Patterns in arthropod abundance and biomass in the semiarid thorn scrub of Bosque Fray Jorge
National Park, north-central Chile: a preliminary assessment

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Keywords: long-term studies, climate change, arthropods, semiarid systems, Chile

Article Type: SI The Fray Jorge LTSER

ABSTRACT

In 2003, we initiated a sampling protocol for arthropods as part of long-term field experiment in a semiarid thorn scrub community in north-central Chile. We utilized pitfall and Malaise traps to sample terrestrial and volant arthropods, respectively. Inventories were conducted for 4 days and nights monthly. We posited that arthropod abundance and biomass would track environmental changes such as high rainfall often due to El Niño Southern Oscillations (ENSOs). Peaks in both abundance and biomass for terrestrial and volant arthropods were in similar months (spring-early summer; August-November); arthropods also tracked high rainfall years in 2004, 2006, and 2011, due mostly to increases in a few dominant groups, i.e., tenebrionid beetles (Coleoptera) in terrestrial sampling, and moths (Lepidoptera: Noctuidae, microlepidoptera) in aerial sampling. However, the same groups increased dramatically in 2008 which was a below-average rainfall year. Numerical decreases in late summer-fall months (January-April) were more abrupt for terrestrial arthropods than for volant ones. Both terrestrial and volant arthropods reached their lowest levels in winter months (June-July). Some evidence suggests long-term shifts in the composition of volant taxa. Arthropods likely are important prey items for insectivorous reptiles (i.e., lizards), birds, and an insectivorous small mammal, the elegant mouse opossum (*Thylamys elegans*), and future efforts are being directed towards examining the evidence for correlated changes in those consumers with arthropod abundance and biomass.

1. INTRODUCTION

Arthropods are an important faunal group in virtually every non-polar terrestrial ecosystem. They fill important niches as herbivores, predators, parasites, pollinators, and symbionts, and they provide food for insectivorous vertebrate groups including lizards, birds, and some small mammals. However, relatively little is known about long-term patterns in their abundance, especially from semiarid systems; semiarid Chile is no exception. Since 1989 we have maintained a multi-factorial field experiment as described in this volume and recent reviews (e.g., Meserve et al. 1996, 1999, 2011). In 2003 we established a sampling protocol to monitor arthropod populations using both pitfall and Malaise traps (terrestrial and volant arthropods, respectively). The initial goals of this effort were modest; to determine if: 1) changes in abundance and biomass of arthropods track environmental changes relating to aperiodic high rainfall events such as those due to El Niño Southern Oscillations (henceforth “ENSOs”); and: 2) if specific consumer groups such as birds and insectivorous small mammals (most notably, the elegant mouse opossum [*Thylamys elegans*]) respond similarly to changes in their prey abundance and biomass. This report focuses on the first goal, but provides some preliminary data for eventually examining the second.

2. Materials and Methods

Fray Jorge (71°40' W, 30°38' S) is a ca. 9,000 ha World Biosphere Reserve about 380 km N of Santiago, Chile and 150 km S of the southern edge of the hyperarid Atacama Desert (see Fig. X in Squeo et al., this volume). The park is dominated by semiarid thorn scrub vegetation, and coastal hills support remnant fog forests, all of which has been protected from grazing and disturbance since 1941. The thorn scrub includes spiny drought-deciduous and evergreen shrubs

and understory herbs on a primarily sandy substrate (Muñoz and Pisano 1947, Muñoz 1985, Gutiérrez et al. 1993a). The climate is semiarid Mediterranean with 90% of the mean annual 125 mm (1989-2013) precipitation falling in winter months (May-Sept.), and warm, dry summers (Dec.-Feb.). Since 1989, there have been 6 El Niño/high rainfall events in this region: 1991-92 (233-229 mm), 1997 (330 mm), 2000-2002 (236-339 mm), 2004 (168 mm), 2006 (147 mm), and 2011 (160 mm); intervening years have been dry (11 to 95 mm).

