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PERSPECTIVA

GENESIS, EVOLUTION, AND FUTURE OF A LONG-TERM STUDY OF SMALL MAMMALS IN SOUTH AMERICA

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ABSTRACT. Since 1989, I have been involved in a long-term ecological study in the semiarid zone of north-central Chile. To date it has uncovered many exciting aspects of the structure and functioning of the unusual biota here. However, the genesis of this project actually dates back to 1973 when I first saw the study area in Parque Nacional Bosque Fray Jorge as a visiting professor at the Universidad Católica de Chile in Santiago. At that time, I initiated a small mammal live-trapping study in collaboration with Eric Le Boulengé of Belgium. Little did we know that the basic data we collected on small mammal populations, diets, and predators then would lead to the installation of what is now the longest running field manipulation in temperate South America. In this experiment, we have altered predator and herbivore access to replicated field enclosures. We have documented strong effects of biotic interactions including herbivory and vertebrate predation on floral and faunal elements; however, abiotic factors due chiefly to periodic rainfall events such as El Niño Southern Oscillations (ENSOs), and most recently climate change have dramatic, overriding effects on virtually all biotic elements. Work continues today with additional experiments and inclusion of other faunal groups such as birds, arthropods and lagomorphs; however, we emphasize that in order to maintain a sustained multifaceted study such as this one, three essential elements are required: 1) good **data**; 2) the **evolution** of objectives and sampling efforts; and 3) to some degree, chance or **serendipity**. We are grateful to many sources of support we have enjoyed over the past 28 years, as well as the dedicated labor of more than 30 technicians and post-doctoral students in the project.

Key words: Climate change. El Niño Southern Oscillations (ENSOs). Long-term studies. North-central Chile. Semiarid ecology.

Recently, following a presentation at the annual SAREM meeting in Santa Fe, Argentina, I was asked how a long-term study such the Fray Jorge project came about. While answering, it occurred to me that this was not a simple question. After all, who anticipates spending nearly a half-century of one's life in one particular area and study? Therefore, I take this opportunity to relate some of the history of the origins, development, and future directions of the project. As one of the two people associated since its very beginning (the other is Julio R. Gutiérrez of the Universidad de La Serena, Chile), perhaps I can offer some unique perspectives and insights that may be of interest to aspiring ecologists contemplating such an endeavor.

Genesis

Every project has a beginning; the actual origin of the Fray Jorge project was not in 1987 when we started the experimental work, but some 15 years before. In 1972 as a new Ph.D. from the University of California, Irvine, I took a position at the Universidad Católica de Chile in Santiago to teach ecology and other courses in the Laboratorio de Ecología there. Little did my wife and I know the situation we were stepping into; with only a rudimentary knowledge of Spanish and the vaguest idea of Latin America (previously, my furthest south had been Baja California!), we arrived in Santiago on a hot, sweltering day in late January 1973. Almost immediately we were confronted with daily political demonstrations and strikes, shortages of virtually every typical commodity (e.g., rice, sugar, flour, cooking oil, even toilet paper!), galloping inflation exceeding 200% annually, and during this, the last year of Salvador Allende's presidency, increasing disorder and chaos in the streets. Amidst the turmoil, in August 1973 I met a Peace Corps volunteer, George Fulk, who invited me to visit his study site in a national park, Parque Nacional Bosque Fray Jorge (then P.N. Fray Jorge; henceforth "Fray Jorge") located about 100 km S of La Serena and 350 km N Santiago near the coast. Driving N on the Pan-American highway (Ruta 5) through a denuded, degraded landscape stretching some 200 km along the ocean between Los Vilos to Coquimbo, I wondered what kind of native vegetation still survived in the region. North

of the Rio Limarí at a small crossing, we turned off the highway, and drove 40 km Won a dirt road to a little (i.e. 10000 ha) island of diversity in Fray Jorge. Here we found a remarkable thorn scrub community with a rich flora of spring ephemerals after winter rains; this community characterized most of the Norte Chico prior to European settlement. On an ocean-facing ridge to the W, relict fog forest (for which the park was created) occurs with tree and liana species typical of Valdivian temperate rainforests 800 km S (**Fig. 1**).

