

# Overview of South American research on interactions between trophic levels

Panorama de la investigación sudamericana sobre interacciones entre niveles tróficos.

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## ABSTRACT

I offer a personal overview of the South American contribution to the study of interactions between trophic levels, as I gathered it from my colleagues' presentations at the Workshop. I provide a diagnosis of the seven areas of research dealt with, offer three conclusions, and attempt to interpret my colleagues in putting forth three ideas for furthering collaboration between us and our North American colleagues.

Key words: Overview, diagnosis, perspective, collaboration.

## RESUMEN

Ofrezco una visión personal de la contribución sudamericana al estudio de las interacciones entre niveles tróficos, tal como me la formé a través de las presentaciones de mis colegas. Entrego un diagnóstico de las siete áreas de investigación tratadas, ofrezco tres conclusiones, e intento interpretar a mis colegas al entregar tres ideas para ampliar la colaboración entre nosotros y los colegas norteamericanos.

Palabras claves: Panorama, diagnóstico, perspectiva, colaboración.

## A PERSONAL OVERVIEW

The following is my personal overview of the state-of-the-art in research on interactions between trophic levels, as presented by the South American participants in August 1986. Given that some South American colleagues have chosen to team up with their North American counterparts in writing their contribution (Castilla & Paine 1987, Brown & Ojeda 1987), that I invited a paper by a researcher who did not actually participate in the Workshop (Fuentes *et al.* 1987), and that some of the papers have been somewhat modified through the review process, my comments below may not exactly be mirrored in the review papers as published. However, I thought it would be valuable to rescue the atmosphere that surrounded the South American contribution, in order to gauge what I think the North American participants may have perceived during the Workshop.

My choice is quite different from that made by Eric Pianka (1987) in overviewing North American research results: he could afford to make broad generalizations and provide provocative guidelines for future

research in North America, because the baseline information is already available. I could not dare to proceed the same way. Although I do not think that we South Americans are at a primitive stage of ecological research, I do believe that attempting generalizations from a still-developing data base would be premature.

My overview is based on three major assumptions: That I have chosen the best experts in the field; that these experts have made balanced reviews of the literature (with restrictions as made explicit); and that their oral presentations adequately represented those reviews.

## DIAGNOSIS

Following is my diagnosis of South American research, as I gathered it from my colleagues' presentations, in their original sequence:

1) Studies of marine predation (Castilla's presentation; see Castilla & Paine 1987) have made parallel advances in comparison to North American research, field experimentation being the usual method of in-

quiry used. Two distinctive features have characterized the South American research effort. One has been that of incorporating the importance of human effects on the outcome of processes that generate the patterns studied. Another has been the emphasis on the spatial and temporal scales under which those patterns are detected. The results indicate that research on interactions between trophic levels should explicitly address whether man is exerting any effect on the habitats under study. The "pristine" condition of such habitats should be assessed rather than assumed. A better understanding of recruitment phenomena seems necessary for further development of this research area.

2) Studies of marine herbivory (Santelices' presentation; see Santelices 1987) have also paralleled those conducted in North America. Field experimentation has been the usual method of research. Comparatively, two features have characterized these studies: An emphasis on laboratory experiments to disentangle factors that cannot be properly evaluated in the field, and an emphasis on non-detrimental aspects of the herbivore-alga interaction. The results indicate that herbivores may sometimes enhance the reproductive capacities of some algae, thus affecting their fitness positively rather than negatively. And also, that the presence of both herbivore and algal species with unique ecological features results in unexpected outcomes of interaction. Further knowledge on the temporal and spatial patterns of propagule availability is necessary for a better understanding of some phenomena under study.

