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The importance of biogeographical history and extant environmental conditions as drivers of freshwater decapod distribution in southern South America

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SUMMARY

1. A topical issue in macroecology is whether the distribution of organisms is related to biogeographical history or current environmental conditions. Distributions of freshwater decapods in southern South America have been mainly attributed to historical factors, such as geoclimatic events, marine ingressions, tectonic uplifts and glaciations. Here, we test the hypothesis that current distributions are strongly influenced by local environmental conditions.
2. Generalised linear models were used to quantify the importance of altitude, stability of the waterbody, annual temperature range (ATR), pH and conductivity on the distribution of five freshwater decapod families in Argentina (Sergestidae, Palaemonidae, Parastacidae, Aeglidae and Trichodactylidae), while accounting for effects of latitude and longitude.
3. Decapod occurrence was strongly associated with interacting spatial and environmental factors. Latitudinal and/or longitudinal gradients were important predictors for the occurrence of *Acetes paraguayensis* (Sergestidae), Palaemonidae, Aeglidae and Trichodactylidae. However, the longitudinal pattern for Palaemonidae was reversed, increasing from east to west, when environmental variables were included in the analyses, whereas for Trichodactylidae, the longitudinal pattern was sufficiently explained by inclusion of local environmental variables.
4. Altitude, water stability and ATR were important predictors of all families, while Palaemonidae, Parastacidae and Trichodactylidae were significantly associated with pH and Palaemonidae and Aeglidae with conductivity. Interactions terms were often significant, especially with latitude.
5. Our results show that the macrodistribution of freshwater decapods is not solely a result of historical processes, a finding that disagrees with current understandings. Significant relationships between decapod occurrence and environmental variables indicates limited plasticity and strong adaptation to local habitats, highlighting the importance of including environmental factors in studies of crustacean biogeography and macroecology.

Keywords: *Acetes paraguayensis*, Aeglidae, biogeography, environmental features, Parastacidae

Introduction

There is an ongoing debate as to how biogeographical histories of continents determine distributional patterns of biota and their ranges (Potter, 1997; Lovejoy, Bermingham & Martin, 1998). In South America, decapod species distributions have been generally assumed to be driven by historical factors. Several descriptive studies have considered the distribution of freshwater decapods to be exclusively delimited by spatial traits

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related to dispersal corridors (Collins, Williner & Giri, 2002; Collins, Giri & Williner, 2009), modifications in the land topography and the formation of continental aquatic environments caused by marine ingressions that imposed physical barriers to dispersion (Feldmann, 1984; Breinholt, Pérez-Losada & Crandall, 2009). In this regard, Ringuelet (1956) posited the geographical distribution of some Argentinean crustaceans, and Crandall & Buhay (2008) the global distribution of crayfish in fresh water, to be exclusively related to hydrographic webs developed historically and/or physiographic and weather changes in the past. In addition, Oyanedel *et al.* (2011) and Pérez-Losada *et al.* (2004) attributed current geographical distributional patterns of aeglids to vicariance and migration processes that took place during drainage extension/coalescence, to orogenic phases that occurred during the formation of the Andean chain and to the existence of multiple island glacial refuges. Meanwhile, Giri & Collins (2014) described clinal patterns of *Aegla uruguayana* (Schmitt, 1942) (Aeglidae) revealing their isolation and/or connection to different basins and sub-basins associated with genetic drift in response to geoclimatic events that occurred where they evolved. Moreover, Yeo *et al.* (2008) attributed the distribution of South American trichodactylid crabs to dispersal patterns and vicariance processes produced by phases of tectonic uplift. It is noteworthy that these authors mentioned that distribution may also be influenced by abiotic (e.g. climate, hydrology, topography and altitude) and biotic factors (e.g. vegetation and inter-specific competition), but no evidence was provided supporting this conjecture. In contrast to the history-driven distributional pattern hypothesis, Murphy & Austin (2004) conducted phylogenetic analyses of *Macrobrachium* prawns, suggesting a complicated history of long distance dispersal, even across biogeographical barriers imposed by the tectonic collisions. In addition, Miserendino (2001) documented the local environmental variables that affected the distributions of *Aegla neuquensis* (Schmitt, 1942) within Andean Patagonian rivers and streams.

Landscape characteristics of southern South America vary greatly over relatively short distances, making this an ideal area to study the interplay between biogeography and local environmental conditions on distribution patterns. For example, the range of altitudes is almost 7000 m (the peak of Aconcagua Mountain is 6962 m a.s.l. in the Andean region), whereas variation in air temperature is almost 34 °C and latitudes span 30° from the Tropic of Capricorn. The extent of endorheic and exorheic systems of southern South America is vast in the Littoral region (e.g. the Parana-Plata drainage basin is the second largest South American fluvial system). Waterbodies present diverse characteristics, depending on their geographical locations and geological origins (Fig. 1a–c). At north-eastern sites (Littoral region), for example, the prevailing aquatic systems are large rivers with low variability in their main channel flow (e.g. Paraguay, Paraná and Uruguay rivers) (Williner, Giri & Collins, 2010). In these environments, oscillations in hydrometric levels are associated with variability in precipitation and the degree of connections with the tributary streams, but the main channels never dry out. At southern sites (Patagonia region), river flow is lower and hydrometric levels are influenced by thawing. The freshwater environments also vary markedly in mineral content and composition, mainly due to the source-rock composition. Other sources of variation in environmental conditions of the waterbodies include prevailing climate, diversity of vegetation and anthropogenic effects.

Decapods are functionally important invertebrates due to their role in trophic webs (e.g. some species have an ontogenetic shift from herbivore–detritivore to omnivore) (Burres, Gangloff & Siefferman, 2013), their high population densities and their nutritional value (Williner, Giri & Collins, 2009). The families Sergestidae, Palaemonidae, Parastacidae, Aeglidae and Trichodactylidae occur in continental environments of the southern Neotropical region (Martin & Davis, 2001). We analysed the distribution of these five freshwater decapod families in Argentina to address: (i) that environmental factors are more important than previously acknowledged for the distribution of freshwater decapods at a macroecological level and (ii) that spatial gradients traditionally ascribed to historical processes can be partly explained by local environmental conditions.

Methods

Study area and source of the data

The study area comprises most of Argentinean aquatic systems. This area extends approximately from the Tropic of Capricorn to 46°S (>2500 km), ranges in longitude from 53° to 73°W, has an altitudinal range of approximately 7000 m a.s.l. and a surface area of around 3 million km^2. Stability values ranges from 1 to 20, while the annual temperature range (ATR) varies between 20 and 34 °C. pH and water conductivity range from 5.3 to 9.2 and from 12.8 to 19 900 μ cm^{-1}, respectively (Fig. 1).

