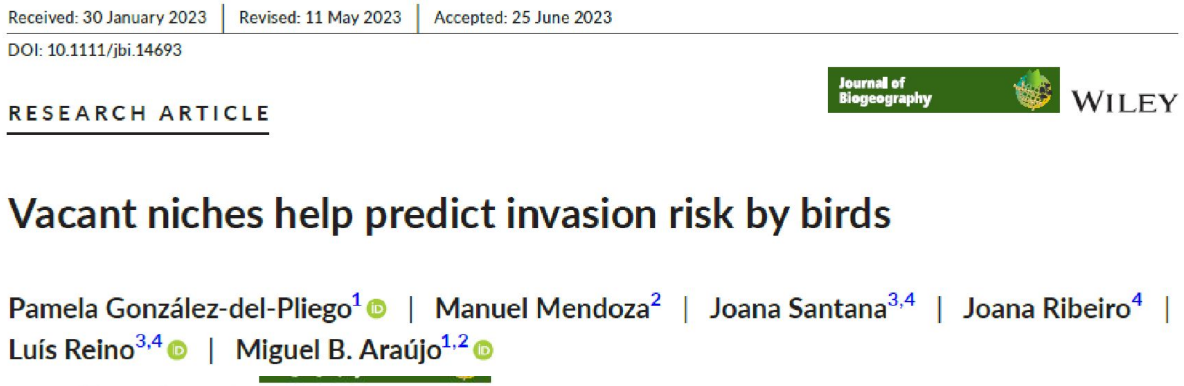
FIGURE 3.2
The ecomorphs.

Empty / vacant niches

The resources that are unused by anyone but are potentially usable.

Lawton (1984): “Evolutionarily novel suites of environmental conditions for which no species in a region are well adapted”.

Rohde (2005): “The vacant niche is the possibility that in ecosystems or habitats more species could exist than are present at a particular point in time, because many possibilities are not used by existing species.”



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Journal of Biogeography WILEY

RESEARCH ARTICLE

Vacant niches help predict invasion risk by birds

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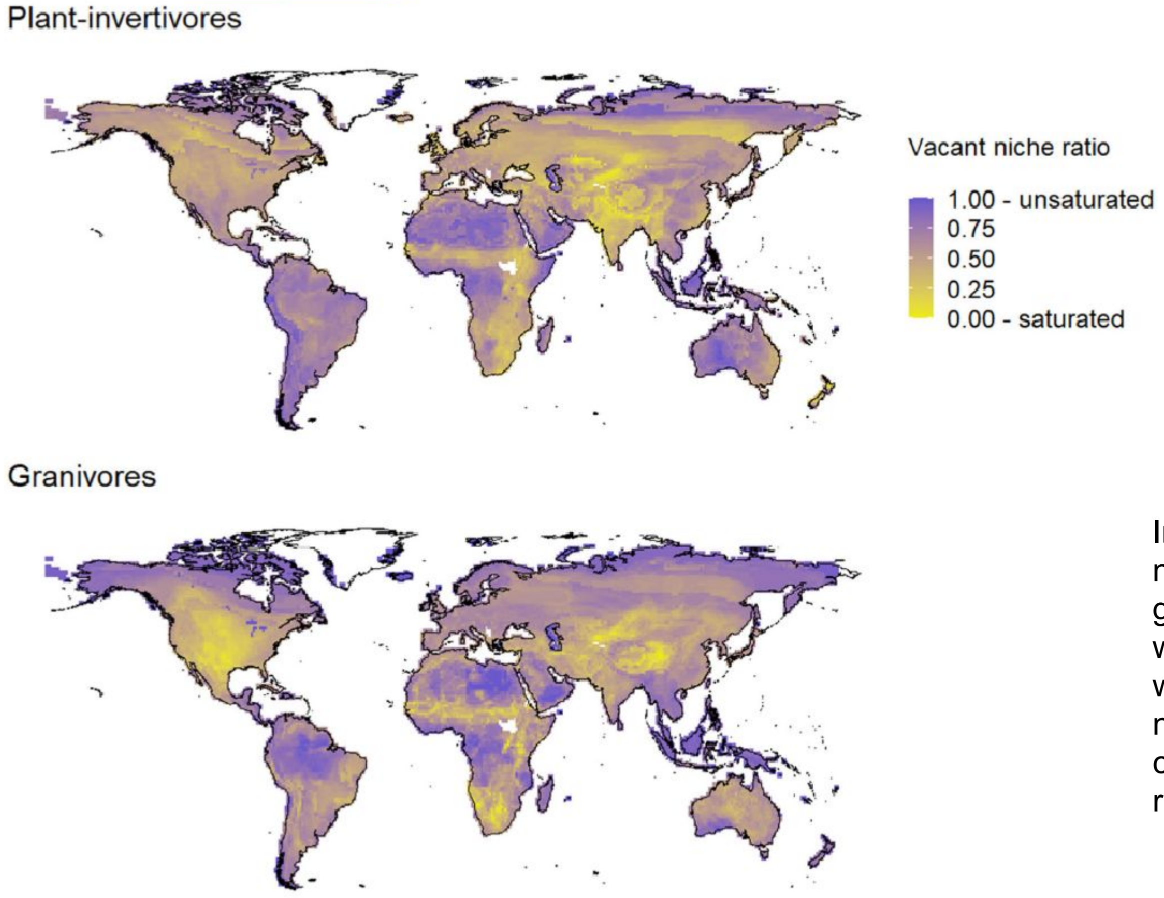