Fulk was finishing up his work here and returning soon to the U.S.; as I had worked in a fairly similar community (the California coastal sage scrub) for my Ph.D. dissertation, he encouraged me to follow up on his work. So, less than two months after the military overthrow of the Allende government on 11 September 1973, my wife Jan and I made our way up to Fray Jorge and began a live-trapping study of small mammals in an interior valley (Quebrada de las Vacas) using live traps kindly loaned by Bill Glanz of UC Berkeley, then conducting his Ph.D. dissertation research in the International Biome Project, based at Universidad Católica. At the same time, we initiated ancillary studies on small mammal diets, spatial utilization, and other ecological aspects similar to what I had done for my Ph.D. in the coastal sage scrub. In mid-1974, we were joined by Eric and Paule Le Boulengé of Belgium; Eric was also teaching at the Laboratorio de Ecología.

After returning to the U.S., my research focus shifted away from Fray Jorge to fieldwork in the Midwest near where I taught at Northern Illinois University (DeKalb, Illinois). Although I published results from our Chile work, and later returned to southern Chile in the early-mid 1980's to work in Valdivian temperate rainforests, this had little to do with the Fray Jorge project. Then in 1985, I was invited to submit a paper on South American small mammals as part of a commemorative volume honoring Phil Hershkovitz at the Field Museum of Natural History (Chicago). I traveled to Belgium to collaborate with Le Boulengé (at the Université de Louvain, Louvain-la-Neuve), and the paper that resulted (Meserve and Le Boulengé, 1987) was one of the first to utilize sophisticated modeling techniques to examine small mammal mark-recapture data.

What emerged from this effort were some rather intriguing questions. For example, during the ca. 1 ½ years of work in Fray Jorge in the 1970's, we had observed dramatic increases in numbers of some small mammals such as the degu (*Octodon degus*), and yet, rather constant numbers in other species such as the olivaceous field mouse (*Abrothrix olivacea*) and Darwin's leaf-eared mouse (*Phyllotis darwini*). Further, there was a remarkable diversity of trophic specializations among the small mammal consumers here—herbivores, granivores, insectivores, omnivores. What factors might be explaining this difference—life history, intrinsic population

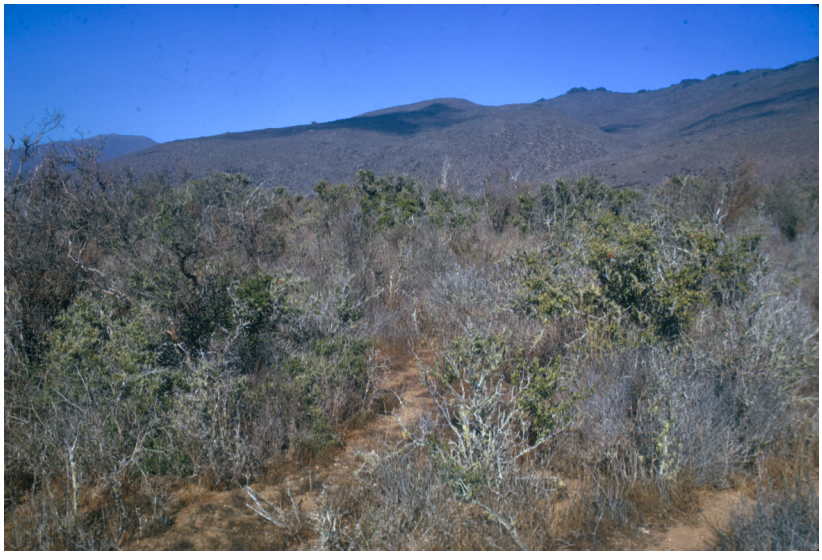

Fig. 1. Thorn scrub vegetation in Fray Jorge; patches of relict fog forest are visible on the ridge facing the Pacific Ocean

regulation, extrinsic biotic factors (predation, competition, etc.), or extrinsic abiotic ones (i.e., rainfall)? Without careful experimentation, the answers to these questions were intractable.