The occurrence of freshwater decapods was obtained from 362 sites (locations with at least one presence) during fieldworks between 2001 and 2013. The sites were

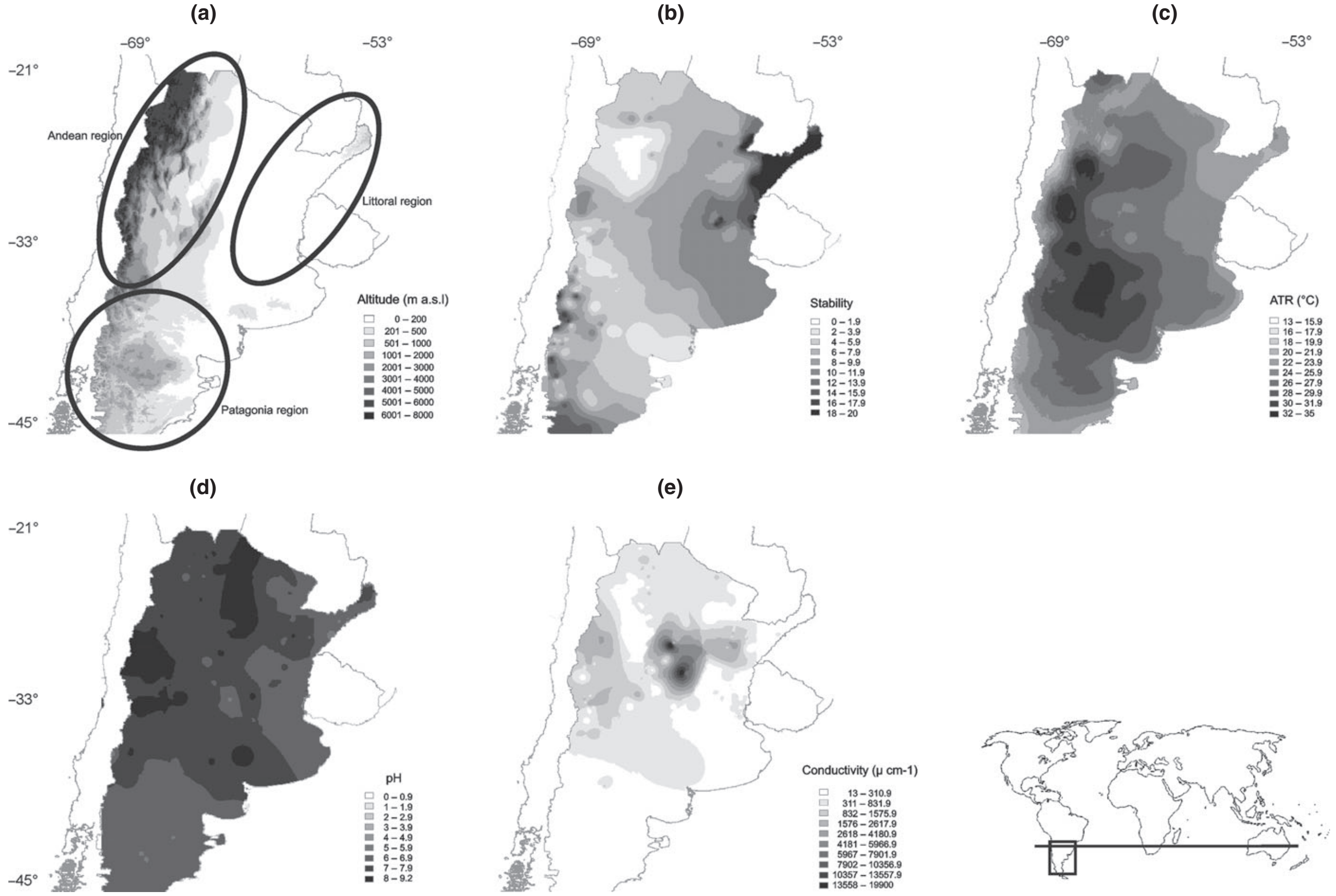

Fig. 1 Maps showing environmental gradients (represented by grey scales) of the area studied: (a) altitude (m a.s.l.) and regions; (b) aquatic stability; (c) annual temperature range (ATR °C); (d) pH and (e) water conductivity (µ cm^{-1}). The inset shows the location of the study area in a world map and the Tropic of Capricorn (black line).

representative of all zones and habitats (e.g. open rivers, coasts with or without vegetation, lakes, ponds, water columns, waterfalls, caves and bottoms with sand, clays and/or rocks). The capture methods used included bottom and hand nets, funnel traps and manual capture. The animals obtained in the samples were anaesthetised by exposure to cold temperatures and fixed in 70% alcohol. In addition, the data on the occurrence of shrimp (Sergestidae), prawns (Palaemonidae), crayfish (Parastacidae), aeglids (Aeglidae) and crabs (Trichodactylidae) were supplemented using the information from museum collections [Argentina: Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' in Buenos Aires, Museo de La Plata in La Plata, Museo Provincial de Ciencias Naturales 'Florentino Ameghino' in Santa Fe, Museo Provincial de Ciencias Naturales y Antropología 'Prof. Antonio Serrano' in Paraná, the Crustacean Collection of the Instituto Miguel Lillio in Tucumán; Brazil: Crustacean Laboratory of the Universidade Federal do Rio Grande do Sul (UFRGS) in Porto Alegre; and Germany: 'Senckenberg Museum' in Frankfurt], and by a thorough literature review (Bond-Buckup & Buckup, 1994; Collins, 2000; Collins *et al*., 2002, 2009; Melo, 2003; Pérez-Losada *et al*., 2004; Bond-Buckup *et al*., 2010).

Decapod species were determined according to relevant identification keys (Boschi, 1981; Bond-Buckup & Buckup, 1994; Magalhàes & Türkay, 1996a,b,c, 2008; Magalhàes, 2003).

Independent variables

In the area studied, environmental factors vary along latitudinal and longitudinal gradients (Fig. 1). A first step consisted of running simple models of decapod occurrence with latitude and longitude as the only independent variables (models A) to control for potential confounding or effect modification (effect modification exists when the association between two variables is different at different levels of a third variable, the effect modifier). The main step of the analyses consisted of exploring whether associations between decapod distribution and latitude or longitude were explained by environmental factors (i.e. models A allowed the establishment of significant latitudinal or longitudinal gradients for each family). In a second step, models A results were compared with models (models B) which included all the environmental variables and two-way interactions (see 'Data analysis' below). If a latitudinal or longitudinal gradient identified in model A was explained by covarying environmental factors in model B, then the associations with the former should change or disappear when environmental factors were included in the latter. The environmental variables evaluated in models B were altitude, water stability, ATR, pH and water conductivity. These variables were selected as previous studies have shown them to be important for the distribution, density and diversity of decapods (Daniels *et al.*, 2002; Williner *et al.*, 2009).

Altitude and ATR were determined for each sampling site using ArcGis (version 10.1) by generating the intercept between the georeferenced points and climatic layers freely available from WorldClim (www.worldclim.org). Stability of the waterbody was determined using a subjective scale from 1 to 20, where 1 represented relatively unstable conditions (e.g. a temporary stream), 10 represented intermediate stability (e.g. the riverbank of a foodplain) and 20 represented the most stable waterbodies (e.g. a permanent lake). Values were assigned using satellite and on-site photographs. Determination of stability also included consideration of the precipitation regime, climatic features, hours of sunlight, substratum (particle size, rock, sand, limestone) and the size of the aquatic environment, as well as the connectivity with other aquatic systems. Values for pH, water conductivity and geographical coordinates were recorded at each site using digital equipment (Hanna models HI 98130 and HI 9146 Woonsocket, RI, U.S.A.; and Garmin Dakota 20, Kansas City, MO, U.S.A. respectively). For data obtained from museums or literature, values for pH and water conductivity were estimated using information from the nearest point sampled (max. 25 km Euclidean distance). Latitude and longitude coordinates were obtained from Google Earth (version 6.1.0.5001).