The experimental array of 20 small mammal trapping grids lies in thorn scrub habitat in an interior valley of the park (“Quebrada de las Vacas,” 240 m elev.; see “Central grid complex” in Fig. 1 of Meserve et al., this volume). In late 2003, we installed 40 pitfall traps in two pairs of parallel lines running N-S along the axis of the valley. Each line has 10 traps 100 m apart, and paired traplines are 50 m apart; total area covered is 13.5 ha. Traps consist of plastic 1000 cc jars placed within PVC tubes (25 cm l x 110 mm d) buried flush with the ground. Funnels 110 mm d with 30 mm d holes cover the traps and limit escape. Traps are covered with boards when not in use. Although a few traps start or end inside of experimental grids, neither birds, lizards, or insectivorous small mammals were selectively excluded from these treatments. In March 2004 we initiated complementary sampling with 4 Malaise traps (BioQuip model DGT, 6’ h X 8’ w X 6’ deep with 8” X 4” acrylic collecting tubes and 70% ETOH; www.bioquip.com) arranged in a roughly diagonal line running SW to NE and spanning the pitfall lines. All traps are monitored for 4 consecutive days and nights during monthly small mammal trapping sessions. Pitfall traps are uncovered and captured terrestrial arthropods are collected each morning and evening; captured arthropods are euthanized with ethyl acetate, and placed in labeled flasks. Malaise traps are visited twice daily and captured arthropods euthanized and placed in labeled flasks. All specimens are transported to the laboratory for separation, identification, and counting using a

Nikon SMZ-10 stereoscope. Beginning May 2005 we dried specimens in a forest air Memmert furnace and weighed taxa to the nearest mg with a Sartorius B 310 P balance. Identification was facilitated with published guides and keys for Chilean arthropods (MacAlpine 1981, Borror et al. 1989, Saiz et al. 1989, Chiappa et al. 1990, Artigas 1994, Cepeda 1997, Peña and Ugarte 1997, Peña 2001).

In analyzing the results, we have concentrated on family-level classifications although some arthropods were identified to genus and/or species and some of these became exceptionally abundant during some years (e.g., *Gyriosomus* spp., *Nycterinus* spp., Tenebrionidae in pitfall traps in 2008). To visualize temporal patterns in arthropod assemblage structure (both seasonal and interannual) and to test for differences across seasons, we employed non-metric multidimensional scaling (NMS) in PC-Ord (v. 6.19 - McCune and Mefford 2011) on family-level data. NMS uses the rank order of inter-group distances and not the variables themselves (James and McCulloch 1990), and differs from most ordinations in that sequential axes do not necessarily explain monotonically declining proportions of variance. We used Sorenson's distance metric and applied Varimax rotation to the resulting ordination. NMS operates by iteratively seeking the best positions of n entities (e.g., sites, time periods, etc.) on k dimensions (e.g., ordination axes) such that the stress of this k -dimensional relationship is minimized (Prentice 1977; McCune et al. 2002). Stress is a metric that reflects departure from monotonicity in a graph of inter-sample distances in ordination space versus that in original multivariate space (for details, see McCune et al. 2002).

Within ordination space we applied multi-response permutation procedures (MRPP) in PC-Ord to test the hypothesis that arthropod community composition was similar in different seasons. We defined four seasons as Summer (December – February), Autumn (March – May),

Winter (June – August), and Spring (September – November). MRPP is a nonparametric procedure and as such has limited assumptions concerning the distribution of data (McCune et al. 2002). MRPP applies a test statistic (T) to a weighted mean within-group distance (δ , calculated with Sørensen's distance metric), and provides an effect size ($A = 1 - (\delta_{obs}/\delta_{exp})$, where δ_{obs} is the observed value of this metric, and δ_{exp} is the mean δ calculated over all possible partitions of the data). The test statistic describes variation within groups relative to random expectation; in our case a value of $A = 1$ indicates that arthropod assemblage composition is identical within groups (e.g., seasons), and as the composition of groups differs the value of A declines; if heterogeneity within groups equals that between groups then $A = 0$ (for further detail see McCune et al. 2002). For analyses using Malaise trap results we used data for 123 arthropod taxa over 44 seasons, and for pitfall trap results we used 99 taxa over 46 seasons (see Table 1).

Finally, we applied indicator species analysis (ISA) to evaluate which, if any, higher arthropod groups were good indicators of seasonal assemblage composition. Good indicator species occur predictably in a given grouping (Dufrêne and Legendre 1997), which here refers to taxa that are found in only one season at our study site. ISA determines an “indicator value” of a species as $IV_{kj} = 100(RA_{kj} * RF_{kj})$ where RA_{kj} and RF_{kj} are the relative abundance and relative frequency of species i in season j (for analytic details see McCune et al. 2002). The significance of IV_{kj} is calculated with a Monte Carlo approach in which sample units are randomly reassigned and IV re-calculated; the proportion of such randomized IV values that are as large or larger than the observed IV value is the probability of such an observed value occurring by chance. We ran 1000 such iterations in PC-Ord (McCune and Mefford 2011).