In the 1980's, there was strong interest in the use of reductionist methods in ecology in order to identify the role of biotic vs. abiotic factors in natural communities. The goal of a reductionist approach is to tease apart the role of biotic factors such as predation, herbivory, and interspecific competition, and identify those most responsible for observed changes. This necessitates carefully designed and well-replicated experiments. Field experiments are particularly valuable here because they have greater reality and scale as compared to laboratory experiments. However, at the same time, they have greater problems of site matching and control of environmental factors than do laboratory ones. Certain "simpler" systems lend themselves readily to field experiments—e.g., intertidal zones, temperate grasslands… and semiarid communities. Thus, my previous work in Fray Jorge and the unresolved questions there lured me to return to this unusual community.

In 1987, in collaboration with three Chilean ecologists (Fabián Jaksic, Universidad Católica; Julio Gutiérrez and Luis Contreras, both of Universidad de La Serena), we submitted a proposal to the Environmental Biology Program of NSF requesting $90 000 to initiate a large-scale field experiment in Fray Jorge. Pleasantly, we were funded the first try! On paper, our experimental design seemed simple; we would exclude terrestrial mammal predators and aerial raptors from some areas (i.e., trapping grids), and the larger small mammal herbivore (i.e., the Chilean degu) from others. As a 2-factor experiment, we also had crossed treatments (i.e., both predator and degu exclusions, as well as controls; with 4 randomly assigned grids to each treatment, there were 16-0.56 ha grids in all. Wire overhangs and suspended netting excluded both terrestrial mammal predators and aerial raptors. To allow degu entry to some grids, we cut 5 cm holes at ground level every 5 m along the chicken wire fencing of degu-access grids.

Though simple on paper, installing this design was more difficult in the field. From early through mid-1989, a crew of workmen constructed the central grid complex in a ca. 2 km^2 area in Q. de las Vacas. This entailed importing an enormous amount of material, going through customs, transporting it to the park, and then installing it by hand, grid by grid; no mechanized tools were used. Rough calculations are that we used ca. 1200 wooden posts to support grid fencing, 45 000 m^2 of ca. 20 cm d polypropylene netting, 4 800 m of 1.8 m and 1.0 m wide chicken wire, and vast quantities of nails, staples, and rope. Amazingly, the construction was completed by mid-1989, and we were able to initiate the experiment in June after a 3 month-pre-treatment period.

Evolution

Our initial funding was for 3 years. But even within that short time window, our perspectives were changing. For example, one major initial finding was that predation, a biotic factor that we had posited as being of major significance here, was not as important as we originally thought. Over time, we began to realize that abiotic factors were much more important. Why this was not self-evident given the history of dramatic responses of small mammals to high rainfall during El Niño Southern Oscillations (ENSOs) here and elsewhere remains somewhat of a puzzle to me even today. Perhaps one of the reasons was that we were focused on documenting responses to manipulations of biotic factors within the typical 2-3 year grant funding window. But by a fortuitous coincidence, in 1991-1992, we observed major small mammal (and plant) responses to a high rainfall event in those years. We later recognized that ENSOs periodically "reset the clock" with respect to the role of biotic and abiotic factors. That is, during low rainfall years, conditions appear so limiting that biotic interactions have relatively little importance; during high rainfall years (and immediately ensuing ones), populations are released from environmental limitations and can exert much stronger effects as a result of their interactions. Thus, we posited that biotic and abiotic interactions alternated in importance and control of organismal groups in the community (a so-called "top-down" vs. "bottom-up" view; Meserve et al., 2003). Fortunately, over the next 10 years we have been able to verify this with continued support from the U.S. NSF, and Chile's equivalent agency, FONDECYT.

Changes in perspectives led to interesting side experiments. For example, we initiated food addition experiments on new experimental grids located to the N and S of the central grid complex; we provided rabbit pellets in feeding tubes accessible only by small mammals. Coincidentally, after initiating these additions in 1996, a moderately wet year followed (1997), and then an extremely dry one (1998) resulting from a strong La Niña then. The results were dramatic; whereas food additions had virtually no effects during 1997, they resulted in dramatic increases among herbivorous rodents such as *Octodon degus* and *Phyllotis darwini* in 1998, but not in omnivorous to granivorous ones (e.g., *Abrothrix olivacea*, *Oligoryzomys longicaudatus*).