Data analysis

Prior to the analyses, Pearson's correlation was used to asses collinearity ($r \geq |0.7|$) between environmental variables. The data were analysed using generalised linear models (GLM) with a binomial response. GLMs with binomial response conform well to presence-absence data and assume additive or linear relationships between dependent and independent variables. The dependent variable was decapod occurrence (yes/no) and the independent variables were latitude and longitude (in models A), while models B comprised environmental variables altitude, water stability, ATR, pH and water conductivity and their two-way interactions. Because linearity can be violated under some relationships, all continuous independent variables were assessed using linear and quadratic terms.

Each decapod family was analysed separately. Crayfish (Parastacidae) were represented by only two species [*Parastacus pilimanus* (von Martens, 1869) and *Samastacus spinifrons* (Philippi, 1882) (Appendix S1 in Supporting Information)] restricted to distinct areas (Fig. 2c), with separate analyses conducted for each species. To avoid spatial autocorrelation, only data from the respective distributional areas were used. Similarly, the family Sergestidae was represented by a single species, *Acetes paraguayensis* Hansen, 1919 (Appendix S1), and the subset of data used for its analysis only included data points from the respective distributional area where the species was known to occur.

Grouping crustacean decapod species into families was considered acceptable when analysing for common attributes shared by species (e.g. life history, biological range, single origin, species endemicity). Each decapod family presents a temporally and spatially distinct evolutionary history with respect to its occurrence in freshwater environments (Feldmann & Schweitzer, 2006). Furthermore, using family-level taxonomic resolution reduces uncertainty when studying distribution patterns (Guisan *et al.*, 2006). Feldmann & Schweitzer (2006) also contend that when distributional data on decapod crustaceans is limited or not homogeneous, effects are reduced by conducting analyses at the family level.

The full model (model B) for each family comprised all independent variables, quadratic terms for each independent variable and two-way interactions. The most parsimonious models were found by stepwise elimination of unimportant terms using the Akaike information criterion (AIC) (Akaike, 1974) (a term was not retained if inclusion did not reduce AIC by two units). Interaction terms were eliminated first, followed by single variables. When the AIC values were similar, we removed the variable with the least ecological underpinning (based on knowledge of the ecology of each family). All the analyses were done using R software version 3.1.0 (R Development Core Team, 2008).

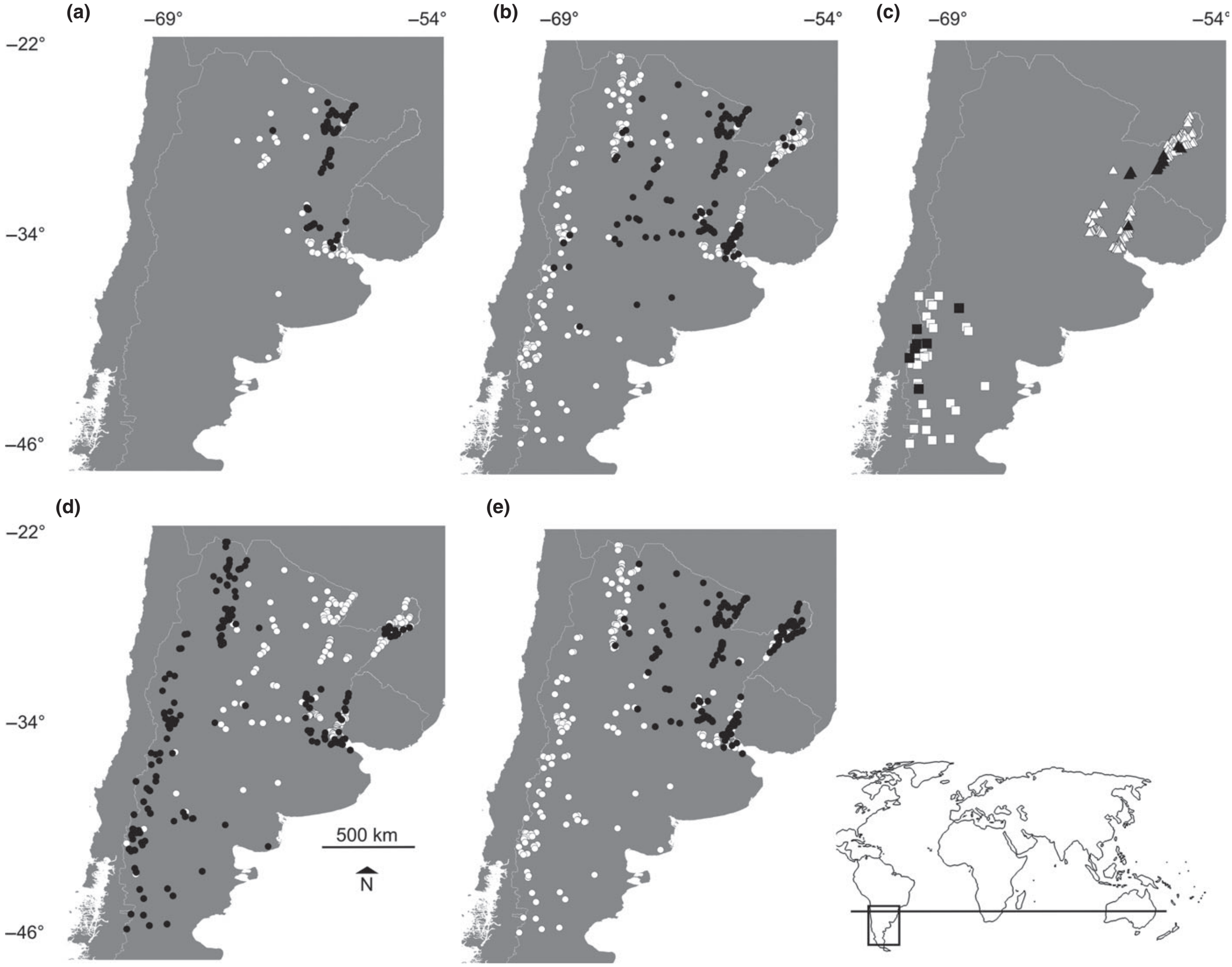

Fig. 2 Occurrence data of: (a) *Acetes paraguayensis*; (b) palaemonid prawns; (c) crayfish (Triangles: *Parastacus pilimanus*; and Squares: *Samastacus spinifrons*); (d) aeglids and (e) crabs in continental environments of southern South America. Black symbols show the presences and white symbols the absences used for each group. The inset shows the location of the study area in a world map and the Tropic of Capricorn (black line).

Results

A total of 39 species were recorded in the study area, including the families Sergestidae (*A. paraguayensis*, a sergestid shrimp), Palaemonidae (freshwater prawns), Parastacidae (*P. pilimanus* and *S. spinifrons* crayfish), Aeglidae (aeglids) and Trichodactylidae (freshwater crabs) (Appendix S1). Distributions ranged from 22° to 46°S, 54° to 72°W and from 0 to 3742 m a.s.l. (Fig. 1 and 2).

