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M P Campos-Soldini, M S García & M E Safenraiter

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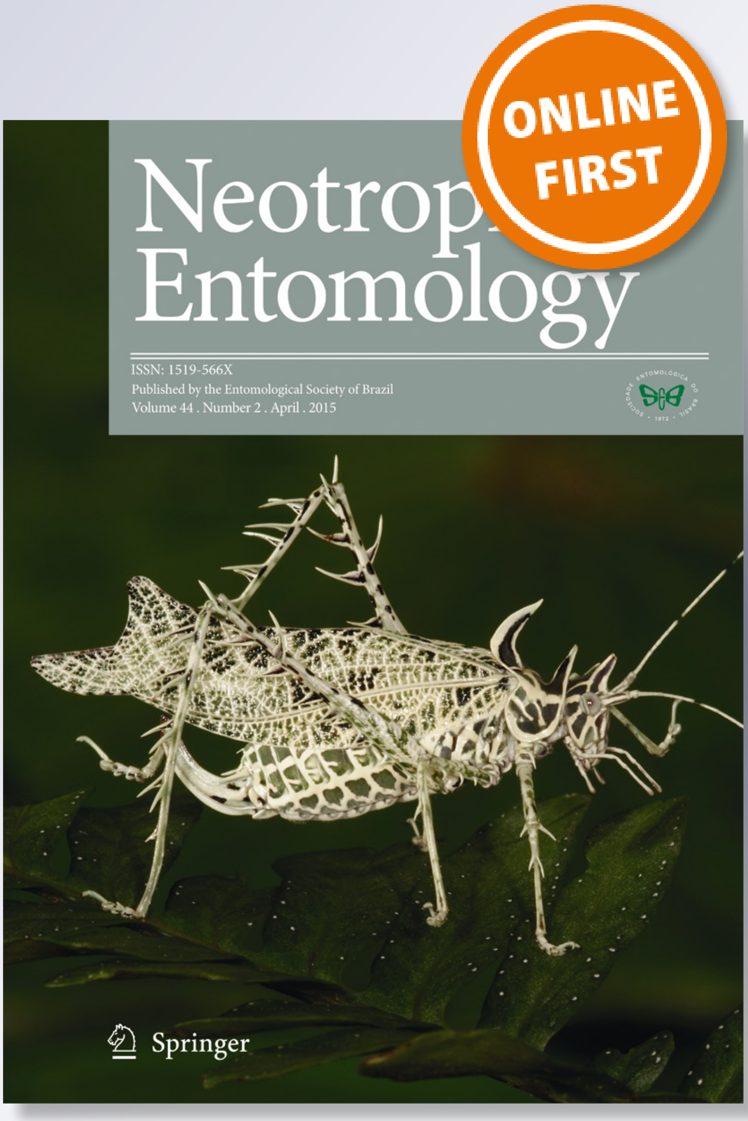

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ECOLOGY, BEHAVIOR AND BIONOMICS

Track Analysis of the North, Central, and South American Species of the *Epicauta maculata* Group (Coleoptera: Meloidae)

MP Campos-Soldini, MS García, ME Safenraiter

Lab de Entomología FCYT-UADER/CICyTTP-CONICET, Diamante, Entre Ríos, Argentina

Keywords

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Correspondence
MP Campos-Soldini, Lab de Entomología FCYT-UADER/CICyTTP-CONICET, Materi y España, Diamante, Entre Ríos, Argentina; mariapaulacampos@gmail.com