FIGURE 2 Geographic distribution of vacant niche ratio. Vacant niche ratio for plant-invertivore (upper panel) and granivore (lower panel) alien bird species globally. Vacant niche ratio ranges from 0 (saturated community with no vacant niches) to 1 (unsaturated community with great degree of niche vacancy). Maps are based on the geographical projection and WGS84 coordinate system.

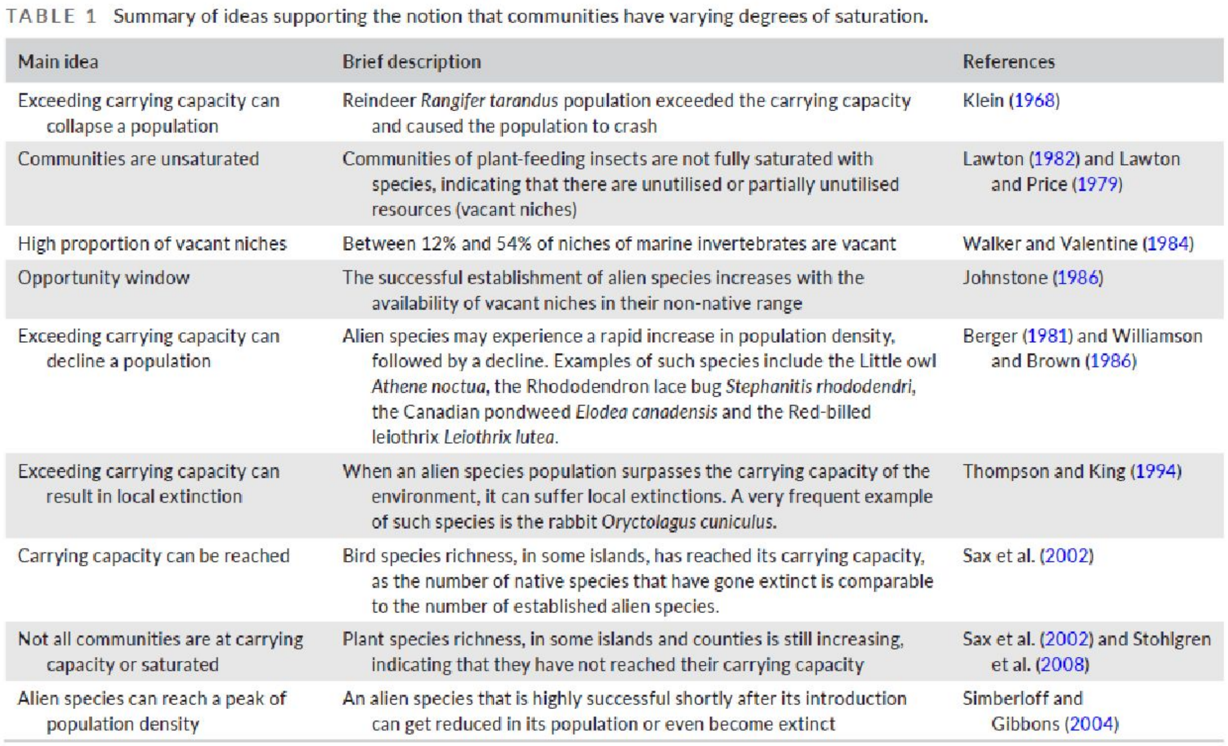

TABLE 1 Summary of ideas supporting the notion that communities have varying degrees of saturation.

Main idea	Brief description	References
Exceeding carrying capacity can collapse a population	Reindeer *Rangifer tarandus* population exceeded the carrying capacity and caused the population to crash	Klein (1968)
Communities are unsaturated	Communities of plant-feeding insects are not fully saturated with species, indicating that there are unutilised or partially unutilised resources (vacant niches)	Lawton (1982) and Lawton and Price (1979)
High proportion of vacant niches	Between 12% and 54% of niches of marine invertebrates are vacant	Walker and Valentine (1984)
Opportunity window	The successful establishment of alien species increases with the availability of vacant niches in their non-native range	Johnstone (1986)
Exceeding carrying capacity can decline a population	Alien species may experience a rapid increase in population density, followed by a decline. Examples of such species include the Little owl *Athene noctua*, the Rhododendron lace bug *Stephanitis rhododendri*, the Canadian pondweed *Elodea canadensis* and the Red-billed leiothrix *Leiothrix lutea*.	Berger (1981) and Williamson and Brown (1986)
Exceeding carrying capacity can result in local extinction	When an alien species population surpasses the carrying capacity of the environment, it can suffer local extinctions. A very frequent example of such species is the rabbit *Oryctolagus cuniculus*.	Thompson and King (1994)
Carrying capacity can be reached	Bird species richness, in some islands, has reached its carrying capacity, as the number of native species that have gone extinct is comparable to the number of established alien species.	Sax et al. (2002)
Not all communities are at carrying capacity or saturated	Plant species richness, in some islands and counties is still increasing, indicating that they have not reached their carrying capacity	Sax et al. (2002) and Stohlgren et al. (2008)
Alien species can reach a peak of population density	An alien species that is highly successful shortly after its introduction can get reduced in its population or even become extinct	Simberloff and Gibbons (2004)

In Europe, we found a significant relationship between alien species and vacant niches, with greater numbers of alien species being found in communities that offered greater numbers of vacant niches overall, and across habitat types. In North America, we found no significant relationship between plant-invertivores and vacant niches, while for granivores, we found that areas with fewer vacant niches had greater numbers of alien species, especially in forests. However, vacant niches alone correctly predict 69% of the presence of alien bird species when combining both regions and trophic guilds.