Correlation showed that no pair of independent variables was highly correlated (all correlation coefficients ≤ |0.7|). The final A and B models for each family are presented in Appendix S2 in Supporting Information.

Latitudinal and longitudinal patterns

In models A, *A. paraguayensis*, palaemonid prawns, aeglids and crabs showed significant latitudinal and/or longitudinal patterns ($P < 0.0001$). Crayfish occurrence (subset of data points), was not significantly related to latitude or longitude alone (models A) or when including local environmental variables and their interactions (models B) ($P > 0.05$). The occurrence of *A. paraguayensis* decreased from north to south (coefficient value −0.32493), while palaemonid prawns increased from west to east (coefficient value −0.13835) ($P < 0.0001$). Aeglids increased from east to west (positive coefficient, $P < 0.0001$) and the probability of occurrence of crabs increased from south to north and from west to east (negative coefficients, $P < 0.05$).

When environmental variables were included in the analyses (models B), the latitudinal gradients in *A. paraguayensis* and crabs and longitudinal pattern in aeglids remained significant and in the same direction. The longitudinal pattern described for palaemonid prawns reversed increasing from east to west (positive coefficient, $P < 0.05$), whereas the longitudinal pattern for crabs was no longer significant (Appendix S2).

Sergestid shrimp

Acetes paraguayensis was recorded in 58 of the 362 sites (16%) and was the only sergestid in the study area (Appendix S1). Sergestid shrimp distribution coincided with the Paraguay, Paraná and Uruguay rivers, in the Littoral region (Fig. 2a).

Latitude, altitude, stability and ATR were the best predictors of *A. paraguayensis* occurrence, although interactions were significant (Appendix S2a). The probability of *A. paraguayensis* occurrence was higher at lower altitudes. This relationship also varied with stability and ATR (Fig. 3a). The association with ATR was strong at low latitudes, but became progressively less important in the south (Fig. 3b).

Palaemonid prawns

Palaemonid prawns were recorded in 138 of the 362 sites (38.1%). The prawns comprised six species in four genera of Palaemonidae (Appendix S1). Prawn distribution was continuous from the north to 39°S, with the exception of the Andes (Fig. 2b). *Palaemonetes argentinus* (Nobili, 1901) was the most frequently recorded species (recorded at 135 sites), whereas *Macrobrachium amazonicum* (Heller, 1862) and *M. jelskii* Miers, 1877 were the least frequently recorded species (both were only found at 16 sites).

Latitude, longitude, altitude, stability, ATR, pH and conductivity were significant predictors of palaemonid prawns occurrence, although interactions were significant. Latitude appeared mainly as an 'effect modifier' (Appendix S2b and Fig. 4b–d). The probability of prawn occurrence declined abruptly as altitude increased above sea level. This relationship was strong and varied only slightly with ATR and conductivity (Fig. 4a). Moreover, palaemonid prawn occurrence depended strongly on aquatic stability and ATR, but relationships varied with latitude (Fig. 4b). In addition, the association between pH and palaemonid prawn occurrence depended on latitude and ATR (Fig. 4c). The association between conductivity and occurrence of palaemonid prawns depended strongly on latitude, stability and ATR (Fig. 4d).

Crayfish

Crayfish were recorded in 20 of 362 sites (5.5%). The crayfish belonged to two species of two genera of Parastacidae (Appendix S1). Crayfish showed marked discontinuity in distribution. *Parastacus pilimanus* was recorded at the northeast and centre-east of the study area (east part of the Littoral region), whereas *S. spini-*

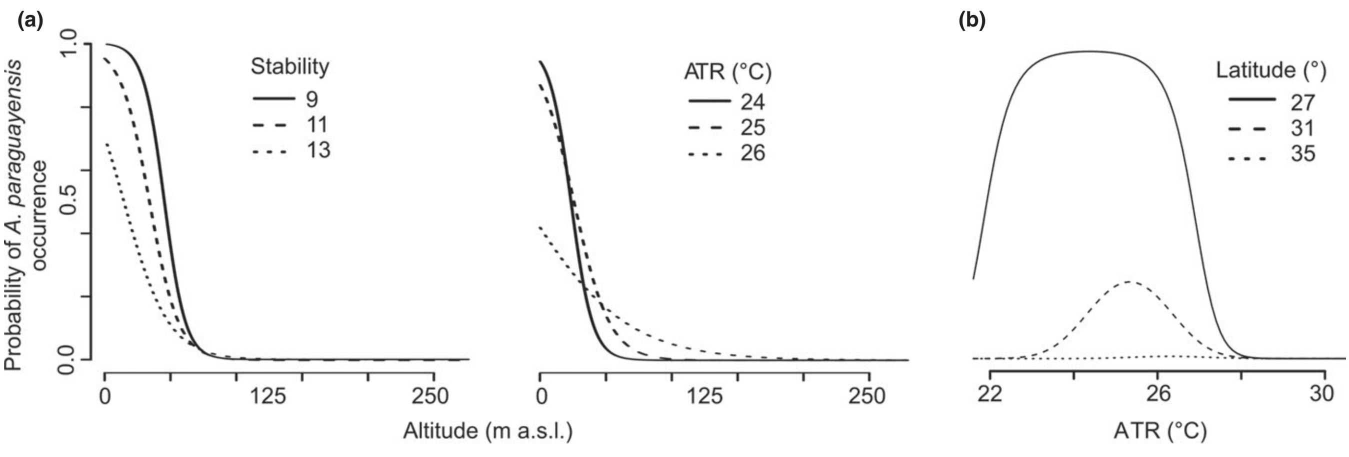

Fig. 3 Variables that significantly influenced the occurrence of *Acetes paraguayensis* in southern South America and their interacting variables: (a) altitude (m a.s.l.) interacted with stability and annual temperature range (ATR °C) and (b) the effect of ATR depended on latitude (°). The figures were constructed with the focal independent variable in the *X* axis. The distinct line types represented the probability of the dependent variable at values of the mean and the first and third quartiles of the interacting variable, while values of the other significant factors were set at their average.