Thus, the conclusion was that food was not limiting on herbivorous rodents in 1997, a wet year, but extremely so during a dry one in 1998 (Meserve et al., 2001).

Additionally, in the mid-1990's we initiated trapping on supplemental grids in peripheral habitats of the park (e.g., riparian habitat, open scrubland, and relict fog forest) to better understand small mammal spatial dynamics. Milstead et al. (2007) showed that some small mammals (e.g., *O. longicaudatus; Abrothrix longipilis*) persist in more mesic habitats, and are "opportunistic" invading the thorn scrub when conditions are mesic. Others (*O. degus, A. olivacea, P. darwini*) are "core" species and persist in the thorn scrub albeit often at low numbers.

Verification of the importance of other biotic interactions such as herbivory by *O. degus* was more difficult; although there was evidence for indirect effects from degu burrowing and runway-making activities as well as shrub-ephemeral plant interactions, evidence of direct herbivory effects was less obvious. However, after a prolonged high rainfall event in 2000-2002 when large increases in lagomorph (i.e., *Lepus europaeus*, *Oryctolagus cuniculus*) and degu populations were observed, we modified the initial experimental design adding all-small mammal and all-small mammal plus lagomorph exclusions. Recently we have begun to observe strong changes in the vegetative community as a result of these efforts. This emphasizes the importance of long-term studies that enable documentation of cumulative effects over long periods of time. In addition, long-term studies need to evolve as new questions become more evident.

Evolution of the project also led to monitoring of other major organismal groups that had previously been ignored. Among these are birds, lizards, and arthropods; results of some of these efforts now have been published (see Armas et al., 2016 and accompanying papers). While emphasizing the importance of Fray Jorge as a major biosphere reserve, changes in these groups also serve to document the effects of on-going climate change in South America. Supported by Instituto de Ecología y Biodiversidad (IEB), Fray Jorge now anchors the N end of a ca. 3000 km long latitudinal transect with two other research sites, the Estación Biológica Senda Darwin on Isla Chiloé, and Parque Etnobotánico de Omora near Puerto Williams, Chile; the latter are located in the center and S extremity of the transect, respectively. As a sentinel site, Fray Jorge is increasingly important in the Norte Chico as the region's population and water demands increase. Changes in rainfall variability and ENSO frequency have already begun affecting its fauna and flora; for example, mean rainfall has increased at the site since 2000 whereas interannual variability has decreased (i.e., $X_{(1989\text{-}99)} = 111.4 \pm 103.8$ mm (Mean ± 1 SD) vs. $X_{(2000\text{-}15)} = 132.8 \pm 82.2$ mm).

The future

As we near the end of our third decade of work, we have transitioned to a multi-disciplinary project incorporating many on-going ecological investigations. We now have a field station at the park headquarters that provides laboratory space and lodging for visiting investigators as well as improved communication and research facilities.

Whereas formerly we had rather a narrow focus on small mammals and plants and the role of biotic interactions in the community, we now recognize that the community cannot be divorced from recent changes in the regional climate and the park's increasing insularity amidst a landscape of badly degraded and greatly altered terrain. A recent survey conducted in artificially replanted areas north of the park revealed a shocking paucity of small mammals in *Atriplex nummularia* monocultures that now characterize much of the Norte Chico. This emphasizes the importance of Fray Jorge as an example of the former biodiversity of the region as well as its uniqueness amidst on-going climate change and habitat alteration.

This brings me back to the original question; how did a project focused on documenting biotic effects on small mammals and plants within a 2-3 year time window become a multi-decadal one with many ancillary investigations on diverse elements of the community? First, and foremost, we needed good **data**. By that, I mean that not only high quality data, but also data on aspects that may not seem important at the time when we initiated work. The data we collected on small mammal diets, and those of potential predators in the area back in the 1970's are examples. Information on the first aspect allowed us to characterize the Fray Jorge small mammal assemblage, and identify important consumer groups (e.g., degus as herbivores) and potential plant-animal interactions. Information on the second verified that predators did consume significant numbers of small mammals especially during and after ENSO's.