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RESEARCH ARTICLE

Functional Ecology BRITISH ECOLOGICAL SOCIETY

Vacant yet invasible niches in forest community assembly

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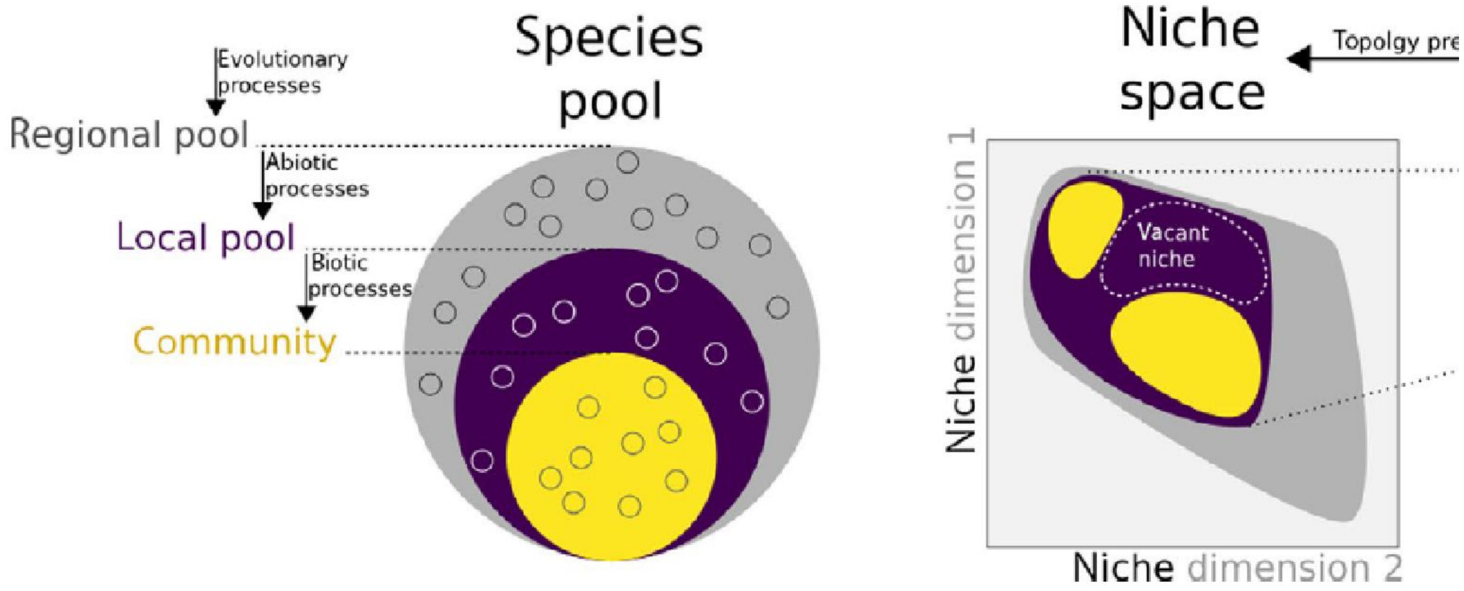
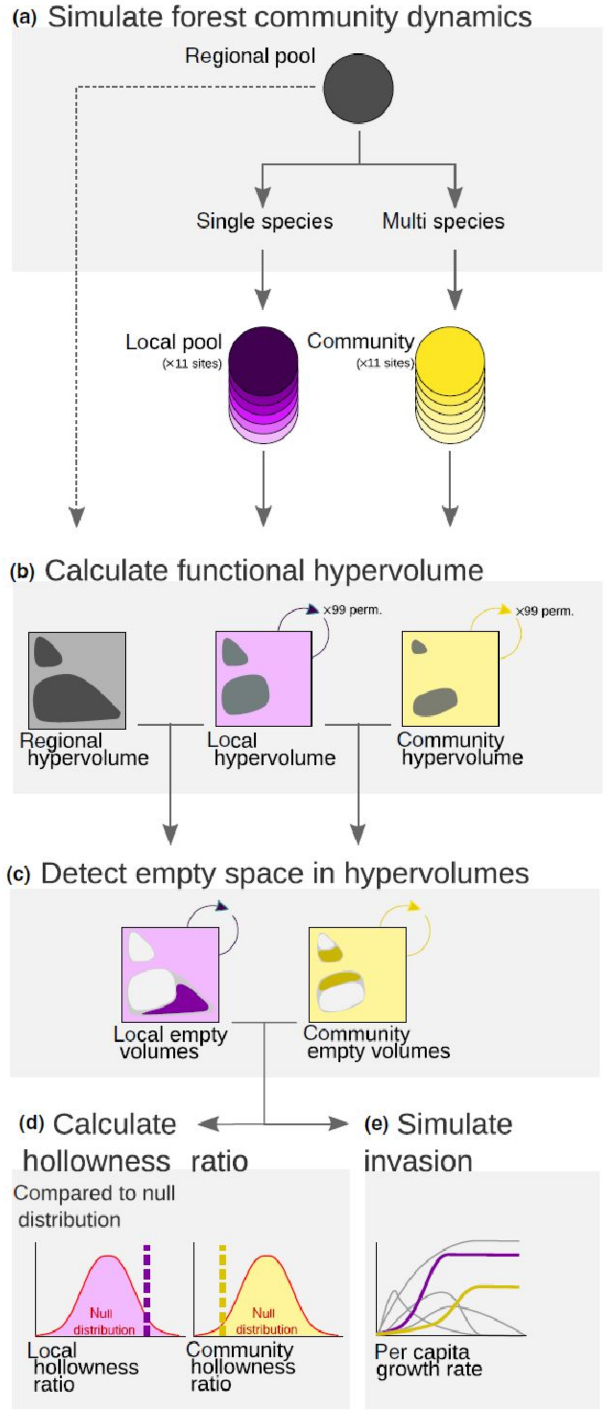
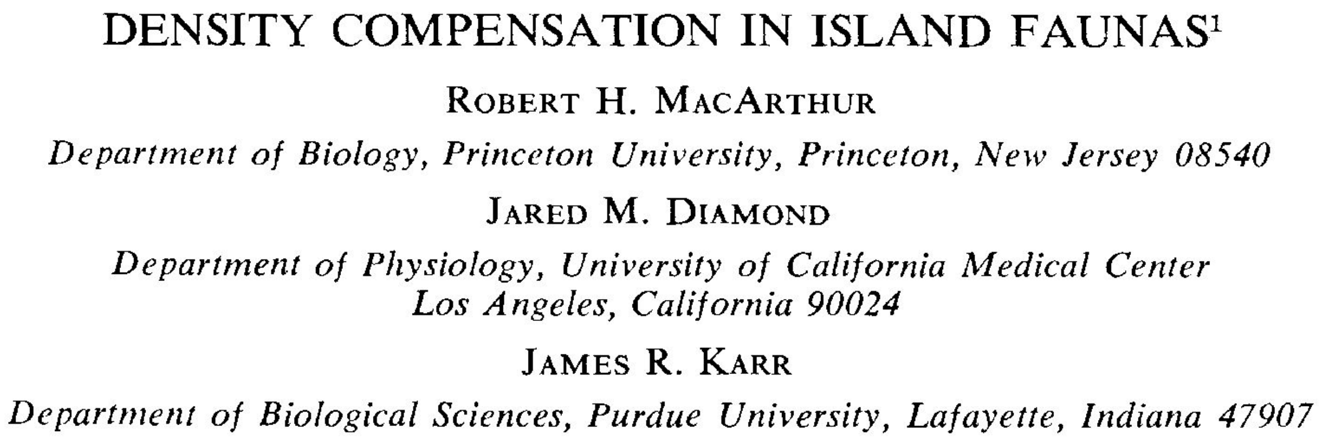
Courtenay Ray[1,4] | Benjamin Blonder[1,4]

