

Differential Responses of Marsh Arthropods to Rainfall-Induced Habitat Loss

Alejandro D. Canepuccia^{1,2,*}, Armando Cicchino^{1,2}, Alicia Escalante^{1,2}, Andres Novaro^{2,3}, and Juan P. Isacch^{1,2}

¹Departamento de Biología (FCEyN), Universidad Nacional de Mar del Plata, CC 573 Correo Central, (B7600WAG) Mar del Plata, Argentina

²Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

³Wildlife Conservation Society USA, Centro de Ecología Aplicada del Neuquén, Neuquén, Argentina

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Alejandro D. Canepuccia, Armando Cicchino, Alicia Escalante, Andres Novaro, and Juan P. Isacch (2009) Differential responses of marsh arthropods to rainfall-induced habitat loss. *Zoological Studies* 48(2): 174-183. The rainfall regime of the Pampas region of Argentina has increased over its historical mean during the last several decades. In this paper we used the unusually rainy year of 2002 to explore possible effects on the abundances and diversity of terrestrial arthropods due to reductions in suitable coastal marsh habitats due to flooding in the eastern Pampas. We assessed 1) the effects of changes in monthly cumulative rainfall totals on habitat availability and diversity, 2) the impacts of changes in habitat availability and diversity on ground arthropods, particularly on beetles species, and 3) arthropod responses to changes in habitat availability according to their dispersal ability, and among beetles species, according to their habitat specialization and trophic group. The increase in rain reduced the areal extent of terrestrial habitats through flooding, and as a consequence, reduced habitat diversity. These changes at the landscape level influenced the abundances and diversity of arthropods (assessed by pitfall traps). The most affected species were those with poor dispersal capabilities, which may have been due to their weaker ability to expand their home range. The most affected among beetle species were those that are habitat specialists, which may have been due to shifts in the habitat to which they are adapted, and at higher trophic levels, an indirect effect, in terms of habitat loss, of a reduction in prey availability was added. Moreover, our results exemplify how large-scale processes like changes in rainfall due to global climate change can affect local ecological patterns, such as fluctuations in abundances and diversity of arthropods in wetlands. <http://zoolstud.sinica.edu.tw/Journals/48.2/174.pdf>

Key words: Arthropods, Beetles, Habitat loss, Rainfall change, Marsh.

Under the global climate change scenario, rainfall regimes have changed worldwide in recent decades (Karl and Trenberth 2003). Total annual rainfall, for example, has markedly increased in regions like Australia, New Zealand (Plummer et al. 1999), southern Brazil, and eastern Argentina (Collischonn et al. 2001, Berbery et al. 2006). Rainfall plays important roles in provoking population fluctuations and generating spatial synchrony of population dynamics (Lima et al.

2002, Sala 2006). Consequently, changes in rainfall regimes may affect species up to the entire ecosystem level by altering biotic interactions (e.g., Martin 2001, Duffy 2003). However, most of the currently available information comes from arid and semiarid ecosystems, where water availability strongly limits primary productivity (Jaksic 2001, Letnic et al. 2005, Holmgren et al. 2006). In such areas, productivity pulses occur in rainy periods, followed by bottom-up effects of climate which

*To whom correspondence and reprint requests should be addressed. Tel/Fax: 54-223-4753150. E-mail: acanepuc@mdp.edu.ar

occur with a lag through the food web (Ostfeld and Keesing 2000, Arim et al. 2007, Farias and Jaksic 2007).

Nevertheless, in ecosystems where plants do not frequently experience strong water deficit constraints (e.g., wetlands), increased rainfall can directly affect habitat biodiversity through flooding-induced loss of terrestrial habitats (Canepuccia et al. 2007 2008). The effects of habitat loss on biodiversity have long been recognized to result in species declines due to increased emigration and decreased survival (Didham et al. 1996, Harrison and Bruna 1999, Driscoll and Weir 2005). Species responses to habitat loss differ according to their life history traits (MacNally et al. 2000, Driscoll and Weir 2005). Dispersal ability (Thomas 2000), habitat specialization, and trophic level (Holt et al. 1999) are among the traits that can most strongly affect the responses of species to habitat loss. Global processes such as climate change (i.e., increments in rainfall) could affect more-specialized components of local communities (Canepuccia et al. 2008) and alter ecological patterns such as biodiversity and community composition. Information about species responses to global processes such as climate change (i.e., increments in rainfall) in different environmental contexts is needed to gain a more-comprehensive understanding of the ecological consequences of climatic change on biodiversity.