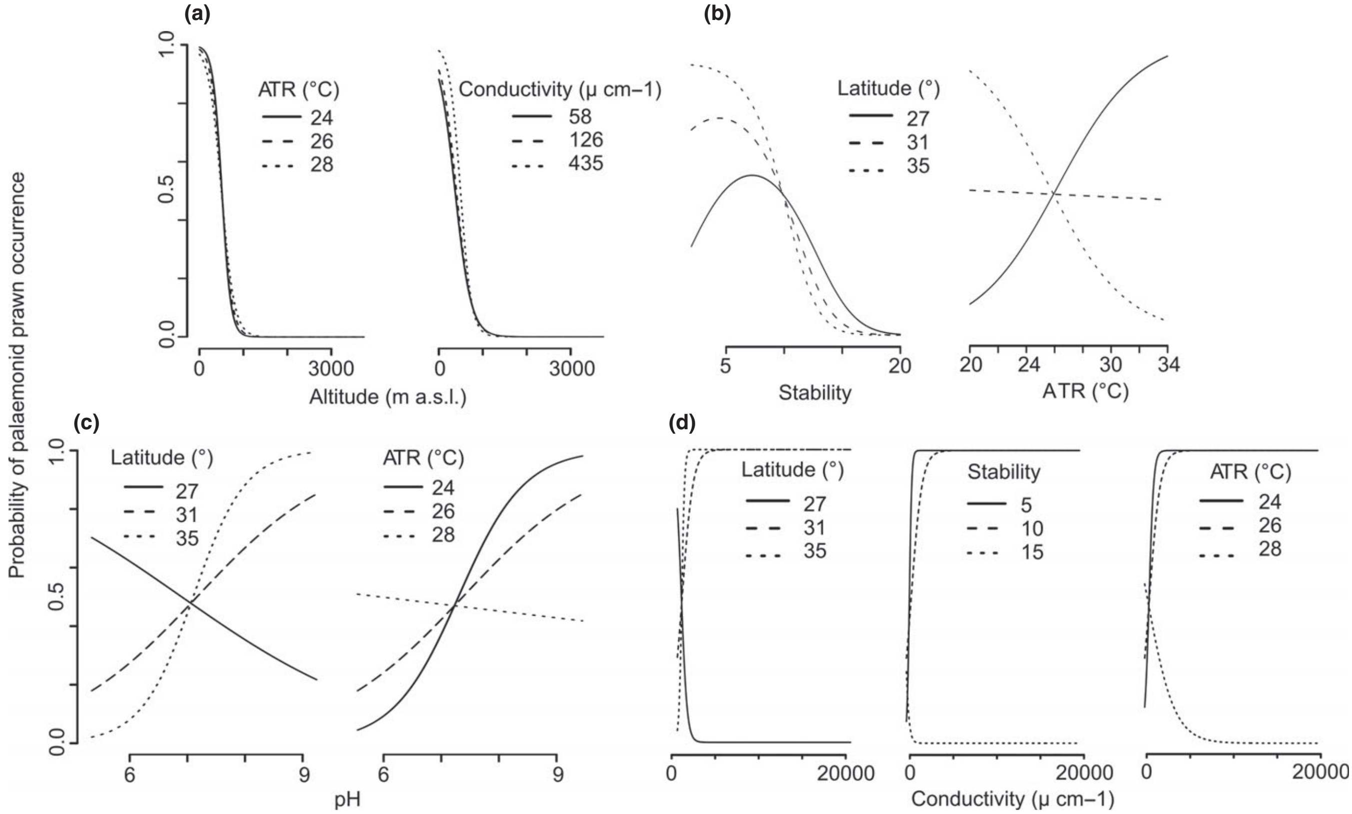

Fig. 4 Variables that significantly influenced the occurrence of palaemonid prawns in southern South America and their interacting variables: (a) altitude (m a.s.l.) interacted with annual temperature range (ATR °C) and conductivity (µ cm^{-1}); (b) stability and ATR interacted with latitude (°); (c) the effect of pH depended on latitude and ATR and (d) conductivity interacted with latitude, stability and ATR. The figures were constructed with the focal independent variable in the *X* axis. The distinct line types represented the probability of the dependent variable at values of the mean and the first and third quartiles of the interacting variable, while values of the other significant factors were set at their average.

frons was recorded around the southwest border, at northwestern Patagonia (Fig. 2c). *Parastacus pilimanus* was the most frequently recorded species of this group (recorded at 13 sites), with *S. spinifrons* only recorded at seven sites. Altitude, stability and ATR were the best predictors of *P. pilimanus* occurrence, although the interaction term altitude × ATR was statistically significant (Fig 5a,c). The occurrence of *S. spinifrons* was significantly related to altitude, stability and pH (Fig 5d–f).

Aeglids

Aeglids, the most frequent morphotype, were recorded at 187 of 362 sites (51.6%). These anomurans belonged to 18 species of a single genus, *Aegla* (Aeglidae), four of which were considered as new species (i.e. their diagnostic characters did not match with currently described species) and represented 22% of the total number of species of the family (Appendix S1). Aeglids were the group with the most extensive distribution (Fig. 2d). *Aegla uruguayana* and *A. neuquensis* were the most frequently recorded species (found at 40 and 39 sampled sites respectively). By contrast, the least frequently recorded species where *Aegla* sp. 1, present at two sites and *A. ringueleti* (Bond-Buckup & Buckup, 1994), *A. saltensis* (Bond-Buckup & Jara in Bond-Buckup *et al*., 2010) and *Aegla* sp. 4, each recorded at a single site.

Latitude, longitude, altitude, stability, ATR and conductivity were significant predictors of aeglid occurrence, although interactions were significant (Appendix S2d). The association between altitude and occurrence of aeglids was strong and generally positive, but this relationship depended on latitude and on stability (Fig. 6a). Aeglid occurrence depended markedly on aquatic stability and ATR, but both associations varied with latitude (Fig. 6b). The association between conductivity and occurrence of aeglids depended on latitude