empty niches are common…







DENSITY COMPENSATION IN ISLAND FAUNAS[1]

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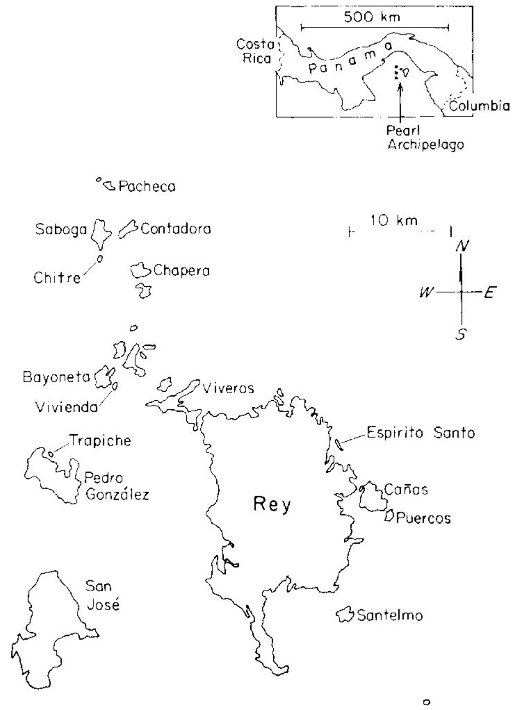
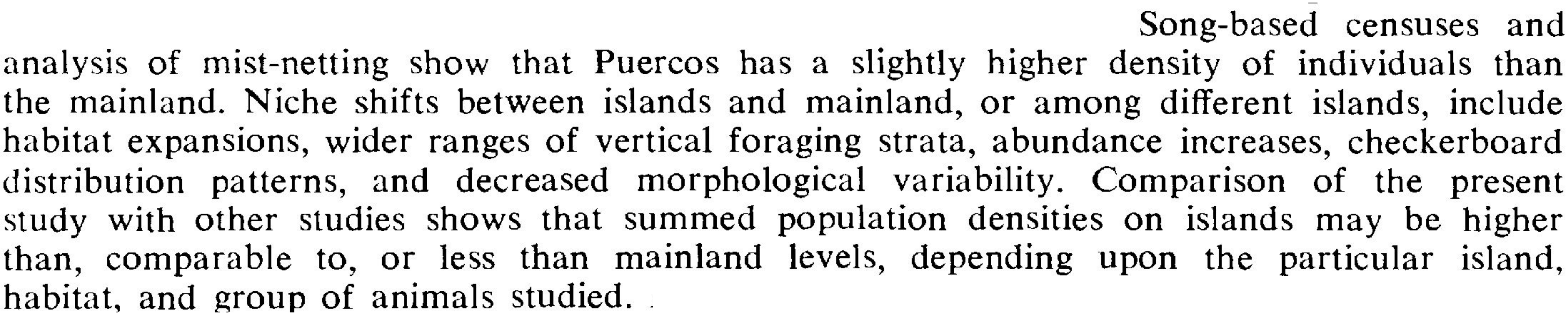