3) Studies of parasitology (George-Nascimento's presentation; see George-Nascimento 1987) have been heavily biased towards taxonomy and systematics, and the whole field of ecological parasitology is just emerging. The little that has been investigated in this topic, however, has covered from parasite-host interactions at the individual through the population to the assemblage level. Most research has been descriptive, but some generalizations have been made based on the comparative method of scientific inquiry. An interesting feature has been the study of complex webs of trophically-transmitted parasites using as study systems a variety of vertebrate predators such as fishes and pinnipeds. The results indicate that both ecological

and phylogenetic characteristics play a role in the distribution and assortment of helminth parasites within food webs. Nothing is known about alterations of behavior or ecology of hosts as caused by parasites.

4) Studies of terrestrial predation (Jaksic's presentation; see Jaksic & Simonetti 1987) have shown asymmetrical co-actions between the prey and predator levels: whereas predators seem to affect mainly the prey's morphology and behavior, the prey base seems to affect mainly the predators' population and assemblage characteristics. Prey have not been considered to be regulated in their numbers by predation. Predators have been viewed as skimming surplus prey, reacting to changes in the prey population levels through adjustments of their functional, numerical, and assemblage level responses (that is, guild structure). The research protocols have been observational-correlational, with generalizations being made based on the comparative method. Emphasis has been placed on recurrence of patterns rather than on establishment of causation. Field or natural experiments have by and large been lacking. Their use should resolve the implicit causal relations that have been abundantly reported.

5) Studies of terrestrial herbivory (Bucher's presentation; see Bucher 1987) have remarked on the complex interplay of introduced grazers (a human disturbance) in modifying patterns of productivity, maintenance and succession of some South American ecosystems (for example, from fire-mediated periodic successions to no succession at all). They have also pinpointed the ignored impact of large mammalian herbivores that are now extinct but that may have left an enduring impact on the life forms of some shrubs and trees (for example, thorns). Some unique features of South American ecosystems include the presence of leaf-cutting ants that not only affect the vegetation through their foraging, but also through their changing the physico-chemical properties of the soil. This type of research has been essentially descriptive, with generalizations having been produced based on comparative studies. However, experiments conducted by agronomists and range managers could be put to good use for understanding the causal phenomena involved in herbivore-plant interactions. Indeed, field experiments

with ecological questions as a primary focus of attention should help very much in resolving some of the intriguing patterns detected. Fuentes *et al.* (1987) complement the review by Bucher (1987), and offer an overview of field manipulations aimed at determining the impact of insect herbivores on shrubs.

6) Studies of frugivory (Armesto's presentation; see Armesto *et al.* 1987) constitute the most recent brand of research on interactions between trophic levels in temperate South America. This interface has been attacked from both sides of the interactors: by studying characteristics of the fruits (such as color, size, seed and pulp contents), and by inferring the plant-dispersal potential afforded by different birds and mammals. Results indicate the importance of historic constraints (such as phylogeny and long term climatic and distributional changes) in determining features of the frugivore-plant interaction. The protocols used have so far been observational-correlational, with patterns still being in need of more exploratory analysis.

7) Studies of granivory (Ojeda's presentation; see Brown & Ojeda 1987) are almost non-existent in South America. Actually, it is yet unclear whether strict granivores have any effect at all on the seed bank. The lack of rodent granivores poses an interesting contrast to the situation in North American deserts. Everything in this area will have to be done from scratch.

#### CONCLUSIONS

Based on the above reviews I conclude the following:

1) In comparison to North American research, South Americans are making adequate progress in the study of marine predation, marine herbivory, and terrestrial predation. Studies of parasite-host, herbivore-plant and frugivore-plant interactions are just starting, but already promise interesting future developments. Studies of granivory lag well behind all other research on trophic interactions.

2) In comparison to North American research, South Americans may be making the same mistakes as their northern colleagues. The heavy emphasis put on studies of interactions and pattern emergence without

regard for the life-history characteristics of the organisms involved in the interactions hampers further development of the discipline. More natural history information is badly needed. Although this aspect of research is essentially descriptive, it seems clear that the predictive capability of ecological research should be greatly improved if a basic understanding of the biology of organisms is gained.