3. Results

Over 11 years of monitoring we documented 5 classes, 26 orders, and 85 families of arthropods in pitfall traps, and 2 arthropod classes, 17 orders, and 111 families with Malaise traps (Table 1). Collections exhibit pronounced seasonality; terrestrial arthropods typically started to increase in early spring (August-September), peaking about November (Fig. 1A). Both numbers and biomass declined through summer and fall (December-April) reaching their minimum levels in May-June (Fig. 1A, 1C). Although volant arthropods showed similar periods of increase, there was more heterogeneity in the months in which they reached both maximum (September-December) and minimum (June-July) numbers and biomass (Fig. 1B, 1D).

Across years, abundance and biomass of arthropods in pitfall traps reached high levels in late 2004 (abundance only), 2006, 2008, and 2011 (Figs. 2A, 2C). This coincided roughly with periods of high abundance and biomass in volant collections (Figs. 2B, 2D). Three of these years (2004, 2006, and 2011) were above-average rainfall years, suggesting that peaks in terrestrial and volant arthropods occur with about a 2-4 month time lag after the winter rainfall period. However, increases in years without high rainfall (e.g., terrestrial and volant insects in 2008) suggest that their abundance does not always track rainfall closely; a similar situation exists for soil seed densities (e.g., Meserve et al. 2011).

Temporal variation in arthropod abundance and biomass is dominated by a few groups. For terrestrial captures, tenebrionid beetles account for fully 88.0%, 97.1%, and 96.9% of the total annual biomass in 2006, 2008, and 2011, respectively; this group, in turn, was dominated by two genera (*Gyriosomas*, *Nycterinus*). Some other noteworthy groups captured were scorpions and spiders. Among volant groups caught in Malaise traps, dipterans (primarily of the family Musidae made up 31.7%, 25.4%, and 62% of the biomass caught in 2006, 2008, and 2011,

respectively. Lepidopterans comprised another 26.0%, 24.3%, and 31.7% of the volant arthropod biomass in the same years, especially moths in the families Noctuidae and the generalist group microlepidoptera. Perhaps surprisingly, ants (Hymenoptera: Formicidae) made up a small proportion of terrestrial insects, and typical diurnal pollinators (Hymenoptera: Apidae) made up small proportions of volant insects captured.

The best NMDS ordination for both Malaise and pitfall trap data included two dimensions, and for all axes the final stress (Malaise, stress = 15.32 after 60 iterations, pitfall, stress = 14.23 after 99 iterations; both $P < 10^{-5}$) was significantly lower than that using randomized data (all $P \leq 0.001$). The resulting axes explained over three-quarters of the variance in the data (Malaise, 61.2% and 17.4%, respectively; pitfall, 48.9% and 26.9%, respectively). When taxon vectors in ordination space are filtered by those exceeding 2 SD in vector length (the gray dashed boxes in Figs. 3, 4) 19 groups appear to merit consideration. With Malaise trap data the first axis polarizes the Anthocoridae and the Andrenidae against an ecologically diverse group including the Culicidae, Apioceridae, and Mordellidae, and to a lesser extent the Dermestidae (Fig. 3). The second axis polarizes Andrenidae, Proctotrupoidea, and Scarabaeidae against Nemopteridae and to a lesser extent, the Dermestidae. The first axis using data from pitfall traps was polarized by millipedes vs. Tenebrionidae and Goemetridae, whereas on the second axis the Colletidae was polarized against the Nitulidae, Halictidae, Tipulidae, Histeridae, Mycetophylidae, and the Entomobryidae (Fig. 4).

Assemblages differed significantly across seasons (Malaise, $t = -21.09$, $P < 10^{-8}$, Fig. 5; pitfall, $t = -39.38$, $P < 10^{-8}$, Fig. 6) and each season was significantly different from all other seasons (Malaise, $T = -5.94$ to -19.18 , $A = 0.03$ to 0.08 , $P = 0.0007$ to 10^{-8} ; pitfall, $T = -11.00$ to -35.14 , $A = 0.05$ to 0.17 , all $P < 10^{-6}$). Indicator species analysis highlighted 66 taxa with

significant indicator values ($P < 0.05$) but most of these did not reflect strong associations; only 13 taxa (Malaise, 6 groups; pitfall, 7 groups) exhibited IV values in excess of 50 (e.g., a 50% likelihood that the given taxon is reliably indicative of a given season; Figs. 3, 4, Table 2). Combining both data sets, melyrids (excluding Dasytidae), tenebrioids, and tettogoniids were indicative of spring, anthicids, chironomids, formicids scorpions, and solifugids, of summer, dolichopodids, tachinids, and tipulids of autumn, and asilids, microlepidopterans, and scarabaeids of winter.