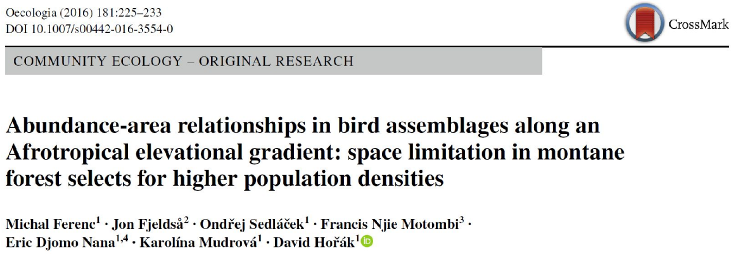
FIG. 1. Map of Pearl Archipelago, showing the location of individual islands whose avifauna is tabulated in Table 2. The inset is on a different scale to illustrate the location of the Archipelago with respect to the Panama mainland.

Absence of species empties ecological space...



Song-based censuses and analysis of mist-netting show that Puercos has a slightly higher density of individuals than the mainland. Niche shifts between islands and mainland, or among different islands, include habitat expansions, wider ranges of vertical foraging strata, abundance increases, checkerboard distribution patterns, and decreased morphological variability. Comparison of the present study with other studies shows that summed population densities on islands may be higher than, comparable to, or less than mainland levels, depending upon the particular island, habitat, and group of animals studied.

“Species scarcity” frees ecological space even in the mountain tops



Oecologia (2016) 181:225–233
DOI 10.1007/s00442-016-3554-0

COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Abundance-area relationships in bird assemblages along an Afrotropical elevational gradient: space limitation in montane forest selects for higher population densities