3) Finally, I think that by focusing their attention on two-level interfaces, both North and South American researchers may be losing sight of the importance of vertical interactions with trophic levels immediately above and below the target interface. What we need is true "community ecology", a consideration of the complex links (not always antagonistic) that bind together organisms disparately different in ecology and phylogeny.

#### PERSPECTIVE

I now summarize what my South American colleagues think (I hope to interpret them well) about the usefulness of this meeting, and about the prospects for future research and collaboration.

1) We have learned that some broad ecological generalizations that have emerged from northern hemisphere research, which have become textbook examples, sometimes do not apply in South America. We think that, for the sake of a better Ecology, we should plan collaborative research in order to incorporate South American research results into the mainstream of Ecology, rather than consider them as oddities, or worse, as incompetent research from this part of the world.

2) We think that, in planning collaborative research, we should not consider the different histories and compositions of North and South American communities and habitats as a hindrance or as "noise". If we really are interested in understanding ecological phenomena on a broad basis, the different historical inertias associated with these two continents should actually be considered an opportunity to test the real value of generalizations produced from research in either continent.

One point requires further elaboration: We want to make a distinction between

“comparative” and “collaborative” research. Comparative ecology has gained a bad reputation in putting too much emphasis on detecting similarities and matching species in different areas as ecological analogs. One can always stretch the facts to detect similarities between different organisms and assemblages, which is what we think the IBP studies did in the past. In our opinion, this is like putting the cart before the horse. In recommending collaborative research we are referring to conducting separate studies of ecological interactions as they affect different communities in both hemispheres, with reciprocal feedbacks of information between North and South American researchers, and ideally, exchanges of visits to the respective research sites. If close similarities emerge, then we may have pinpointed basic constants in the assembly of those communities. If not, consideration of other factors peculiar to either hemisphere may explain why the systems differ.

3) As a final comment, we should like to express that this workshop may well become a benchmark in terms of stating what the state of our art was as of August 1986, thus becoming a useful standard against which to compare further developments of our field in the future. We are curious indeed to see whether our research results have impressed the North Americans somehow, so that in their coming publications they start citing us! This may sound outright selfish, but we think that the time for reciprocation is close, and perhaps already overdue.

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#### LITERATURE CITED

- ARMESTÓ JJ, R ROZZI, P MIRANDA & C SABAG (1987) Plant- frugivore interactions in South American temperate forests. *Revista Chilena de Historia Natural* 60: 321-336.
- BROWN JH & RA OJEDA (1987) Granivory: patterns, processes, and consequences of seed consumption on two continents. *Revista Chilena de Historia Natural* 60: 337-349.
- BUCHER EH (1987) Herbivory in arid and semi-arid regions of Argentina. *Revista Chilena de Historia Natural* 60: 265-273.
- CASTILLA JC & RT PAINE (1987) Predation and community organization on eastern Pacific, temperate zone, rocky intertidal shores. *Revista Chilena de Historia Natural* 60: 131-151.
- FUENTES ER, A POIANI & JD MOLINA (1987) Shrub defoliation in the Chilean matorral: what is its significance? *Revista Chilena de Historia Natural* 60: 275-283.
- GEORGE-NASCIMENTO MA (1987) Ecological helminthology of wildlife animal hosts from South America: a literature review and a search for patterns in marine food webs. *Revista Chilena de Historia Natural* 60: 181-202.
- JAKSIC FM & JA SIMONETTI (1987) Predator-prey relationships among terrestrial vertebrates: an exhaustive review of studies conducted in southern South America. *Revista Chilena de Historia Natural* 60: 221-244.
- PIANKA ER (1987) The subtlety, complexity and importance of population interactions when more than two species are involved. *Revista Chilena de Historia Natural* 60: 351-361.
- SANTELICES B (1987) Marine herbivory studies: the South American contribution. *Revista Chilena de Historia Natural* 60: 153-158.