The Pampas region of central Argentina is characterized by a flat landscape where high precipitation levels frequently cause flooding and result in extensive loss of terrestrial habitats through flooding (Paruelo and Sala 1990, Canepuccia et al. 2007). This region has experienced the greatest recorded increase in annual precipitation during the last century (Berbery et al. 2006), and most native grasslands have simultaneously undergone replacement or modification by agriculture (Bilenca and Miñarro 2004). During the last 4 decades in east-central Argentina, average annual rainfall has been higher than the historic mean (Viglizzo et al. 1995, Berbery et al. 2006), with 10%-30% increases over the last 50 yr, and an associated increase in the occurrence of heavy rainy periods (Berbery et al. 2006, Canepuccia et al. 2008). Annual rainfall reached its maximum level during 2002 (2-fold higher than the annual historic mean, Canepuccia et al. 2007). This represents a natural experiment that can help us understand the effects of increased rainfall on biodiversity.

Lowlands surrounding coastal marshes are particularly vulnerable to changes in flood levels and currently contain many of the protected grasslands in the eastern Pampas (Paruelo and Sala 1990, Bilenca and Miñarro 2004). Comparisons of species responses among taxa or functional groups can highlight essential differences in their spatial dynamics and responses to habitat loss due to global climate change. We used the unusually rainy year of 2002 to explore possible effects of reductions in the amount of suitable habitats in a coastal marsh of the eastern Pampas on the abundances and diversity of terrestrial arthropods. We specifically assessed 1) the effects of changes in monthly cumulative rainfall totals on habitat availability and diversity, 2) the impacts of changes in habitat availability and diversity on ground arthropods, particularly on beetles species, and 3) arthropod responses to changes in habitat availability according to their dispersal ability, and among beetles species, according to their habitat specialization and trophic group.

MATERIALS AND METHODS

Study site

Our study was carried out in a wetland of the Mar Chiquita UNESCO MAB Reserve (37°40'S, 57°25'W, Argentina, Fig. 1), one of the southernmost coastal lagoons along the Atlantic coast of South America (Fasano et al. 1982, Iribarne 2001). It is a shallow lagoon (0.4-0.6 m in mean depth) affected by low-amplitude (< 1 m) tides, with a water surface of 46 km² and a tributary watershed of 10,000 km² (Fasano et al. 1982). The regional climate is characterized as sub-humid to humid mesothermic (León and Burkart 1998). The rainy season extends from Oct. to Mar. and the dry season from Apr. to Sept. (Reta et al. 2001). The area is a topographically variable wetland, where the southern cordgrass *Spartina densiflora* is the dominant species in low and middle marshes throughout the lagoon (Isacch et al. 2006). Where the land is elevated, southern cordgrass is replaced by salt marshes dominated by perennial glasswort *Sarcocornia perennis* (formerly known as *Salicornia ambigua*). High areas, adjacent to perennial glasswort grasslands are dominated by sharp rush *Juncus acutus* grasslands (Isacch et al. 2006). The highest zones, at 5 m above sea level, are dominated by habitats modified by intense

cattle ranching with short pastures comprised of *Stipa papposa*, *Sti. nesiana*, *Bromus* spp., *Platago tomentosa*, *P. australis*, *P. major*, *P. lanceolata*, *Melilotus officinalis*, and *Medicago minima* (Stutz 2001).

Changes in habitat diversity generated by rainfall

Rainfall data were obtained from the US Department of Commerce, National Oceanic and Atmospheric Administration (NOAA; National Environmental Satellite, Data, and Information Service Office, National Climatic Data Center <http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html>) for the Mar del Plata City station (37°56'S; 57°35'W), located 25 km south of our study site but with similar geographic characteristics. The total area occupied by different marsh habitats in non-flooded periods was estimated from a Landsat image of 6 Dec. 2000 (downloaded from the website of the Global Land Cover Facility: <http://glcfapp.umiacs.umd.edu:8080/esdi/index.jsp>). The remote sensing data were classified into 4 main habitat types (i.e., southern cordgrass, perennial glasswort, sharp rush grasslands, and

short pastures used for cattle grazing) using the software ERDAS 8.7 (2003 by Leica Geosystems GIS and Mapping LLC). A set of global-positioning system (GPS) points gathered in the field ($n = 270$) were used to generate the training sites and to assess the accuracy of the classification. For the classification procedure, we used a maximum likelihood probability algorithm (Richards 1986). We used an error matrix analysis to assess the accuracy of the classification procedure by the overall accuracy error (Congalton 1991). The number of reference test pixels used to assess the accuracy varied with the representatives of each class in the subset of the image (i.e., greater coverage required more pixels). The overall accuracy (i.e., the chance of being right) for the classification was 91.4%.