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Abstract

We undertook a panbiogeographic analysis of 23 species of the *Epicauta maculata* group of America—*Epicauta abeona* Pinto, *Epicauta adspersa* (Klug), *Epicauta andersoni* Werner, *Epicauta atomaria* (Germar), *Epicauta apache* Pinto, *Epicauta cavernosa* (Courbon), *Epicauta dilatipennis* Pic, *Epicauta fulvicornis* (Burmeister), *Epicauta horni* Champion, *Epicauta jeffersi* Pinto, *Epicauta koheleri* Denier, *Epicauta lizeri* Denier, *E. maculata* (Say), *Epicauta magnomaculata* Martin, *Epicauta minutepunctata* Borchmann, *Epicauta nigropunctata* (Blanchard), *Epicauta normalis* Werner, *Epicauta ocellata* (Dugès), *Epicauta pardalis* LeConte, *picauta phoenix* Werner, *Epicauta pluvialis* Borchmann, *Epicauta proscripta* Werner, *Epicauta rubella* Denier, and *Epicauta ventralis* Werner—with the purpose of analyzing the distributional data for taxa, to establish patterns of distribution of an ancestral biota and areas where these groups have interacted. Based on the overlap of 20 individual tracks, four generalized tracks constituted by different numbers of species were identified; two of them are located in the Nearctic region and the Mexican transition zone (tracks "A" and "B"), and the other two are distributed in the Neotropical region and the South America transition zone ("C", "D"). Six nodes were recognized: Two of them are included in the Nearctic Region, node 'I' located in northern USA and node 'II' located in southwestern USA, both at the intersection of the tracks "A" and "B". The other four are included in the Neotropical Region at the intersection of the tracks "C" and "D": Node 'III' is located in Chaco province; node 'IV' is located in Parana Forest province; node 'V' is located in the northwest of Argentina in Puna province, and node 'VI' is located in Monte province.

Introduction

Historically, most of the current recognized species with relatively small macula were identified as *Epicauta maculata* (Say) until Werner (1944, 1945), who was the first to examine morphological characters other than the macula. Then, the group was later checked by Pinto (1975, 1980, 1991) and included 13 species—*Epicauta abeona* Pinto, *Epicauta andersoni* Werner, *Epicauta apache* Pinto, *Epicauta horni* Champion, *Epicauta jeffersi* Pinto, *E. maculata* (Say), *Epicauta magnomaculata* Martin, *Epicauta normalis* Werner, *Epicauta ocellata* (Dugès), *Epicauta pardalis* LeConte, *Epicauta phoenix* Werner, *Epicauta proscripta* Pinto, and *Epicauta ventralis* Werner. More recently, Campos-Soldini & Roig-Juñent (In Press) revised this species group in a phylogenetic analysis and added 11 species from South America: *Epicauta adspersa* (Klug), *Epicauta atomaria* (Germar), *Epicauta cavernosa* (Courbon), *Epicauta dilatipennis* Pic, *Epicauta fulvicornis* (Burmeister), *Epicauta koheleri* Denier, *Epicauta lizeri* Denier, *Epicauta minutepunctata* Borchmann, *Epicauta nigropunctata* (Blanchard), *Epicauta pluvialis* Borchmann, and *Epicauta rubella* Denier. So, at present, the *E. maculata* group includes 24 species distributed throughout America (Campos-Soldini & Roig Juñent, In Press).

The *E. maculata* group is distributed in Americas. In North America, the area of greatest diversity takes up central–south Arizona to western Texas where eight species occur; this region encompasses the northern portion of the Chihuahuan Desert and the eastern, higher portion, of the Sonoran Desert. The most widespread species is *E. maculata*, which is distributed along southern Saskatchewan and Manitoba (Canada), through the southern Great Plains (USA) to Mexico and into Guatemala. *Epicauta ventralis* and *E. normalis* are the most widespread species west of the Continental Divide, being most common north of 36°N (Pinto 1980). In South America, its greatest diversity comes from central western Argentina (between 30° and 39°S) to central–north Brazil. The most widespread species are *E. adspersa*, *E. atomaria*, and *E. koheleri* distributed from Río Negro (39°17′16.77″S, 65°39′55.43″W) to northwestern Brazil. Three local species of this group are endemic, and they are distributed throughout central–west and northern Argentina (*E. dilatipennis*, *E. minutepunctata*, and *E. pluvialis*).