Finally, assemblage composition of volant arthropods has changed over the 11 years of sampling, as indicated in a left-to-right shift in ordination space (Fig. 5, bottom). Perhaps surprisingly, however, no such pattern is evident for terrestrial species (Fig. 6, bottom).

4. Discussion

To our knowledge, data reported here comprise the first long-term assessment of arthropod abundance and biomass for semiarid Chile. Most prior work has focused primarily on characterizing the fauna (e.g., Saiz et al. 1989, Rau et al. 1998, Cepeda 1997). Such efforts often are needed before ecologically insightful studies are possible. Here we show that arthropod abundance and biomass change dramatically across seasons and years in the Fray Jorge system, and that this is at least partially explained by rainfall. However, the observation of a large increase in both terrestrial and volant arthropods in 2008, a below-average rainfall year (96 mm) suggests that other factors may be important. For example, there was a significant increase in ephemeral plant cover in 2008 after a very dry rainfall year in 2007 (48 mm—see Fig. 3 in Meserve et al., this volume). Hence, the increase in both tenebrionid beetles and moths may have been triggered by the response of ephemeral plants to increased rainfall even though this

was below the long-term average rainfall for this site. These observations suggest a “storage effect” due to carryover of soil nutrients from a prior dry period when few ephemerals germinated, and may complement similar evidence for annual plants (Gutiérrez and Meserve 2003).

The linkages that may exist between arthropod populations and their food (foliage, seeds, other arthropods, etc.), and their consumers (e.g., insectivorous reptiles, birds, and small mammals) are poorly known at present, but with these preliminary data, we can begin to examine them. For example, tenebrionid beetles are primarily scavengers, whereas noctuid and microlepidoperan moths are primarily nectarivorous. The former exhibit well-documented increases during high rainfall years in the north-central semiarid zone (Peña 2001), whereas changes in the latter group are less well-known.

Ordination of these data further reveal seasonal patterns in familial associations. The distribution of families in ordination space is not readily interpreted in ecological terms. For example, volant species (Fig. 3) appear to polarize (on the first axis) the predatory Anthocoridae and to some extent spring bees (Andrenidae) against a diverse group including mosquitoes (Culicidae), tumbling flower beetles (Mordellidae), non-feeding flower-loving flies (Apioceridae), and detritivorous beetles (Dermestidae). Data from pitfall traps appears more difficult to interpret (Fig. 4); larvae of geometrid moths (e.g., “inchworms”) and darkling beetles (Tenebrionidae) are modestly polarized against millipedes. Whereas these ordinations appear poorly explained in ecological terms, they may illustrate temporal changes to the arthropod community that parallel similar changes observed for birds (Kelt et al. 2012, this volume), and this is more apparent for Malaise trap data than for pitfall trap data. In particular, the second NMS axis using Malaise trap results appears to highlight seasonal shifts in community

composition, with late spring and summer months (November through February) low on this axis, and winter months (June through August) located high on this axes (Fig. 5). The first NMS axis illustrates a long-term temporal trend, with data gradually shifting from the left side of the ordination (2004) to the far right side (2014) (Fig. 5). Whether this reflects lingering consequences of a prolonged dry period or a longer-term response to broader influences (anthropogenic changes to regional habitat, e.g., agricultural lands, or climate change) is not clear. Pitfall data also appear to show a diagonal shifting in ordination space, with summer in the upper right quadrat and winter in the lower left, but in contrast to data for volant there is no indication of a temporal shift over the 11 years of data (Fig. 6). These observations suggest that apparent changes in the volant arthropod fauna are only partially matched by the terrestrial arthropod fauna, and raise questions concerning the ecological interpretation of these results. Are terrestrial arthropods more resistant to extrinsic influences that may be altering the volant fauna, or do the results from Malaise traps suggest a gradually changing filter as terrestrial larvae metamorphose to volant adults? Further monitoring may help resolve these and other questions. Regardless, this comprises a call for additional research on this diverse and otherwise unstudied fauna.

Previously we have noted evidence for a biannual cycle in numbers of the insectivorous llaca or elegant mouse opossum (*Thylamys elegans*; Meserve et al. 1995, 2001). Given that results from pitfall traps suggest a similar biannual oscillation in terrestrial arthropod densities and biomass (Fig. 2A, 2C), it is tempting to speculate on a relationship between these two components. In addition, smaller insectivorous passerines may exhibit similar patterns. Finally, our site supports two larger insectivorous owls (the chuncho or austral pygmy-owl, *Glaucidium nanum*, and the pequén or burrowing owl, *Athene cunicularia*). Spiders, scorpions, and

tenebrionid beetles have been found in their pellets (unpubl. data). Other synergistic relationships may become evident as we integrate the arthropod data set with changes in components of the Fray Jorge system.