Rainfall regimes are known to have strong effects on landscape configuration because the study area is located on a low-lying coastal plain (Isla and Gaido 2001, Canepuccia et al. 2007). When rainfall increases, there is a quick change in water levels due to the excess rainwater that inundates the wetlands (Isla 1997, Canepuccia et al. 2007 2008). This process results in a positive relationship between rainfall and wetland water surface and a negative relationship between rainfall and the marsh habitat surface (Canepuccia et al. 2007). For each habitat, the percentage of the flooded area was estimated by direct observations in each field survey described below, by standing on elevated points to maximize observations. These percentages were weighted by the proportion of the total area covered by each habitat and summed to obtain the total percentage of marshes flooded. A simple linear regression (Zar 1999) was used to assess the relationships of monthly rainfall with the area (log-transformed to fit the assumptions of linearity and normality of the analyses, Zar 1999) of each habitat and habitat diversity. Habitat diversity was assessed using the Shannon diversity index ($H' = -\sum p_i \log p_i$, where p_i is the proportion contributed by the i th habitat area to the total landscape area). Tukey's tests after analysis of variance (ANOVA) were used to evaluate the null hypothesis of no differences in the regression coefficients among habitat areas and rainfall (Zar 1999).

Responses of arthropod abundances and diversity to habitat loss

The abundances of arthropods were assessed from spring 2001 to summer 2002 and

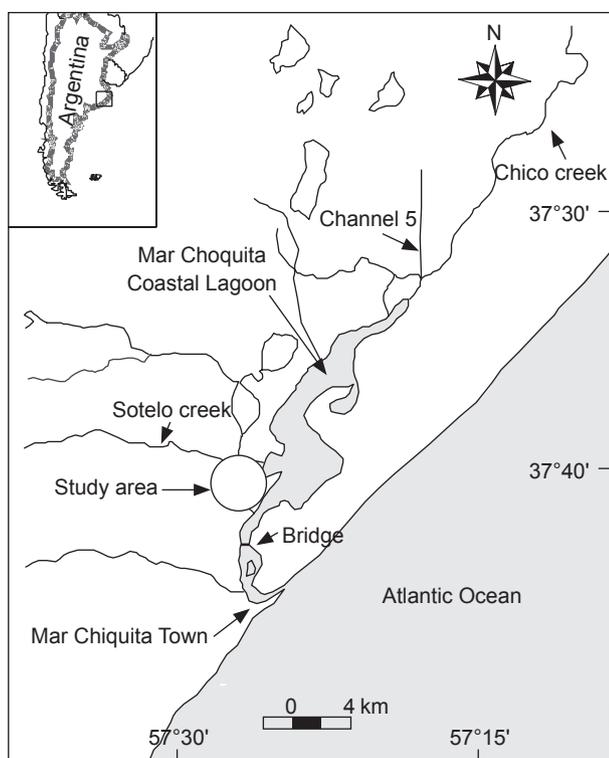


Fig. 1. Sampling site (circle) at Mar Choiquita coastal lagoon, Mar Choiquita Reserve along the Argentinean coast.

from winter 2003 to autumn 2004. Arthropod abundances were surveyed near Sotelo Creek (Fig. 1), using a transect of 5 pitfall traps located 10 m apart in the middle of each of the 4 main habitat types described above. Pitfall traps (12 × 15 cm, with eight 2 × 3 cm lateral holes drill in each one, 1 cm below the top) were buried to the lower edge of the drilled holes and covered with a plastic roof to prevent the entrance of vegetation and small mammals and to reduce the impact of rain. They were filled with a formalin-saturated NaCl solution and detergent as a tensioactive agent (Lemieux and Lindgren 1999). Transect locations in each habitat were the same during the entire study period. Each pitfall trap was emptied after 30 d, and arthropods were determined to the lowest taxonomic level possible and grouped according to taxonomic family. From the total arthropods captured in each habitat, we determined the richness (mean number of taxa by habitat) and relative abundance (mean abundance of individuals captured in each habitat).

The analyses were carried out at the family level for all arthropods captured and to species level for beetles. Due to a lack of normality, Dunn's test after the Kruskal-Wallis test (Zar 1999) was used to evaluate the null hypothesis of no differences in arthropod abundances among the months sampled. The most abundant groups of arthropods (Hymenoptera, Arachnida, Diptera Hemiptera, and Coleoptera) in the area were classified according to their relative dispersal abilities (i.e., Parker and Mac Nally 2002) as: 1) poor dispersal ability for walking arthropods (Hymenoptera and arachnids); 2) good dispersal ability for flying Diptera, and 3) intermediate dispersal capability for Hemiptera and beetles, which utilize both dispersal methods. Although this is a rough classification, we believe that it is suitable for analyzing the effects of the dispersal capability at the level of the arthropod community. In order to evaluate the beetles' responses to habitat loss according to trophic levels, the mean abundances of herbivorous, omnivorous, and predator beetles in each habitat were assessed. In the same way, we grouped beetles according to their habitat specialization, considering specialists to be those species that live in 1 or few habitats and generalists to be those species that inhabit a great variety of habitats (after Cicchino 2003).