The species of this group are dispersed in several biogeographic areas (Darlington 1957, Ringuelet 1961, Rapoport 1968, Cabrera & Willink 1980, Morrone & Lopretto 1994, Morrone 1994, 2001a,b, 2004, 2006, Maury *et al* 1996). In North and Central America, this group is distributed in the following biogeographic provinces (Udvary 1975, Morrone *et al* 1999): Sierra-Cascade (Fig 1a) extends from southern British Columbia through Washington and Oregon to Northern California; Californian (Fig 1b) is a coastal area in the northern portion of the Baja California Peninsula, from Sierra of San Pedro Mártir and Juárez, extending northwards along the Sierra Nevada into southwestern United Sates; the Great Basin (Fig 1c) in northern USA is the largest, contiguous endorheic watersheds area and extends from Nevada and south–central Oregon to central–west Utah; the Rocky Mountains (Fig 1d) run from the northernmost part of British Columbia, in western Canada and New Mexico in the southwestern United States; the Canadian Taiga Province (Fig 1e) is a broad lowland region extending across, eastern British Columbia to the Quebec state; the Grassland (Fig 1f) province is a broad lowland region which is located in the north together with Canadian Taiga province and Mexican Gulf in the south, and between Eastern Forest and the Rocky Mountain respectively; the Eastern Forest (Fig 1g) is a broad land that extends along several eastern American states; the Sonoran (Figs 1h and 2a) is a coastal area in northwestern Mexico extending from the northeastern portion of Baja California to the Piaxtla River basin in the south; the Mexican Plateau (Fig 2b) is a large, arid to semiarid plateau that occupies much of northern and central Mexico, extending from the United States border in the north to the Trans-Mexican Volcanic Belt in the south and is limited by the Sierra Madre Occidental to the west and east respectively; the Sierra Madre Occidental (Fig 2c) is a mountain range in western Mexico, extending alongside the Pacific coast of Mexico, from south of the Arizona–Sonora border southeast through eastern Sonora, western Chihuahua, Sinaloa, Durango, Zacatecas, Nayarit, and Jalisco 1,000 m bellow sea-level (bsl); the Transmexican Volcanic Belt (Fig 2b) extending through Central Mexico in the states of Guanajuato, Mexico, Distrito Federal, Jalisco, Michoacan, Puebla, Oaxaca, Tlaxcala, and Vera Cruz; the Balsas basin (Fig 2e) is a broad lowland region which is located between Neovolcanic and Sierra Madre del Sur; this depression occupies a major portion of the states of Michoacan, Guerrero, Morelos, and Puebla, 2,000 m bsl; Sierra Madre del Sur (Fig 2g) is a mountain range in southern Mexico that is joined with the transverse Volcanic Belt of central Mexico in Northern Oaxaca but is separated from this range further west by the valley of the Balsas river and its tributary, the Tepaltcatepec river; the Mexican Pacific Coast (Fig 2f) comprises a narrow strip in the Pacific Coast of Mexico (the states of Sinaloa, Nayarit, Colima, Jalisco, Michoacán, Guerrero, Oaxaca, and Chiapas); the Mexican Gulf (Fig 2h) extends along the coast of the Mexican Gulf in eastern Mexico, Belize, and northern California; Chiapas (Fig 2i) extends along southern Mexico, Guatemala, and Nicaragua, basically corresponding to the Sierra Madre de Chiapas, between 500 and 2,000 m bsl.