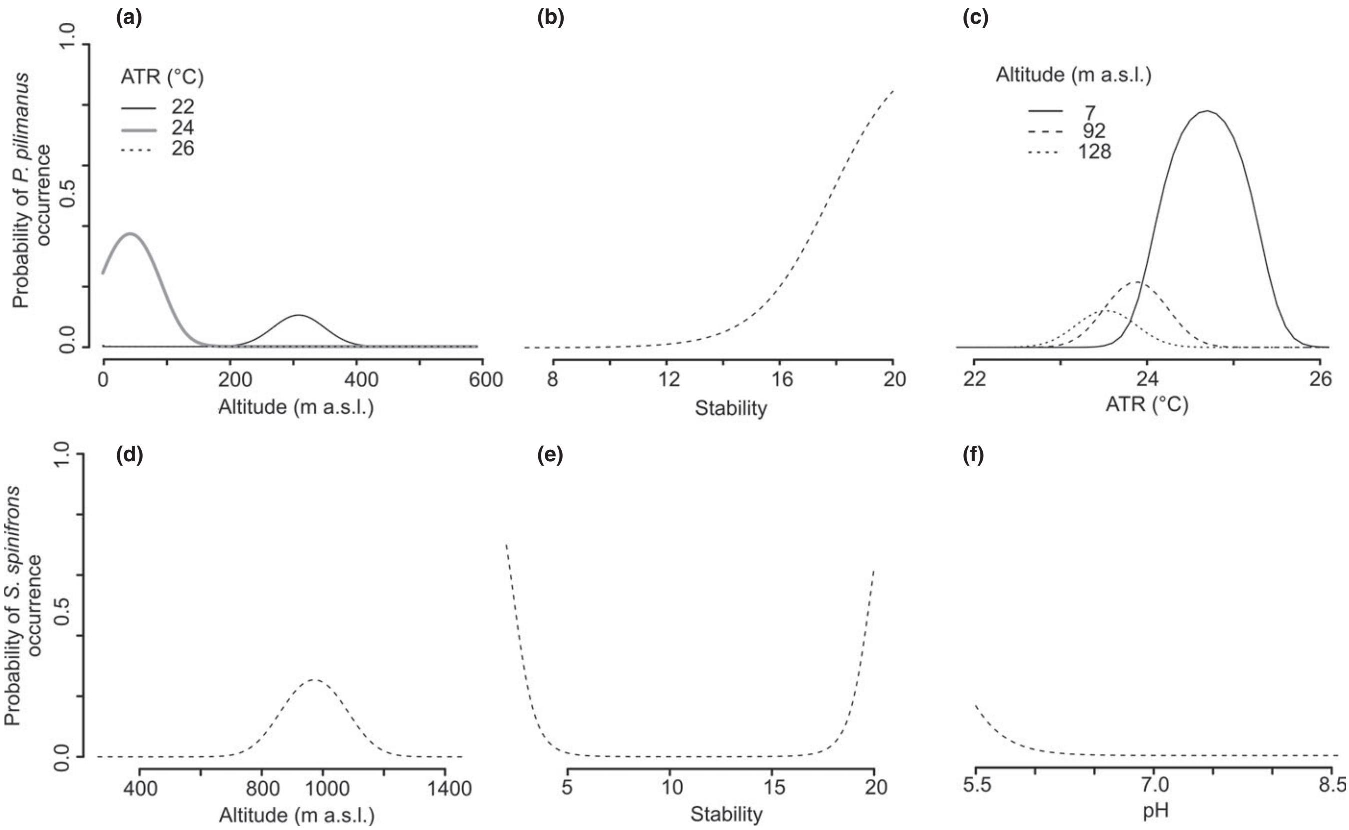

Fig. 5 Variables that significantly influenced the occurrence of *Parastacus pilimanus* in southern South America: (a) altitude (m a.s.l.) [and the effect modified by annual temperature range (ATR °C)]; (b) stability and (c) ATR (and the effect modified by altitude); and the occurrence of *Samastacus spinifrons* as affected by different values of: (d) altitude; (e) stability and (f) pH. The figures were constructed with the focal independent variable in the X axis. The distinct line types (Figs 5a and c) represented the probability of the dependent variable at values of the mean and the first and third quartiles of the interacting variable, while values of the other significant factors were set at their average. Where no interactions were present (Figs 5b, d–f), other variables were set at their mean values.

and ATR. The pattern for conductivity was decisively different at northern sampling sites (Fig. 6c).

Crabs

Crabs were recorded at 164 of 362 sites with decapod occurrence (45.3%) and comprised 13 species in seven genera of freshwater crab Trichodactylidae (Appendix S1). Crab distribution was continuous across the centre and north of the study area, with the exception of the Andes (similar to palaemonid prawns) (Fig. 2e). *Trichodactylus borellianus* (Nobili, 1896) was the most frequently recorded species, found at 107 sites, whereas *T. panoplus* (von Martens, 1869) and *T. fluviatilis* Latreille, 1828 were the least frequently recorded species, found at 15 and 14 sites respectively.

Latitude, altitude, stability, ATR and pH were significant predictors of crab occurrence. Altitude had no significant interaction terms. However, importance of the remaining environmental variables was confounded by significant interactions (Appendix S2e). The association between altitude and occurrence of crabs was strong and negative (Fig. 7a). Moreover, crab occurrence also depended strongly on aquatic stability and ATR, and these relationships varied with latitude (Fig. 7b). Finally, the association between pH and occurrence of crabs depended on stability (Fig. 7c).

Discussion

Using a quantitative analytic approach at a biogeographical scale, we found support for our hypothesis that the current distribution of each freshwater decapod family in the southern region of South America (Argentina) is strongly influenced by local environmental factors.

The southern region of South America has had a dynamic history of continental basin formation and certain events that produced changes in the location of

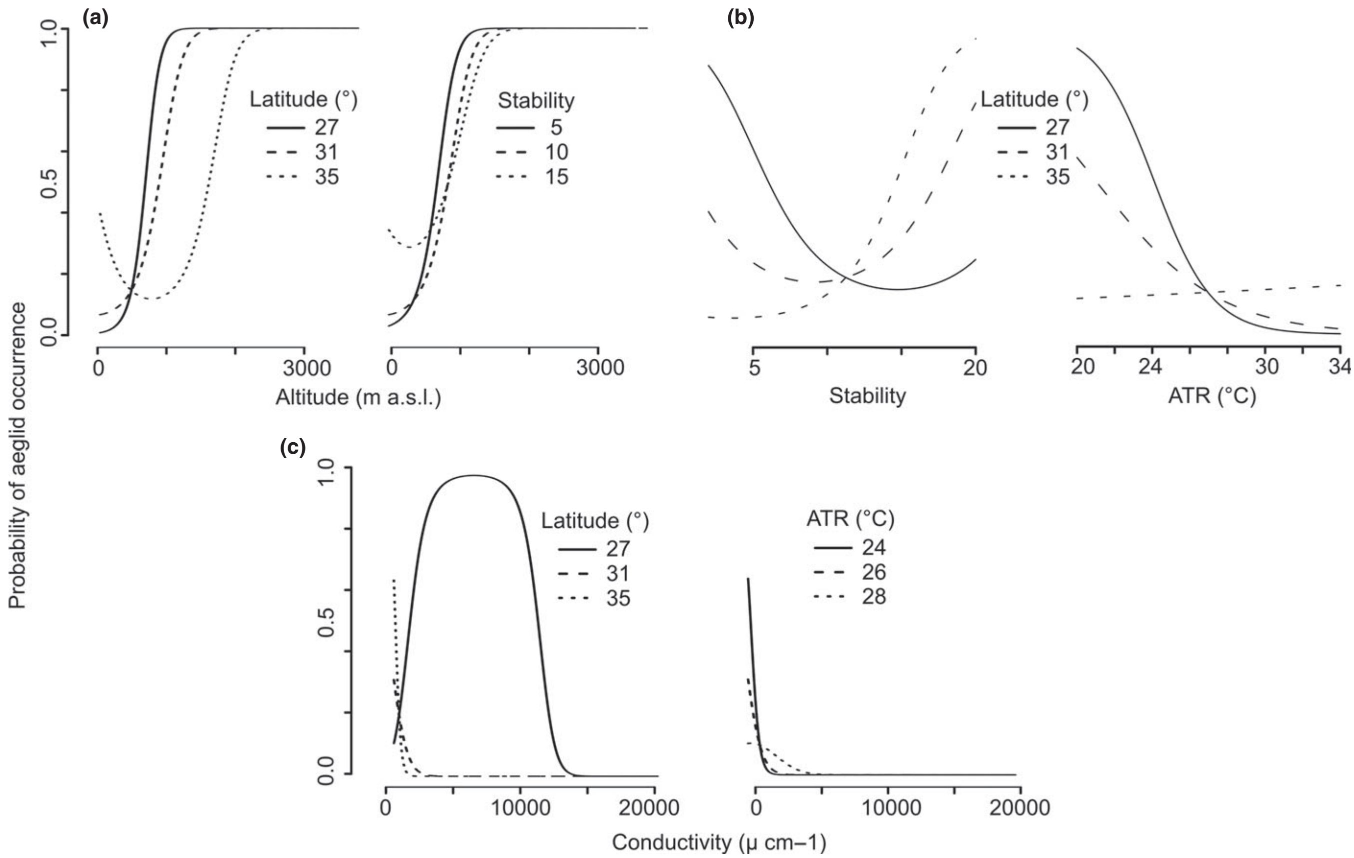

Fig. 6 Variables that significantly influenced the occurrence of aeglids in southern South America and their interacting variables: (a) altitude (m a.s.l.) interacted with latitude (°) and stability; (b) the effect of stability and annual temperature range (ATR °C) depended on latitude and (c) conductivity (μ cm^{-1}) interacted with latitude and ATR. The figures were constructed with the focal independent variable in the *X* axis. The distinct line types represented the probability of the dependent variable at values of the mean and the first and third quartiles of the interacting variable, while values of the other significant factors were set at their average.