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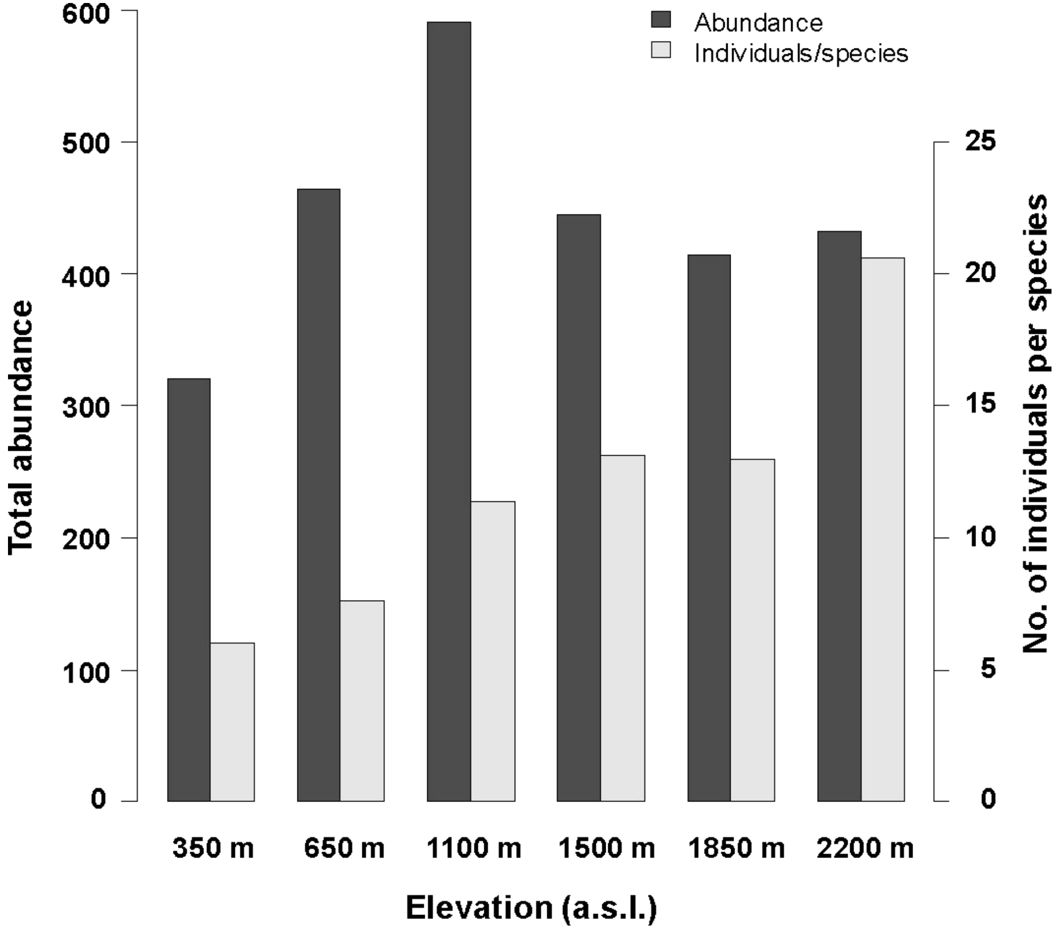
Eric Djomo Nana[1,4] · Karolína Mudrová[1] · David Hořák[1]



Niche construction

is the process whereby organisms actively modify their own and each other's evolutionary niches (Odling-Smee et al. 2003)

Termite muds

Beaver's dams

Okavango islands

SUMMARY

- *niche* is a controversial concept
- there is no *one* niche, Grinnell and Elton used different perspectives
- dimensionality of niche makes niche (concept) difficult to grasp
- remember Hutchinson
- both properties of the environment and species may characterize a niche
- *niche* space translates to *physical* space
- niche packing and expansion contribute to species richness levels
- still it seems, there is “empty“ ecological space

- see next time, if *traits* will help…

discussion + niche construction by humans

SPECIAL FEATURE: PERSPECTIVE

Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions

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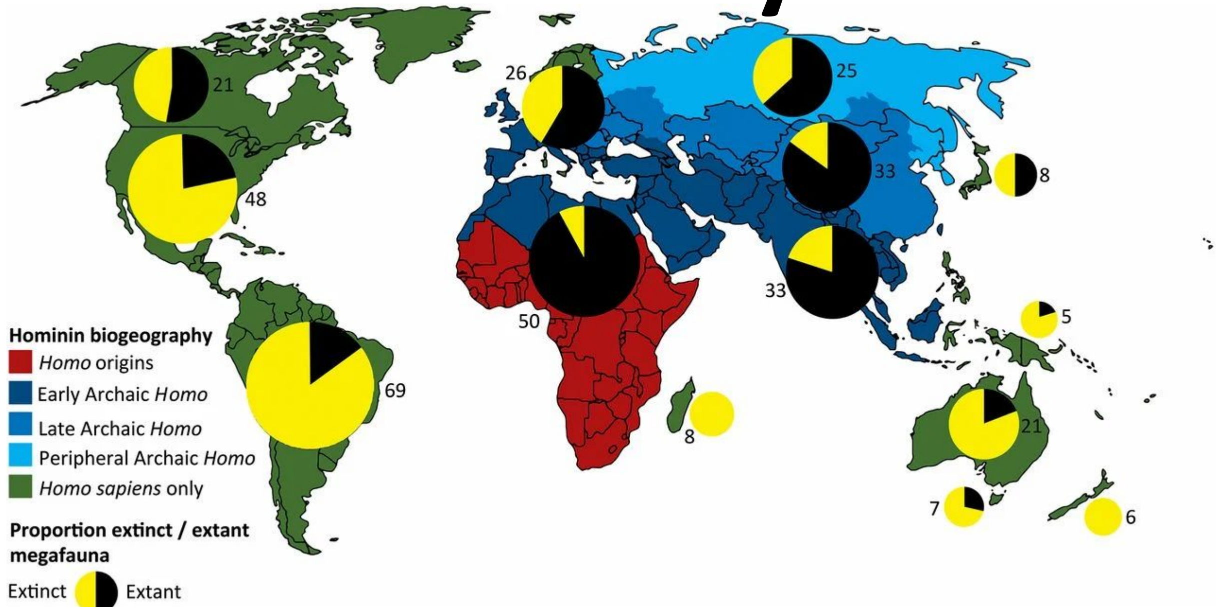
SPECIAL FEATURE:
PERSPECTIVE