The South American taxa are located in several provinces (Morrone 2000, 2001a,b, 2006). Pantanal province (Fig 2j) comprises southern and central Brazil, northwestern Bolivia, and northern Paraguay; Yungas province (Fig 2k) extends from northern Peru to northwestern Argentina; Puna province (Fig 2l) comprises eastern Bolivia, northern Argentina and Chile and southern Peru; Chaco province (Fig 2m) comprises southern Bolivia, western Paraguay, southern Brazil, and central–north Argentina; Pampa province (Fig 2n) comprises central and western Argentina (between 30° and 39°S), Uruguay, and the south eastern Brazilian state; Parana Forest province (Fig 2o) comprises southeastern Brazil, northeastern Argentina, and eastern Paraguay; Prepuna province (Fig 2p) comprises central and northwestern Argentina, and the Monte province (Fig 2q) comprises central Argentina, between 24° and 43°S. Finally, few species are distributed in the central Patagonia province (Fig 2r) which extends in southern Argentina from central Mendoza, widening through and occupying the eastern part of the southern tip of South America.

These taxa are more commonly found in semiarid and arid zones that have undergone extensive anthropogenic changes. They are often abundant in low-lying roadsides habitats adjacent to grazing areas or crops lands. Despite of the

Fig 1 North American biogeographic provinces. The obtained map is from Udvary (1975): **a** Sierra Cascade province; **b** Californian province, **c** Great Basin province, **d** Rocky Mountain province, **e** Canadian Taiga province, **f** Grassland province, **g** Eastern Forest province, and **h** Sonoran province.

interest in the group, their large-scale distribution has received little attention. We provide an analysis on the distributional data for taxa belonging to *E. maculata* group and established patterns of distribution of the ancestral biota and areas where species of this group have interacted.

Material and Methods

Geographical records were mainly obtained from specimens examined in Campos-Soldini & Roig-Juñent (In Press) deposited in the following collections: CICyTTP-CONICET (María Paula Campos-Soldini): *Centro de Investigaciones Científicas y Transferencia de Tecnología a la Producción* (Entre Ríos-Argentina), IADIZA, CCT-CONICET (Sergio Roig-Juñent): *Instituto Argentino de Investigaciones de las Zonas Áridas* (Mendoza-Argentina), FIMLA (Gustavo Scrocchi): *Fundación Instituto Miguel Lillo* (Tucumán-Argentina), MLPC (Analía Lanteri): *Museo de La Plata* (La Plata-Argentina); MCNFA (Carlos Virasoro): *Museo Provincial de Ciencias Naturales* "*Florentino Ameghino*" (Santa Fe-Argentina), MACN (Arturo Roig-Alsina): *Museo Argentino de Ciencias Naturales* "Bernardino Rivadavia" (Buenos Aires-Argentina), Florida Department of Agriculture and Consumer Services Division of Plant Industry (Kyle E. Schnepp), and from the literature (Bruch 1914, Bosq 1934, 1943, Hayward 1942, Viana & Williner 1974, Pinto 1980, 1991, Martínez 1992, Di Iorio 2004).

The distributional data of 24 species of the *E. maculata* group from America, previously treated in a phylogenetic analysis by Campos-Soldini & Roig-Juñent (In Press), have been analyzed: thirteen of them from North and Central America—*E. abeona*, *E. andersoni*, *E. apache*, *E. horni*, *E. jeffersi*, *E. maculata*, *E. magnomaculata*, *E. normalis*, *E. ocellata*, *E. pardalis*, *E. phoenix*, *E. proscripta*, and *E. ventralis*—and eleven from South America—*E. adspersa*, *E. atomaria*, *E. cavernosa*, *E. dilatipennis*, *E. fulvicornis*, *E. koheleri*, *E. lizeri*, *E. minutepunctata*, *E. nigropunctata*, *E. pluvialis*, and *E. rubella*. Species with one local or with imprecise data were excluded from analysis (*E. rubella*).