The effects of flooding on arthropod abundances were tested by means of a simple linear regression (Zar 1999) of the abundances and diversity of different arthropod groups and

their dispersal ability (poor, intermediate, and good dispersal abilities) with the percentage of non-flooded habitats. Analyses were done using PopTools (vers. 2.6.9; Hood 2005). As data of arthropod abundances were used for multiple analyses, henceforth, the levels of significance for multiple tests were adjusted by the sequential Bonferroni method (Rice 1989). In the case of the most elevated habitats (grasslands modified into cattle grazing pastures) which were rarely flooded, we used a simple regression between arthropod abundances described above and total habitat loss from all habitats in the study area. The independent variables were appropriately transformed to comply with the methodological assumptions (Neter et al. 1991). The same methodology was used to analyze the responses of beetles according to their trophic groups (predators, omnivores, and herbivores), and their habitat specificity (specialists and generalists) with habitat area, and habitat diversity. Statistical significance was assessed using *F*-tests for partial correlation coefficients (Sokal and Rohlf 1995). To avoid the complications of possible effects of seasonality on arthropod abundances (see Cicchino 2003), the cold months in the study period (July, Aug., and Sept.) were excluded from the analysis, since arthropod abundances naturally decrease during this period.

RESULTS

Changes in habitat area generated by rainfall

The linear model showed negative relationships between monthly rainfall and areas of the 3 habitats (sharp rush: $R^2 = 0.88$, $F = 104.9$, $p < 0.05$, $n = 16$; perennial glasswort: $R^2 = 0.58$, $F = 19.6$, $p < 0.05$, $n = 16$; and cordgrass: $R^2 = 0.74$, $F = 40.1$, $p < 0.05$, $n = 16$). However, monthly rainfall had no effect on the area of short-pasture habitat ($R^2 = 0.19$, $p = 0.1$, $n = 16$). A comparison of the regression coefficients showed that this effect was greater on topographically lower habitats (cordgrass $b = -0.004$, perennial glasswort $b = -0.002$, and sharp rush $b = -0.0005$; $F = 37.98$, $p < 0.05$; *d.f.* = 3; Tukey's test, $p < 0.05$ for all comparisons). A negative relationship was also observed between habitat diversity and rainfall ($R^2 = 0.88$, $F = 100.9$, $p < 0.05$, $n = 16$).

Responses of arthropod abundances and diversity to habitat loss

We observed a total of 14,700 arthropods, the predominant groups being ants (Formicidae: 36%), spiders (Arachnida: 19%), muscoids (Diptera 16%), and beetles (Carabidae: 7%). The regression analysis showed a positive relationship between the total habitat area and the mean total arthropod number ($R^2 = 0.60$, $F = 16.75$, $p < 0.01$, $n = 12$, Fig. 2). This positive relationship was also detected for the perennial glasswort ($R^2 = 0.89$, $F = 79.9$, $p < 0.01$, $n = 12$, Fig. 3a) and cordgrass habitats ($R^2 = 0.86$, $F = 331.7$, $p < 0.01$, $n = 12$, Fig. 3b), but not for the sharp rush ($R^2 = 0.33$, $F = 4.44$, $p = 0.06$, $n = 12$) or short pasture habitats ($R^2 = 0.02$, $F = 1.76$, $p = 0.21$, $n = 12$). A similar response was observed between habitat area and richness of arthropod families (cordgrass: $R^2 = 0.86$, $F = 68.01$, $p < 0.01$, $n = 12$; perennial glasswort: $R^2 = 0.87$, $F = 68.9$, $p < 0.01$, $n = 12$; sharp rush: $R^2 = 0.02$, $F = 0.19$, $p = 0.67$, $n = 12$; and short pastures: $R^2 = 0.09$, $F = 1.01$, $p = 0.34$, $n = 12$). There were also differences among the abundances of arthropods for the same month during the sampling period. For example, the months of Dec. 2001, and Mar. and May 2002 (rainy years), showed lower arthropod abundances than the same months of 2003 and 2004 (dry years; Kruskal-Wallis test, $H = 148.4$, $d.f. = 15$, $p < 0.01$, Fig. 2).

All dispersive groups (poor, intermediate, and good dispersers) increased in abundance in

relation to the area of cordgrass and perennial glasswort habitats, but the slope was greater for poorly dispersing arthropods than for intermediate and good dispersers ($F = 16.10$ in perennial glasswort; $F = 8.1$ in cordgrass; $p < 0.05$, $d.f. = 2$; Tukey's test, $p < 0.05$). There was a negative relationship between habitat area and the abundance of arthropods with good dispersal ability in the sharp rush habitat ($R^2 = 0.50$, $F = 7.58$, $p < 0.01$, $n = 12$), while in short pastures, there was no relationship between any disperser and total habitat area.