5. Acknowledgements: We are grateful to many sources of financial support for this project over 26 years including the U.S. National Science Foundation (most recently DEB-1456729 to DAK and PLM), FONDECYT Chile, MIDEPLAN ICM PO5-002, CONICYT PFB-23, the U.S. AID Program, Northern Illinois University, and the University of California, Davis. Many people too numerous to mention have contributed to the project. Steve Heydon (UC Davis Bohart Museum of Entomology) helped us to update the taxonomy of arthropods and provided insight to the natural history of key groups. Finally, we gratefully acknowledge the cooperation of the Corporación Nacional Forestal (CONAF) in Chile which has allowed us to transform the study area to a living laboratory.

6. References Cited

- Artigas, J. N. 1994. Entomologia economica: Insectos de interés agrícola, forestal, medico y veterinario. Ediciones Universidad de Concepción, Concepción, Chile.
- Borror, D. J., C. A. Triplehorn, and N. F. Johnson. 1989. Borror and Delong's introduction to the study of insects, 6th ed. Brooks and Cole, CENGAGE Learning, Independence, Kentucky.
- Cepeda, J. (ed.). 1997. Insectos de la alta montaña del Valle de Elqui. Ediciones de la Universidad de la Serena, La Serena. Chile.
- Chiappa, E., N. Rojas, G. I., and G.T. Toro. 1990. Clave para los géneros de abejas de Chile (Hymenoptera-Apoidea). Revista Chilena de Entomología 18:67-81.
- Dufrêne, M. and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345-366.
- Gutiérrez, J.R. and P.L. Meserve. 2003. El Niño effects on the soil seed bank dynamics in north-central Chile. Oecologia 134:511-517.
- James, F. C. and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's box? Annual Review of Ecology and Systematics 21:129-166.
- Kelt, D.A., A. Engilis, Jr., J. Monárdez, R. Walsh, P.L. Meserve, and J.R. Gutiérrez. 2012. Seasonal and multiannual patterns in avian assemblage structure and composition in northern Chilean thorn-scrub. Condor 113:30-43.
- Kelt, D. A., H. Cofre, C. Cornelius, A. Engilis, Jr., J. R Gutiérrez, P. A Marquet, R. Medel, P. L Meserve, V. Quirici, H. Samaniego, R. A Vasquez. This volume. The avifauna of Bosque Fray Jorge National Park and Chile's Norte Chico Journal of Arid Environments.
- McAlpine, J. F. 1981. Manual of Nearctic Diptera, Volume 1. Research Branch, Agriculture Canada, Ottawa, Canada.

- McCune, B., and M. J. Mefford. 2011. PC-ORD. Multivariate analysis of ecological data. Version 6.19. MjM Software, Gleneden Beach, Oregon.
- McCune, B., J. B. Grace, and D. L. Urban. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.
- Meserve, P. L., and 12 authors. 1995. Heterogeneous responses of small mammals to an El Niño Southern Oscillation in north-central semiarid Chile and the importance of ecological scale. *Journal of Mammalogy* 76:580-595.
- Meserve, P. L., J. R. Gutiérrez, J. A. Yunger, L. C. Contreras, and F. M. Jaksic. 1996. Role of biotic interactions in a small mammal assemblage in semiarid Chile. *Ecology* 77:133-148.
- Meserve, P. L., W. B. Milstead, J. R. Gutiérrez, and F. M. Jaksic. 1999. The interplay of biotic and abiotic factors in a semiarid Chilean mammal assemblage: results of a long-term experiment. *Oikos* 85:364-372.
- Meserve, P. L., W. B. Milstead, and J. R. Gutiérrez. 2001. Results of a food addition experiment in a north-central Chilean small mammal assemblage: evidence for the role of “bottom-up” factors. *Oikos* 94:548-556.
- Meserve, P.L., D. A. Kelt, M. A. Previtali, W. B. Milstead, and J. R. Gutiérrez. 2011. Global climate change and small mammal populations in north-central Chile. *Journal of Mammalogy* 92:1223-1235.
- Meserve, P. L., D. A. Kelt, J. R. Gutiérrez, A. Previtali, and W. B. Milstead. This volume. Biotic interactions and community composition in a semiarid thorn scrub community in Bosque Fray Jorge National Park, north-central Chile: a paradigm revisited. *Journal of Arid Environments*.