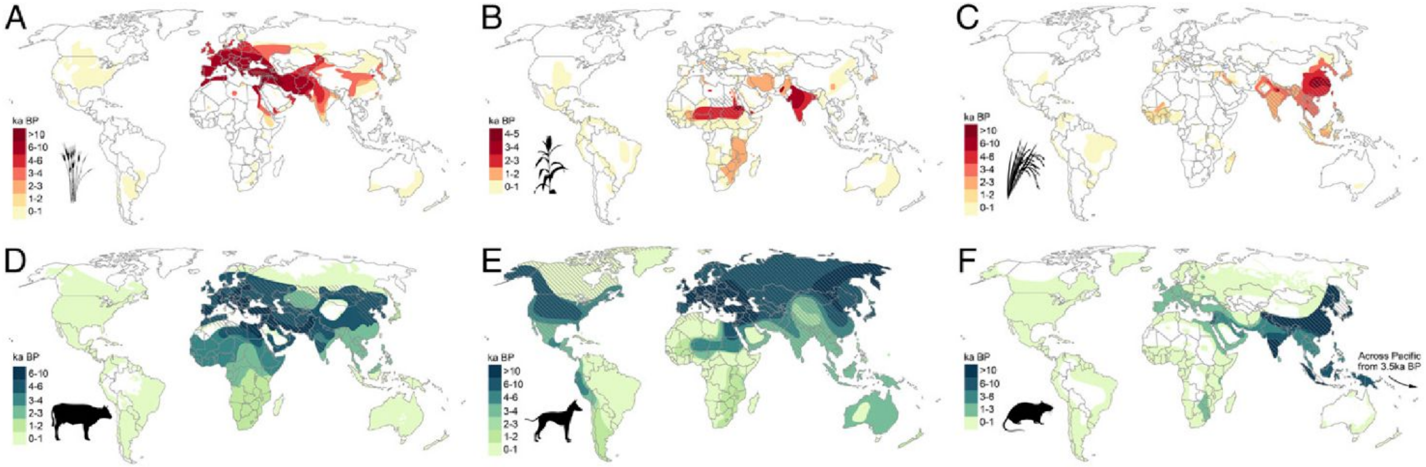


Fig. 3. Global spread of selected food crops (red) and domesticated and commensal animals (blue) through time. (*A*) Wheat (*Triticum* spp.). (*B*) Sorghum (*Sorghum bicolor*). (*C*) Rice (*Oryza sativa*, *Oryza glaberrima*). (*D*) Cattle (*Bos taurus*, *Bos indicus*). (*E*) Dog (*Canis familiaris*). (*F*) Rat (*Rattus rattus*, *Rattus tanezumi*, *Rattus norvegicus*, *Rattus exulans*). The major spread of rats to global islands beginning by 3 ka is not apparent at the scale shown. (Note that maps use different temporal scales, appropriate to individual species and their temporality of spread; hatching indicates natural distribution.)