Ground beetle species (Carabidae) distributions differed among habitats. *Argutoridius chilensis* (Dejean 1828), *Brachinus marginellus* (Dejean 1826), and *Feroniola montevideana* (Straneo 1952) showed a positive association with the cordgrass habitat. *Argutoridius bonariensis* (Dejean 1831), *Anisostichus posticus* (Dejean 1829), and *Loxandrus planicollis* (Straneo 1991) were exclusively associated with short pasture habitats. *Aspidoglossa intermedia* (Dejean 1831), *Bra. pallipes* (Dejean 1826), *Bra. intermedius* (Brullé 1838), *Nothonepha palidegutula* (Jensen-Haarup 1910), and *Scarites anthracinus* (Dejean 1831) showed no association with any habitat (see Appendices in Supplemental material).

In the lowest habitats, beetle abundances decreased in response to decreases in habitat areas (perennial glasswort: $R^2 = 0.93$, $F = 142.9$, $p < 0.01$, $n = 12$, Fig. 3c; cordgrass: $R^2 = 0.77$, $F = 33.5$, $p < 0.01$, $n = 12$, Fig. 3d), but there was no significant relationship for sharp rush ($R^2 = 0.11$,

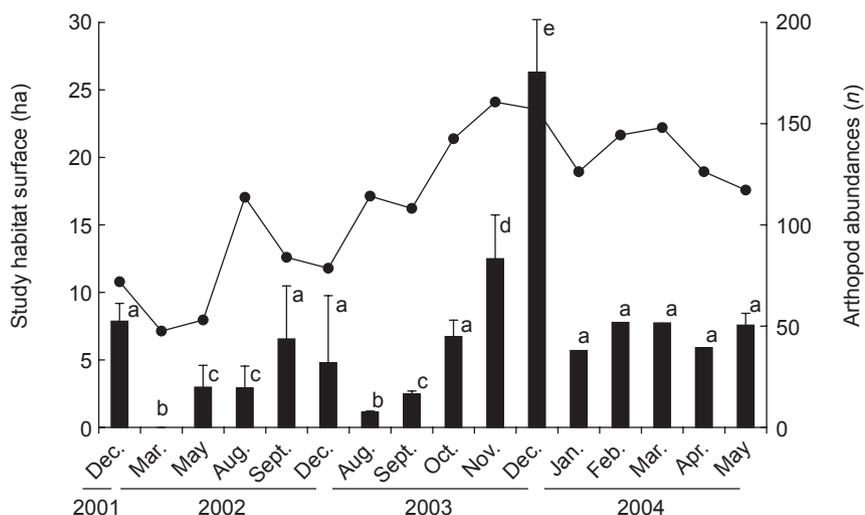


Fig. 2. Monthly mean of arthropods (bars) and total habitat area (points connected by lines), from Dec. 2001 to May 2004. Letters indicate differences among the average of arthropod numbers by Dunn's test, after the Kruskal-Wallis test, $H = 148.4$, $d.f. = 15$, $p < 0.001$.

$F = 1.41$, $p = 0.26$, $n = 12$) or short pasture ($R^2 = 0.04$, $F = 1.76$, $p = 0.21$, $n = 12$) areas. Similar results were obtained for beetle richness (cordgrass, $R^2 = 0.82$, $F = 355.37$, $p < 0.01$, $n = 12$, perennial glasswort, $R^2 = 0.93$, $F = 125.2$, $p < 0.01$, $n = 12$; sharp rush: $R^2 < 0.01$, $F = 0.03$, $p = 0.08$, $n = 12$; and short pastures: $R^2 = 0.28$, $F = 3.81$, $p = 0.08$, $n = 12$).

When habitat specialization of beetle species was considered, both groups (generalists and specialists) showed decreases in their abundances in response to a reduction in the area of the lowest habitat (cordgrass, generalists: $R^2 = 0.62$, $F = 28.6$, $p < 0.01$, $n = 12$; specialists: $R^2 = 0.69$, $F = 24.1$, $p < 0.01$, $n = 12$). This effect was more marked for specialists than generalists ($t = 13.60$, $p < 0.05$, $d.f. = 1$). This pattern was also found for specialists in the perennial glasswort habitat ($R^2 = 0.80$, $F = 41.1$, $p < 0.01$, $n = 12$). There was no relationship between habitat area and abundance of generalist beetles in short pastures ($R^2 = 0.54$, $F = 0.22$, $p = 0.02$, $n = 12$) after applying the Bonferroni sequential correction ($p < 0.01$, Rice 1989). There was no relationship of the abundances of generalist and specialist beetles

with the area of the sharp rush habitat (generalists: $R^2 = 0.04$, $F = 0.40$, $p = 0.54$, $n = 12$; specialists: $R^2 = 0.001$, $F < 0.05$, $p = 0.97$, $n = 12$).