- Muñoz, M. 1985. Flores del Norte Chico. Dirección de Bibliotecas, Municipalidad de La Serena, La Serena, Chile.
- Muñoz, P. C., and E. Pisano. 1947. Estudio de la vegetación y flora de los Parques Nacionales de Fray Jorge y Talinay. *Agricultura Técnica* (Santiago, Chile) 2:71-190.
- Peña, L. E. 2001. Introducción al estudio de los insectos de Chile, 6th ed. Editorial Universitaria, Santiago, Chile.
- Peña, L. E., and A. J. Ugarte. 1997. Las Mariposas de Chile. Editorial Universitaria, Santiago, Chile.
- Prentice, I. C. 1977. Non-metric ordination methods in ecology. *Journal of Ecology* 65:85-94.
- Rau, J. R., C. Zuleta, A. Gantz, F. Saiz, A. Cortés, L. Yates, A. E. Spotorno, and E. Couvé. 1998. Biodiversidad de artrópodos y vertebrado terrestres del norte grande de Chile. *Revista Chilena de Historia Natural* 71:527-554.
- Saiz, F., J. Solervicens, and P. Ojeda. 1989. Coleópteros del Parque Nacional La Campana y Chile central. Ediciones Universitarias de Valparaíso, Universidad Católica de Chile, Valparaíso, Chile.

Table 1. List of arthropod classes, orders, and families collected in Malaise and pitfall traps in 2003-2014.

Class	Order	Family	Malaise	Pitfall
Arachnida	Acarina	Ixodidea		X
Arachnida	Acarina	Not identified		X
Arachnida	Araneae	Not identified	X	X
Arachnida	Pseudoscorpionida	Not identified	X	X
Arachnida	Scorpiones	Not identified		X
Arachnida	Solifugae	Not identified	X	X
Chilopoda	Centipedes	Not identified		X
Diplopoda	Millipedes	Not identified		X
Insecta	Coleoptera	Anobiidae	X	X
Insecta	Coleoptera	Anthicidae	X	X
Insecta	Coleoptera	Bostrichidae	X	X
Insecta	Coleoptera	Buprestidae		X
Insecta	Coleoptera	Carabidae	X	X
Insecta	Coleoptera	Cerambycidae	X	X
Insecta	Coleoptera	Chrysomelidae (excl. Bruchinae)	X	X
Insecta	Coleoptera	Chrysomelidae, Bruchinae	X	X
Insecta	Coleoptera	Cleridae	X	X
Insecta	Coleoptera	Coccinellidae	X	X
Insecta	Coleoptera	Curculionidae (excl. Scolytinae)	X	X
Insecta	Coleoptera	Curculionidae, Scolytinae	X	
Insecta	Coleoptera	Dermentidae	X	X
Insecta	Coleoptera	Elaterridae	X	X
Insecta	Coleoptera	Histeridae		X
Insecta	Coleoptera	Latridiidae		X
Insecta	Coleoptera	Melyridae (excl. Dasytinae)	X	X
Insecta	Coleoptera	Melyridae, Dasytinae	X	X
Insecta	Coleoptera	Mordellidae	X	X
Insecta	Coleoptera	Mycteridae	X	
Insecta	Coleoptera	Nitulidae		X
Insecta	Coleoptera	Oedemeridae	X	
Insecta	Coleoptera	Ptinidae	X	X
Insecta	Coleoptera	Scarabaeidae	X	X
Insecta	Coleoptera	Scydmaenidae		X
Insecta	Coleoptera	Staphilinidae	X	X
Insecta	Coleoptera	Tenebrionidae	X	X
Insecta	Coleoptera	Trogossitidae, Diontolobus	X	
Insecta	Coleoptera	Trogossitidae		X