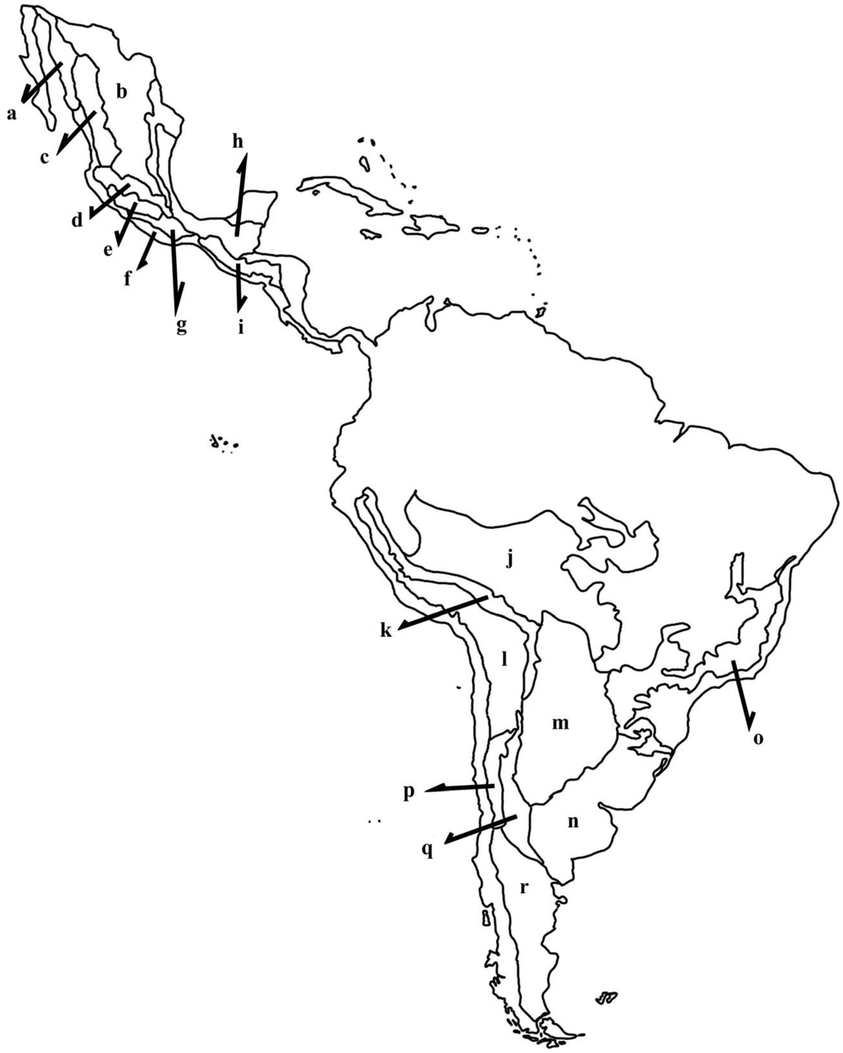

Fig 2 Central America and South America biogeographic provinces. The obtained map is from Morrone (2000): **a** Sonoran province; **b** Mexican Plateau; **c** Sierra Madre Occidental province; **d** Transmexican Volcanic Belt province, **e** Balsas Basin province, **f** Mexican Pacific Coast province, **g** Sierra Madre del Sur province, **h** Mexican Golf province, **i** Chiapas province, **j** Pantanal province, **k** Yunga province, **l** Puna province, **m** Chaco province, **n** Pampa province, **o** Parana Forest province, **p** Prepuna, **q** Monte province, and **r** Central Patagonia province.

The Croizat's method was basically to plot distributions of organisms on maps and connect the disjunct distribution areas or collection localities together with lines called tracks. Individual tracks for unrelated groups of organisms were then superimposed, and if they coincided, the resulting summary lines were considered generalized tracks. Generalized tracks indicate the preexistence of ancestral biotas, which subsequently became fragmented by tectonic and/or climatic changes. There are three basic panbiogeographic concepts. The *individual track* represents the spatial coordinates of species or group of related species and operationally is a line graph drawn on a map of their locations or distribution areas, connected according to their geographical proximity (Craw 1983, 1988, 1989, Croizat 1958, Croizat *et al* 1974, Craw & Page 1988, Grehan 2001). The *generalized track* represents coinciding tracks for unrelated taxa or groups that constitute a generalized or standard track (Page 1897, Craw 1979, 1989), which provides a spatial criterion for biogeographic homology (Grehan 1988). The *node* is the area where two or more generalized track intersects. It means that different ancestral biotic and geological fragments interrelated in space/time as a consequence of the collision, docking, or suturing of the terrain, thus constituting a composite area (Morrone & Crisci 1995, Craw *et al* 1999).