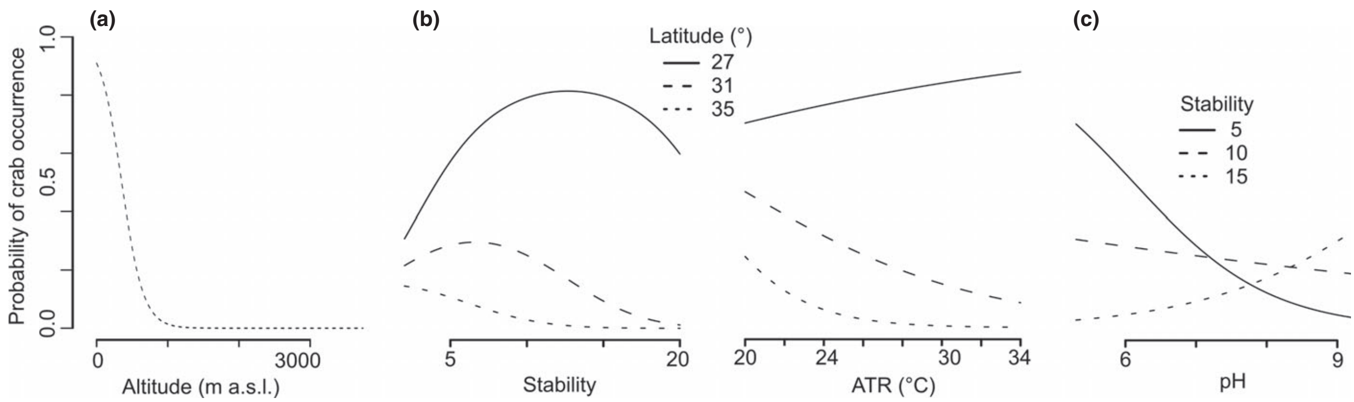

Fig. 7 Variables that significantly influenced the occurrence of crabs in southern South America and their interacting variables: (a) altitude (m a.s.l.); (b) the effect of stability and annual temperature range (ATR °C) depended on latitude (°); and (c) pH interacted with stability. The figures were constructed with the focal independent variable in the *X* axis. The distinct line types (Figs 7b and c) represented the probability of the dependent variable at values of the mean and the first and third quartiles of the interacting variable, while values of the other significant factors were set at their average. Where no interactions were present (Fig. 7a), other variables were set at their mean values.

streams and rivers (Collins, Giri & Williner, 2011). The low dispersion capacity and/or sedentary behaviour plus the parano-platense character in the distribution of some species of shrimps, prawns, aeglids and crabs are evidence of their possible route of dispersion. In this sense, the axis formed by the rivers Paraguay, Paraná and Uruguay is the main dispersal corridor from where these decapods from the Amazon and the Atlantic forest invaded continental systems since the upper Miocene (Ringuelet, 1956; Collins *et al.*, 2002, 2009). Concerning the distinct distribution of crayfish throughout the region sampled, this is likely the result of Myr of isolated evolution, adapting to environmental features and geoclimatic phenomena, such as marine water ingressions during the late Paleozoic, among others (Babcock *et al.*, 1998). Furthermore, the low dispersion capacity of crayfish, scavenger habits and cave life, in addition to potential competitors and predators could have restricted the colonisation of new habitats with a suitable environment. The current distribution of aeglids may be influenced by modifications in the land geography and the formation of continental aquatic environments in southern South America. Thereafter, aeglids could have moved (i.e. a dispersion event) or been restricted (i.e. a vicariant event) to high altitudes, as suggested by our results. The process of aeglid species differentiation began in these original populations and the current high degree of endemism is a result of the loss of connectivity (Collins *et al.*, 2011).

These historical contexts may partially explain our finding of relatively strong associations between the occurrence of some freshwater decapod families and latitude and/or longitude. In four of the five families (i.e. Sergestidae, Palaemonidae, Aeglidae and Trichodactylidae), a latitudinal and/or longitudinal pattern was observed. Palaemonid prawns and crabs occurred more frequently in the east, while aeglids were found to occur more frequently in the west. *Acetes paraguayensis* and crab occurrence increased from south to north. In fact, even after adjusting for local environmental variables, latitude significantly influenced the distribution of shrimp, prawns, aeglids and crabs. Longitude was associated with the occurrence of palaemonid prawns and aeglids, which might be related to historical factors, but also to geographical accidents (e.g. the Andes mountain chain) or environmental variables not included here. Three of the five latitudinal or longitudinal patterns established in a first step of our analysis (model A), maintained their significance and direction when environmental variables were considered (model B), that is, the latitudinal gradient in *A. paraguayensis* and crabs and the longitudinal pattern of aeglids. This finding implies that patterns are not consequence of co-variation of the selected environmental variables along spatial gradients represented with latitude and longitude. However, the longitudinal gradient for distribution of palaemonid prawns was reversed in the model B, after adjusting for altitude, stability, ATR, pH and conductivity. In addition, the longitudinal pattern established for crabs in model A was sufficiently explained by the variables considered in model B.

In most cases, interactions terms were significant, especially with latitude. The global diversity gradients for a wide range of taxa follow a classic latitudinal pattern, characterised by a decrease in richness from the tropics to the poles. However, there are exceptions to this pattern mainly because latitude is correlated with many environmental factors (Keith, Kerswell & Connolly, 2014). The common finding of interactions with latitude reported here might contribute to better understand exceptions. For example, the probability of occurrence of *A. paraguayensis* decreased with increasing latitude, especially at sites with average ATR values, whereas for palaemonid prawns their occurrence increased with latitude at sites with low stability, or high conductivity. Aeglids either decreased or increased with latitude, depending on altitude, stability, ATR and conductivity. These findings also support the contention of Hillebrand (2004) that the latitudinal diversity decline from the tropics to the poles is weaker in fresh water than in marine or terrestrial environments.

The dominant influence of historical factors proposed by previous studies (Ringuelet, 1956; Breinholt *et al.*, 2009; Collins *et al.*, 2009) is based on descriptive analyses. Here, our quantitative approach revealed that environmental variables significantly affect decapod distribution. Altitude and stability were found to be strong predictors of the occurrence of all families studied here. Annual temperature range was also a significant predictor of all decapods, with the exception of the crayfish *S. spinifrons*. The occurrence of palaemonid prawns, *S. spinifrons* and crabs was also influenced by pH, whereas palaemonid prawns and aeglids were also associated with conductivity. However, in most cases, interactions were significant, except for the crayfish *S. spinifrons* (no significant interaction terms remained in the final model B).