The abundances of both predator and omnivorous beetle species decreased in response to a reduction in the area of the lowest cordgrass habitat (predators: $R^2 = 0.75$, $F = 30.2$, $p < 0.01$, $n = 12$; omnivores: $R^2 = 0.59$, $F = 14.4$, $p < 0.01$, $n = 12$). This response was greater for predator species ($F = 2.88$ cordgrass; $p < 0.05$; $d.f. = 2$; Tukey's test $p < 0.05$). There was a positive relationship between habitat area and predator beetles in the perennial glasswort habitat ($R^2 = 0.93$, $F = 120.9$, $p < 0.01$, $n = 12$). There was no relationship between habitat area and the abundance of predator beetles in short pastures ($R^2 = 0.51$, $F = 8.20$, $p = 0.02$, $n = 12$) after applying the Bonferroni sequential correction ($p < 0.01$, Rice 1989) or in the sharp rush habitat ($R^2 = 0.01$, $F = 0.14$, $p = 0.72$, $n = 12$). Abundances of omnivorous and herbivorous beetles in the cordgrass and perennial glasswort habitats were too low to make inferences from the data.

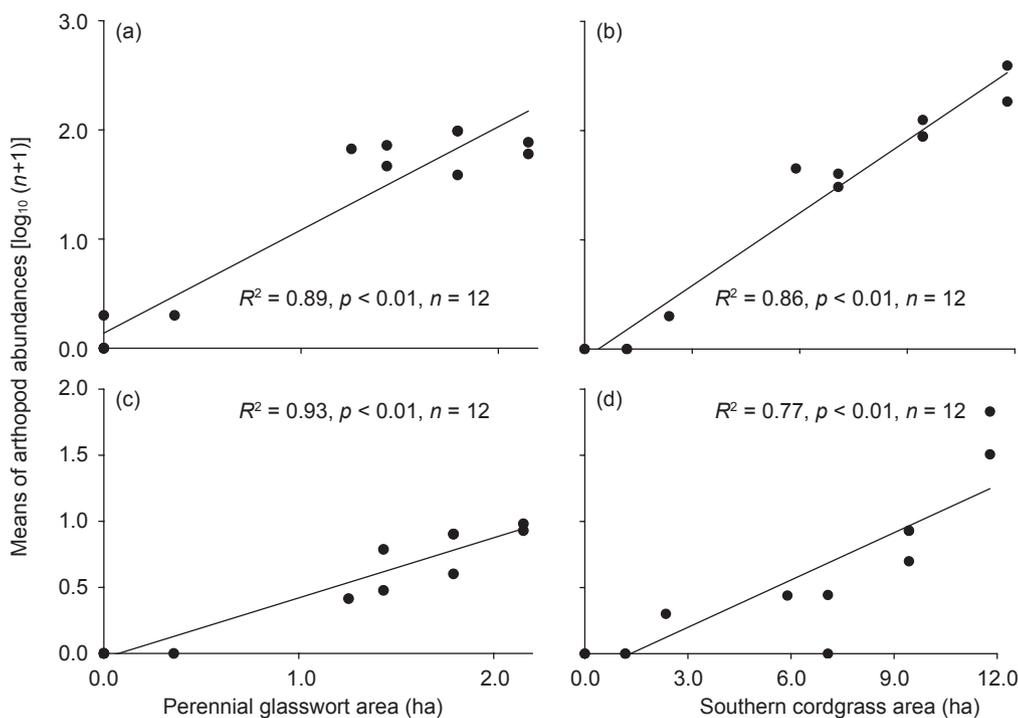


Fig. 3. Relationships between habitat areas, and means of arthropod abundances determined by pitfall traps placed in (a) perennial glasswort and (b) cordgrass, and relationships between habitat areas and means of beetle abundances determined by pitfall traps placed in (c) perennial glasswort and (d) cordgrass, from Dec. 2001 to May 2004.

DISCUSSION

As a result of global climate change, rainfall regimes have changed in many regions (e.g., Collischonn et al. 2001, Plummer et al. 1999, Berbery et al. 2006). In the eastern Pampas, rainfall increased above its historical mean over the last century (Berbery et al. 2006, Canepuccia et al. 2007). Given that our study area is in a low-lying coastal plain, the rainfall increase translates into changes in water levels and flooding (Isla and Gaido 2001, Canepuccia et al. 2007). This flooding due to additional rainfall could diminish the areal extent of terrestrial habitats and habitat diversity on a local scale, with strong consequences for the native fauna (Canepuccia et al. 2008). This could result in reduced species abundances and diversity. Among arthropods, the most seriously affected groups were those with a poor dispersal capability, and among beetle species, those that are habitat specialists and belong to higher trophic levels.