Insecta	Coleoptera	Trogossitidae, Peltinae	X	X
Insecta	Diplura	Campodeidae		X
Insecta	Diptera	Acroceridae	X	X
Insecta	Diptera	Agromizyidae	X	X
Insecta	Diptera	Anisopodidae	X	
Insecta	Diptera	Anthomyiidae	X	
Insecta	Diptera	Apioceridae	X	
Insecta	Diptera	Asilidae	X	X
Insecta	Diptera	Bibionidae	X	X
Insecta	Diptera	Bombyllidae	X	X
Insecta	Diptera	Calliphoridae	X	
Insecta	Diptera	Cecidomyiidae	X	
Insecta	Diptera	Ceratopogonidae	X	X
Insecta	Diptera	Chironomidae	X	X
Insecta	Diptera	Chloropidae	X	
Insecta	Diptera	Culicidae	X	
Insecta	Diptera	Dolichopodidae	X	X
Insecta	Diptera	Drosophilidae	X	
Insecta	Diptera	Empididae	X	X
Insecta	Diptera	Ephydriidae	X	
Insecta	Diptera	Heleomyzidae	X	
Insecta	Diptera	Muscidae	X	X
Insecta	Diptera	Mycetophylidae	X	X
Insecta	Diptera	Mydidae	X	
Insecta	Diptera	Nemestrinidae	X	
Insecta	Diptera	Phoridae	X	X
Insecta	Diptera	Pipunculidae	X	
Insecta	Diptera	Psychodidae	X	
Insecta	Diptera	Sarcophagidae	X	
Insecta	Diptera	Sciaridae	X	X
Insecta	Diptera	Simuliidae	X	
Insecta	Diptera	Sphaeroceridae	X	
Insecta	Diptera	Stratiomyidae	X	X
Insecta	Diptera	Syrphidae	X	
Insecta	Diptera	Tabanidae	X	X
Insecta	Diptera	Tachinidae	X	X
Insecta	Diptera	Tephritidae	X	X
Insecta	Diptera	Therevidae	X	X
Insecta	Diptera	Tipulidae	X	X
Insecta	Diptera	Xylophagidae		X
Insecta	Entomobryomorpha	Entomobryidae	X	X
Insecta	Hemiptera	Anthocoridae	X	
Insecta	Hemiptera	Aphididae	X	X
Insecta	Hemiptera	Aphrophoridae		X

Insecta	Hemiptera	Berytidae		X
Insecta	Hemiptera	Cercopidae	X	X
Insecta	Hemiptera	Cicadellidae	X	X
Insecta	Hemiptera	Coccidae	X	
Insecta	Hemiptera	Dictyopharidae	X	
Insecta	Hemiptera	Fulgoridae	X	X
Insecta	Hemiptera	Lygaeidae	X	X
Insecta	Hemiptera	Miridae	X	X
Insecta	Hemiptera	Nabidae	X	X
Insecta	Hemiptera	Psyllidae	X	X
Insecta	Hemiptera	Rhopalidae	X	
Insecta	Hymenoptera	Andrenidae	X	
Insecta	Hymenoptera	Anthophoridae	X	
Insecta	Hymenoptera	Apidae	X	X
Insecta	Hymenoptera	Bethylidae	X	
Insecta	Hymenoptera	Braconidae	X	X
Insecta	Hymenoptera	Chysididae	X	
Insecta	Hymenoptera	Colletidae	X	X
Insecta	Hymenoptera	Formicidae	X	X
Insecta	Hymenoptera	Halictidae	X	X
Insecta	Hymenoptera	Ichneumonidae	X	
Insecta	Hymenoptera	Megachilidae	X	X
Insecta	Hymenoptera	Mutillidae	X	X
Insecta	Hymenoptera	Plumeriidae	X	X
Insecta	Hymenoptera	Pompilidae	X	X
Insecta	Hymenoptera	Sphecidae s.l.	X	X
Insecta	Hymenoptera	Superfam. Chalcidoidea	X	X
Insecta	Hymenoptera	Superfam. Proctotrupeoidea	X	
Insecta	Hymenoptera	Tenthredinidae	X	
Insecta	Hymenoptera	Thynnidae	X	X
Insecta	Hymenoptera	Vespidae	X	
Insecta	Isoptera	Not identified	X	
Insecta	Lepidoptera	Geometridae	X	X
Insecta	Lepidoptera	Hesperiidae	X	
Insecta	Lepidoptera	Lycaenidae	X	
Insecta	Lepidoptera	Microlepidoptera	X	X
Insecta	Lepidoptera	Noctuidae s.l.	X	X
Insecta	Lepidoptera	Nymphalidae	X	
Insecta	Lepidoptera	Pieridae	X	
Insecta	Lepidoptera	Pterophoridae	X	
Insecta	Lepidoptera	Pyralidae	X	X
Insecta	Lepidoptera	Saturniidae	X	
Insecta	Mantodea	Mantidae		X
Insecta	Microcoryphia	Machilidae		X