A second crucial aspect is follow-up or **evolution**. By that, I mean exploring the implications and potential significance of trends that may indicate important new directions and foci of work. A case in point was the finding in the mid-1990's that although predation was important in affecting small mammal numbers and survival rates in Fray Jorge, especially those of a larger herbivore, the degu, ENSO's had greater effects on virtually all elements of the small

mammal assemblage as well as the surrounding community. As the project evolved, changes in the experimental design as well as shifts in the focus of work after 2002 enabled verification of strong herbivore effects following the dramatic increase of degu and lagomorph numbers following 2000-2002.

Lastly, mention needs be made of chance or **serendipity**. Who could have predicted that the 1991-1992 ENSO would demonstrate the importance of abiotic factors in this system—or that one in 2000-2002 would trigger a fundamental shift in the small mammal assemblage composition? Had we terminated work in this community before 2002, we would have missed the opportunity to observe major changes in the Fray Jorge plant community, largely as a result of the changes in numbers of degus after then. We posit that these demographic changes have resulted from declining interannual variation in precipitation since 2000; increases in mean annual precipitation have also occurred. Thus, we have shown that climate change effects are complex in semiarid regions and can have unanticipated consequences.

What does the future hold for Fray Jorge project? Our current funding extends through 2020, signifying the maintenance of the project through 3 decades; with the IEB's involvement, the project will continue in some shape or form for the foreseeable future. While my own involvement in it has declined as I pass the reigns to younger investigators, I continue to be strongly committed to its success and development.

In closing, I must acknowledge all those who have made this project possible and successful. First and foremost, I owe a great debt of thanks and appreciation to Julio Gutiérrez (Universidad de La Serena) for his continuous support, patience, and invaluable contributions to the project's success; as a leading plant ecologist, he provided essential breadth and perspective on semiarid systems that I lacked. Further, he procured financial support from FONDECYT Chile without which it would not have continued, nor enjoyed as much success. Fabián Jaksic provided important initial support, and helped us navigate the convoluted process of importing and obtaining building materials and their transportation to the park. My former student, colleague, and now lead PI on the project, Doug Kelt, has readily assumed the mantle of directing the U.S. side of the project; I am grateful for his continuing dedication to its goals and diversification. Many people have served as technicians on the project, and I gratefully acknowledge their hard work and commitment to quality data collection (see **Appendix 1**); in particular Brian Lang, W. Bryan Milstead, and Andrea Previtali deserve special mention for their important contributions. I also thank the Corporación Nacional Forestal (CONAF) who allowed us to establish a living laboratory and field experiment in P.N. Bosque Fray Jorge and have been especially cooperative. And finally, special thanks go to my wife Jan and our sons, Jeffrey and Stephen, who tolerated my frequent absences over the past 35 years, and accepted that this was to be my life's work and scientific contribution.

Acknowledgements: I thank Enrique Lessa for the opportunity to provide a written record of the history of this project. I hope that it may stimulate future researchers to engage in long-term studies that are so crucial for our understanding of ecological processes in a constantly changing world.

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APPENDIX 1

List of personnel who have served as technicians and post-docs on the Fray Jorge project (approximately chronological).

Technicians: Kenneth Cramer (USA), Miguel Angel Torrealba (Chile), Elier Tabilo (Chile), Brian K. Lang (USA), Sergio Silva (Chile), Sergio Herrera (Chile), Víctor Valverde (Chile), Victor Lagos (Chile), Hernán Vásquez (Chile), Alvaro Levicán (Chile), Francisco López (Chile), W. Bryan Milstead (USA), Andrea Campanella (Italy), Alexandra Minn (USA), Juan Monárdez Robles (Chile), Jorge Albinaña (Spain), Alex Cea (Chile), Leticia Sánchez (Chile), Patricia Vidiella (Venezuela), M. Ángeles Moreno (Chile), Andrea Previtali (Argentina), Lazaro Guiñazú (Argentina), Héctor Veas (Chile), Juan Calderón (Chile), Sandra Uribe (Chile), Camila Holzapfel (Chile), Daniela Rivariola (AR), José Luis Cortés (Chile).

Post-doctoral Students: Jaime Madrigal (Chile), Aurora Gaxiola (Chile), Cristina Armas (Spain)