In our study, arthropod abundances decreased in response to habitat loss by flooding. Nevertheless, the responses differed among ecological groups and were determined by species attributes. Among them, the dispersal capability of animals constitutes one of the ecological attributes most reported in relation to the ability of species to respond to habitat loss (mammals and birds, Wright 1981; reptiles, Driscoll 2004; beetles, De Vries et al. 1996, Davies et al. 2000, Driscoll and Weir 2005). In our study, the dispersal ability was a strong predictor of abundance declines due to habitat loss. The abundant poor dispersers (ants and spiders) in the study area were more affected by habitat loss than were highly mobile species. This may have been due to the highly mobile species being able to expand their home ranges (Andr n 1994) and acquire resources in other areas (landscape compensation, Dunning et al. 1992).

The impacts of climate change on biodiversity will probably be dwarfed by interactions with other human impacts. For example, when the low-lying habitats (cordgrass and perennial glasswort) were reduced by flooding, arthropods could only disperse toward higher habitats, such as sharp rush (non-disturbed vegetation), or unflooded habitat such as short pastures (more-disturbed vegetation due to intense livestock grazing). The abundances of good dispersers only increased in the sharp rush habitat but not in short pastures. This may have been due to the

condition of the 'remaining habitat', which may have impacted species abundances, especially loss of vegetation, refuge, and food in short pastures due to livestock grazing (Brown 2001, Driscoll 2004). Shifts in habitat choice by species can result in a species moving out of habitats to which it is adapted into new habitats where it may incur substantial biotic costs (e.g., Martin 2001). The choice among habitats seems to be related not only to the capabilities of dispersers, but also to the quality of the remaining habitats (Driscoll 2004). In this study, both generalist and specialist beetles were affected by habitat reduction through flooding. This response was stronger for habitat specialists like *Bra. marginellus* (which inhabits wet oligohaline soils), *Pachymorphus* sp. nov. b (which inhabits halophile grasslands, Cicchino 2003), and *Pelmatellus* sp. b, (which inhabits sharp rushes). Generalist species seemed to be less affected by habitat loss (i.e., *Pachymorphus chalceus*, Dejean 1826, *Pac. striatulus*, Fabricius 1792, and *Argutoridius bonariensis*), since they may use the remaining habitats as a continuum (Tscharnkte et al. 2002) and colonize the low cover of highly disturbed short pastures. Meanwhile, specialist species seemed to be more dependent on specific natural habitats.

Finally, species at the highest trophic level are more susceptible to extinction in response to habitat loss (Holt et al. 1999, Komonen et al. 2000), even though empirical evidence is contradictory (Mikkelsen 1993, Kruess and Tscharnkte 1994). Several surveys of vertebrates and plants showed no tendency for species of 1 trophic group to go extinct more often than any other (Mikkelsen 1993). In our study, predators were more vulnerable to local extinction than those species from lower trophic levels. Predator beetles were most affected in habitats with greater loss of area due to flooding. The higher effect on predator species may have been due to the fact that they were affected by habitat loss through flooding, and also indirectly by the effects of flooding on prey abundances. Among them, *Aspidoglossa intermedia*, *Bra. pallipes*, and *Incagonum lineatopunctatum* (Dejean 1831) diminished in relation to habitat loss. Omnivorous beetles showed no effects of habitat loss, and the lower abundances of herbivorous beetles did not allow evaluation of any effect on this group.

In summary, climate change is likely to have considerable ecosystem-level impacts (Sala 2006). Factors such as changes in humidity, indirect effects such as plant quality changes, or changes

in direct and indirect interactions among species might also be involved in arthropod responses to rainfall increases found in our study. However, our results suggest that in wetlands, an increase in rainfall can produce a quick reduction in the availability of terrestrial habitats, and influence biodiversity. Two possible responses by wetland communities to increased rainfall can be predicted: direct changes in their abundances and diversity, and indirect changes in their community structure (vertical relationships). Nevertheless, not all species were affected in the same way. Those arthropods that have poor dispersal capabilities and those beetle species which are habitat specialists and in higher trophic levels were more affected. As these traits are not necessarily correlated, the search for a single ecological attribute of a species as an indicator of habitat loss, may be of little predictive value (Davies et al. 2000, Driscoll and Weir 2005). Our results constitute an example of how global climate change (i.e., increments in rainfall) can affect ecological patterns, (abundances and diversity of arthropod communities on wetlands). Overall, this study exemplifies how the interaction of 2 major components of global change (i.e., changes in land use and climate; Karl and Trenberth 2003) acting at a regional scale, as predicted by some theoretical models (Ryall and Fahrig 2006), can severely impact more-specialized components of local communities.