Insecta	Neuroptera	Chrysopidae	X	
Insecta	Neuroptera	Coniopterygidae	X	
Insecta	Neuroptera	Hemerobiidae	X	
Insecta	Neuroptera	Mantispidae	X	X
Insecta	Neuroptera	Myrmeleontidae	X	X
Insecta	Neuroptera	Nemopteridae	X	X
Insecta	Orthoptera	Acrididae	X	X
Insecta	Orthoptera	Gryllacrididae	X	
Insecta	Orthoptera	Gryllidae	X	X
Insecta	Orthoptera	Proscopiidae		X
Insecta	Orthoptera	Tettigoniidae	X	X
Insecta	Plecoptera	Not identified	X	
Insecta	Poduromorpha	Poduridae		X
Insecta	Psocodea	Not identified	X	X
Insecta	Siphonaptera	Not identified	X	X
Insecta	Symphyleona	Sminthuridae		X
Insecta	Thysanoptera	Thripidae	X	X
Insecta	Trichoptera	Not identified	X	
Insecta	Zygentoma	Lepismatidae		X
Malacostraca	Amphipida	Not identified		X
Malacostraca	Isopoda	Not identified		X

Table 2. Taxa exhibiting IV values in excess of 50% (e.g., a 50% likelihood that the given taxon is reliably indicative of a given season); seasons and significance values are shaded. See text for months corresponding to seasons.

	Class	Order	Family	Obs. IV	Mean (SD) IV	p	Spr	Sum	Aut	Wtr
Malaise	Insecta	Diptera	Chironomidae	53.2	16.6 (4.24)	0.000	0	53	7	1
Malaise	Insecta	Diptera	Tipulidae	50.9	9.3 (3.61)	0.000	0	0	51	0
Malaise	Insecta	Diptera	Dolichopodidae	60.3	20.7 (4.65)	0.000	3	5	60	2
Malaise	Insecta	Diptera	Tachinidae	52.2	31.9 (3.39)	0.000	14	21	52	13
Malaise	Insecta	Lepidoptera	microlepidoptera	53.9	33.8 (4.04)	0.000	11	4	30	54
Malaise	Insecta	Diptera	Asilidae	51.3	17.4 (4.02)	0.000	4	1	5	51
Pitfall	Insecta	Coleoptera	Scarabaeidae	60.8	17.6 (3.41)	0.000	2	0	12	61
Pitfall	Insecta	Coleoptera	Melyridae (excl. Dasytinae)	49.8	8.6 (3.32)	0.000	50	0	0	0
Pitfall	Insecta	Orthoptera	Tettigoniidae	49.8	14.9 (3.12)	0.000	50	10	0	1
Pitfall	Arachnida	Scorpiones	Not identified	51.8	25.1 (2.52)	0.000	21	52	19	1
Pitfall	Arachnida	Solifugae	Not identified	56.8	23.4 (2.89)	0.000	23	57	15	0
Pitfall	Insecta	Coleoptera	Anthicidae	56.9	17.4 (3.09)	0.000	19	57	2	0
Pitfall	Insecta	Hymenoptera	Formicidae	57.8	31.7 (3.8)	0.000	21	58	17	3
Pitfall	Insecta	Coleoptera	Tenebrionidae	52.3	42.9 (9.09)	0.153	52	44	2	1

Figure 1. Monthly means $\pm$ 1SE (vertical lines) of numbers of terrestrial (A) and volant (B) arthropods captured in pitfall and Malaise traps, respectively, and biomass (in g) of terrestrial (C) and volant (D) arthropods caught in pitfall traps and Malaise traps, respectively.

Figures 2. Variation in monthly numbers of terrestrial and volant arthropods caught in pitfall (A) and Malaise traps (B), respectively, and biomass of terrestrial (C) and volant (D) arthropods caught in pitfall traps and Malaise trap, respectively. Years with above-average rainfall are shaded (the rainfall year starts in May of a current year and ends in April of the following one).

Figure 3. Principal vectors from NMS ordination of major volant arthropod families captured at Fray Jorge with Malaise traps (2004-2014). “Species” refers to taxa (see Table 1).

Figure 4. . Principal vectors from NMS ordination of major terrestrial arthropod families captured at Fray Jorge with pitfall traps (2003-2014). “Species” refers to taxa (see Table 1).

Figure 5. Nonmetric multidimensional scaling ordination of volant arthropod data from Malaise traps in Fray Jorge (2004-2014), illustrating predictable seasonal variation in arthropod assemblages (top panel) and a gradual long-term shift in assemblage composition over the 11 years of data collection (bottom panel).

Figure 6. Nonmetric multidimensional scaling ordination of terrestrial arthropod data from pitfall traps in Fray Jorge (2003-2014), illustrating predictable seasonal variation in arthropod assemblages (top panel) but unlike volant species (Fig. 5) no evidence of longer temporal changes in assemblage composition (bottom panel).