A number of variables co-vary with altitude, mainly air temperature, atmospheric pressure and solar radiation. The change in environmental conditions along an altitudinal gradient influences organisms that are generally adapted to local conditions, with evolutionary adaptation occurring over short spatial distances (Körner, 2007). In our study, relationships with altitude differed among families, and were generally influenced by other variables. Shrimp, prawns, the crayfish *P. pilimanus* and crabs were more likely to occur at low altitudes. However, these associations were highly dependent on stability (*A. paraguayensis*), on ATR (shrimp, prawns and *P. pilimanus*) and on conductivity (prawns). On the other hand, aeglids were the dominant family at the highest altitudes of the decapod occurrence range. Although occurrence increased with altitude, this relationship was strongly related to latitude and stability.

Variation in stability of the aquatic environment was one of the main drivers of decapod occurrence. Stability was related to the flood pulse in large river systems and to the period between two rainy seasons and/or by the frost-free period in small waterbodies. However, relationships differed among southern South American decapod families. Probability of occurrence of *A. paraguayensis* decreased with increased stability, especially at low altitude values. The crayfish *P. pilimanus* was mainly found at high stability, while the other crayfish species studied, *S. spinifrons*, was mainly present at extreme stability values (lowest and highest stabilities); a finding which merits further exploration. On the other hand, relationships between palaemonid prawns, crabs and aeglids and stability were highly dependent on latitude. These variable patterns could be related to the existence of diverse niches occupied by the different species. Latitude co-varies with stability in the study area, and niches differ between the northern and southern waterbodies. At low latitude sites (especially to the east), the prevailing aquatic systems are large river systems with low variability in their main flow (high stability), whereas high latitude sites have low water flow and may freeze in winter. Previous descriptive studies also found stability of the waterbody to be an important predictor, as it is related not only to freshwater decapod species occurrence and richness, but also densities, movements/migrations, reproductive activities, feeding rhythms, intraspecific and interspecific relationships (Williner *et al.*, 2010). Low precipitation, related to stability, likely limits the dispersal capacity of shrimps, prawns and aeglids, as a decrease in hydrologic levels results in reduced connectivity and surface of the waterbodies (Williner *et al.*, 2009; Torres, Giri & Collins, 2014). If a particular environmental setting tends to disappear temporarily, the probability of death is higher due to extreme chemical conditions, limited food availability, lack of refuges, desiccation and predation. All of these factors could cause local extinctions of decapod species and increase the time needed for the populations to recover (Fernández & Collins, 2002; Williner *et al.*, 2009). Notwithstanding, the construction of burrows in swampy areas (e.g. by crayfish, crabs and aeglids) during periods of stress is important for survival. In addition, some crab species could perform active widespread terrestrial movements or migrations into other channels or streams to seek improved conditions during periods of low rainfall (Fernández & Collins, 2002; Daniels, Gouws & Crandall, 2006; Williner *et al.*, 2009; Collins, Williner & Montagna, 2010; Noro & Buckup, 2010).

Climatic conditions, including temperature, define niches and therefore the potential distributional range of any given species. Seasonal changes in waterbody temperature closely follow seasonal trends in air temperature (Allan, 1995). Abrupt changes in temperature induce physiological alterations and stress in crustaceans, affecting the fitness, life cycle and community composition of species, and therefore play a major role in their life history (Pruitt, 1990) and distribution (Jackson, Peres-Neto & Olden, 2001; Williner *et al.*, 2010). In our study, ATR significantly influenced the occurrence of most families (all except the crayfish *S. spinifrons*), but relationships were complex as they depended on latitude (for shrimp, prawns, aeglids and crabs) and/or altitude for shrimp, prawns and the crayfish *P. pilimanus*, as well as other interacting variables. Another study found that the distribution of the estuarial Indo-Pacific prawn *M. rosenbergii* De Man, 1879 was associated with temperature ranges (Nelson *et al.*, 1977). Furthermore, Allan (1995) described an interaction between waterbody temperature and latitude. Additionally, the temperature range of a region could largely govern distributional patterns of freshwater decapods and establish biogeographical boundaries playing a role in the determination of their evolutionary biology, as explained for freshwater crabs of South Africa by Daniels *et al.* (2002).

pH and conductivity are two factors that strongly affect the distribution of decapods. Populations of decapods cannot be successfully established in environments with extreme pH values, as effective moulting and an appropriate ionic equilibrium are impaired (Fryer, 1993; Collins *et al.*, 2010; Williner *et al.*, 2010). However, our results suggest that optimal pH values depended on the environmental context (i.e. latitude or stability) for palaemonid prawns and crabs. There is a paucity of data on the distribution of crustaceans in relation to pH (but see Potts & Fryer, 1979), especially for macrocrustaceans. The apparent context-dependent pH tolerance suggested by our results warrants further investigations. Water conductivity is crucial for decapod fitness and survival, as it influences physiological (e.g. moult, metabolic rate) and ecological (e.g. assemblages, reproduction, predation) processes (Anger *et al.*, 1994; Bialetzki *et al.*, 1997; Dick & Platvoet, 2000; Miserendino, 2001; Williner *et al.*, 2010). In our study, the occurrence of palaemonid prawns and aeglids was associated with water conductivity. For palaemonid prawns, the relationship with conductivity was complex and highly dependent on latitude, stability and ATR. The relationship of aeglids with conductivity was dependent on latitude and ATR. We are not aware of previous quantitative studies investigating the influence of variability in conductivity on macrocrustacean distribution. Besides relationships with the environmental variables studied here, decapod occurrence could be related to other environmental variables not included in this study. Furthermore, freshwater decapod distributions may also be influenced by ecological interactions (e.g. trophic relationships, biological competition), and disturbances produced by rapid human alterations of the biosphere. In agreement with Haydon, Crother & Pianka (1994), we conclude that the distribution of organisms, including decapods, is determined by a triangular structure, where biogeographical patterns are the result of the interaction among ecological, historical and stochastic processes.

Our results provide evidence to support our hypothesis that environmental variables influence the distributions of freshwater decapods in southern South America (Argentina). This conclusion complements the extant literature that recognises the influence of the biogeographical history of the continent on freshwater decapod distributional patterns. Offering a new quantitative approach to the study of this group's biogeography in the region, we found that several environmental factors are important determinants of their macrodistribution. This finding suggests limited plasticity and strong adaptation to the local habitats.

Our study combined field, museum collections and literature to broaden our knowledge of freshwater decapod biogeography in southern South America, representing the first study of this type providing quantitative information of macroecological preferences. Studies like this are central to many fundamental questions in macroecology and conservation biology. Further studies should be aimed at elucidating the mechanisms behind the associations and interactions found, as well as providing more detailed analysis within each family (i.e. among the species that compound them) and other relevant ecological aspects.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of freshwater decapod species registered in southern South America (Argentina).

Appendix S2 Tables of GLMs showing the assessment of latitude and longitude alone (models A) plus the most parsimonious models describing the most important determinants of occurrence (models B) for (a) *Acetes paraguayensis*; (b) palaemonid prawns; (c) crayfish; (d) aeglids and (e) crabs.

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