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APPENDIX. The presence of beetle species in each studied habitat in Mar Chiquita, Argentina. The food habits and the degree of habitat specialization of each species are indicated to the right of Carabid species (in parentheses): o, omnivore; h, herbivore; p, predator; -, unknown; g, habitat generalist; and s, habitat specialist

Beetle/Habitat	Short pastures	Sharp rush	Perennial glasswort	Cordgrass
<i>Anisostichus posticus</i> , (Dejean, 1829), (h, g)	x			
<i>Argutoridius bonariensis</i> , (Dejean, 1831), (o, g)	x	x		
<i>A. chilensis ardens</i> , (Dejean, 1828), (o, s)				x
<i>Argutoridius</i> sp. nov. a (o, g)	x			
<i>Aspidoglossa intermedia</i> , (Dejean, 1831), (p, g)		x	x	x
<i>Brachinus</i> sp. N 1, (p, g)		x	x	x
<i>Bra. immarginatus</i> (Brullé, 1838), (p, s)			x	
<i>Bra. intermedius</i> , (Brullé, 1838), (p, g)		x	x	x
<i>Bra. marginellus</i> , (Dejean, 1826), (-, s)				x
<i>Bra. pallipes</i> , (Dejean, 1826), (p, s)	x	x	x	x
<i>Bra. vicinus</i> , (Dejean, 1826), (p, s)				x
<i>Bradycellus</i> sp. nov. a (h, g)	x			
<i>Bradycellus</i> sp. nov. b (h, s)		x		
<i>Bradycellus</i> sp. nov. c (-, s)		x		
<i>Brd. viduus</i> , (Dejean, 1829), (h, g)	x			
<i>Calosoma retusum</i> , (Fabricius, 1775), (-, g)	x			
<i>Carbonellia platensis</i> , (Berg, 1883), (p, g)	x			
<i>Ega montevidensis</i> , (Tremoleras, 1917), (p, s)			x	
<i>Feroniola montevideana</i> , (Straneo, 1952), (p, s)				x
<i>Galerita collaris</i> , (Dejean, 1826), (p, g)			x	
<i>G. lacordairei</i> , (Dejean, 1826), (p, g)		x		
<i>Incagonum brasiliense</i> , (Dejean, 1828), (p, g)		x		x
<i>I. discosulcatum</i> , (Dejean, 1828), (p, s)			x	
<i>I. lineatopunctatum</i> , (Dejean, 1831), (p, g)	x	x		x
<i>I. fuscoaeneum</i> , (Gemming and Harold, 1868), (p, s)			x	x
<i>Incagonun</i> sp. nov. a (p, s)			x	x
<i>Incagonun</i> sp. nov. b (p, s)		x		
<i>Loxandrus planicollis</i> , (Straneo, 1991), (p, g)	x			
<i>Metius circumfusus</i> , (Germar, 1824), (o, g)		x	x	x
<i>Notaphiellus solieri</i> , (Germain, 1906), (-, g)	x			x
<i>Notaphus brullei</i> , (Gemm and Harold, 1868), (p, s)				x
<i>N. fischeri</i> , (Solier, 1849), (p, g)	x	x		
<i>N. laticollis</i> , (Brullé, 1838), (p, g)	x			
<i>Nothonepha pallideguttula</i> , (Jensen-Haarup, 1910), (p, g)	x	x	x	x
<i>Notiobia cupripennis</i> , (Germar, 1824), (o, g)	x			
<i>Paraclivina breviscula</i> , (Putzeys, 1866), (o, g)	x	x		x
<i>Paranortes cordicollis</i> , (Dejean, 1828), (p, g)	x	x	x	
<i>Paratachys bonariensis</i> , (Steinheil, 1869), (p, s)				x
<i>Pelmatellus</i> sp. nov. b (h, s)		x		
<i>Polpochila flavipes</i> , (Dejean, 1831), (h, s)		x		x
<i>Scarites anthracinus</i> , (Dejean, 1831), (p, g)		x	x	x
<i>Selenophorus anceps</i> , (Putzeys, 1878), (o, g)	x	x		
<i>S. punctulatus</i> , (Dejean, 1826), (o, g)	x			
<i>Semiclivina parvula</i> , (Putzeys, 1866), (p, s)		x		
<i>S. platensis</i> , (Putzeys, 1866), (p, s)				x
<i>Tachys argentinicus</i> (p, s)		x		
<i>Tetragonoderus aeneus</i> , (Dejean, 1831), (p, s)	x			
<i>Thalpius brunneus</i> , (Liebke, 1929), (-, s)		x		
<i>Pachymorphus chalceus</i> , (Dejean, 1826), (o, g)		x	x	x
<i>Pachymorphus</i> sp. nov. a (o, s)		x	x	x
<i>Pachymorphus</i> sp. nov. b (o, s)				x
<i>Pac. striatulus</i> , (Fabricius, 1792), (o, g)	x		x	