Locations, individual and generalized tracks, and nodes were represented on maps using QGIS 2.4.0 (Quantum GIS 2.4.0). Localities were connected according to their geographical proximity, using minimum spanning tree methods. Generalized tracks and nodes were characterized following the regionalization of Morrone (2000, 2006, 2010) for Mexico Central America and South America, and Udvary (1975) and Katinas *et al* (2004) for the USA.

Results

Individual tracks

The individuals track (Figs 3 and 4) corresponds to the species of the *E. maculata* group listed above.

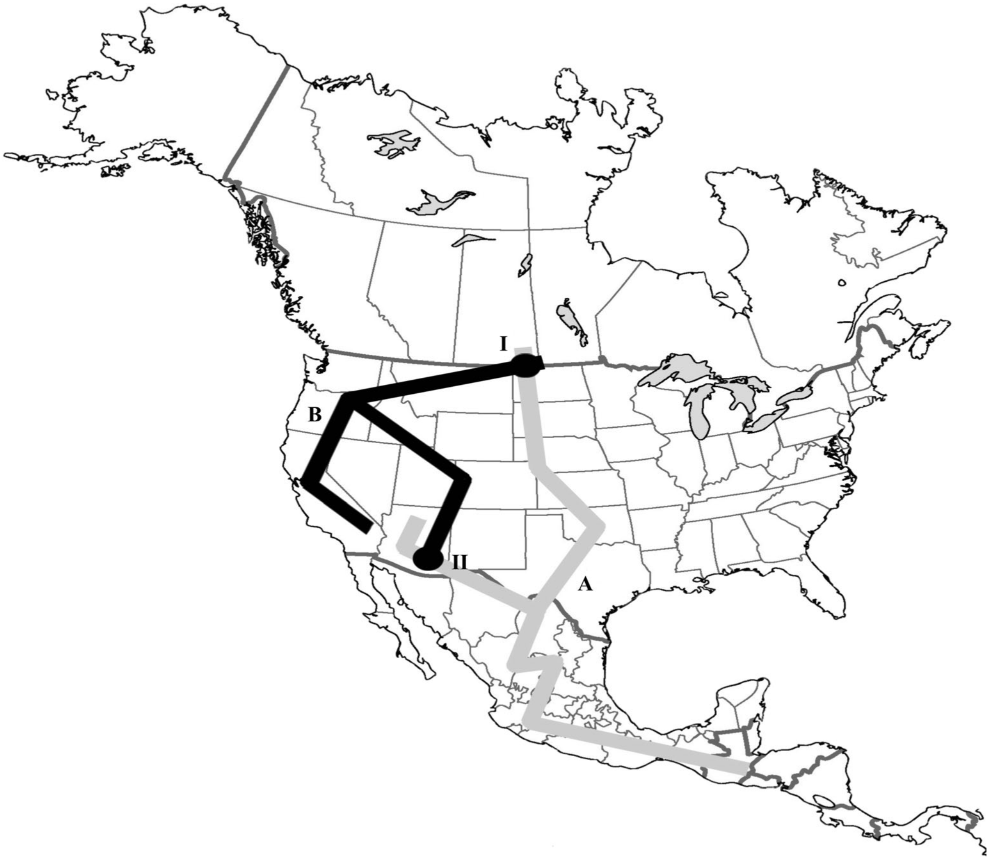

Fig 3 North–Central generalized tracks represented by 13 species: Track "*A*" (*Epicauta abeona*, *Epicauta andersoni*, *Epicauta apache*, *Epicauta horni*, *Epicauta jeffersi*, *Epicauta maculata*, *Epicauta ocellata*, *Epicauta pardalis*, *Epicauta phoenix*, and *Epicauta proscripta*); Track "*B*" (*Epicauta magnomaculata*, *Epicauta normalis*, and *Epicauta ventralis*); nodes '*I*' located in northern USA and '*II*' located in southwestern USA at the intersection of the generalized tracks "*A*" and "*B*".

In North and Central America (Fig 3)

Epicauta abeona (17 specimens) is distributed in central Mexico (Aguascalientes, Distrito Federal, Durango, Jalisco, Mexico, Michoacan, and Nayarit). *Epicauta andersoni* (38 specimens) is distributed from south and central United States to northern and central Mexico; and in the USA (Arizona, Colorado, Kansas, New Mexico, Oklahoma, Texas, and Utah). *Epicauta apache* (86 specimens) is distributed from southern and central United States to northern and central Mexico; and in USA (Arizona, Kansas, Nebraska, New Mexico, Oklahoma, and Texas). *Epicauta jeffersi* (16 specimens) is endemic to United States and is distributed in southern and central USA (Arizona, Colorado, New Mexico, Oklahoma, and Texas). *Epicauta maculata* (188 specimens) is distributed from south and central Canada, through middle United States, Mexico to Guatemala; in Canada (Manitoba, Ontario, and Saskatchewan); and in the USA (Arizona, Colorado, Illinois, Iowa, Kansas, Missouri, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, and Texas); in Mexico (Aguascalientes, Chihuahua, Coahuila, Distrito Federal, Durango, Guanajuanto, Hidalgo, Jalisco, Mexico, Michoacan, Nuevo Leon, Oaxaca, Querétaros, Sonora, and Zacatecas); and in Guatemala (Chichicastenango and Huehuetenango). *Epicauta magnomaculata* (12 specimens) is endemic to the United States and is distributed in Midwest USA (California). *Epicauta normalis* (79 specimens) is distributed from south and central Canada to Midwest United States; in Canada (Alberta, Saskatchewan); and in the USA (Arizona, California, Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oregon, Utah, and South Dakota). *Epicauta ocellata* (12 specimens) is endemic to Mexico and is distributed across central Mexico (Coahuila, Durango, Morelos, Oaxaca, Puebla, and San Luis Potosí). *Epicauta pardalis* (59 specimens) is distributed from south and central United States to north and central Mexico; in USA (Arizona, New Mexico, Texas); and in Mexico (Aguascalientes, Chihuahua, Coahuila, Durango, Jalisco, Sonora). *Epicauta phoenix* (15 specimens) is distributed from southwest United States to northwest Mexico; in USA (Arizona and California); and in Mexico (Baja California). *Epicauta ventralis* (120 specimens) is distributed from central Canada to Midwest United States; in Canada (Alberta, Saskatchewan); and in the USA (Arizona, California, Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, Oregon, Utah, Washington, Wyoming).

In South America (Fig 4)

Epicauta adspersa (35 specimens) is endemic to Argentina and is distributed in Buenos Aires, Córdoba, Entre Ríos, Mendoza, Neuquén, La Pampa, La Rioja, Río Negro, San

Fig 4 South America generalized tracks represented by 11 species: Track "*C*" (*Epicauta dilatipennis*, *Epicauta koheleri*, *Epicauta minutepunctata*, and *Epicauta nigropunctata*); Track "*D*" (*Epicauta adspersa*, *Epicauta atomaria*, *Epicauta cavernosa*, *Epicauta fulvicornis*, *Epicauta lizeri*, and *Epicauta pluvialis*). Neotropical nodes '*III*' to '*VI*' at the intersections of the generalized tracks "*C*" and "*D*".

Juan, Santa Fe, and Santiago del Estero. *Epicauta atomaria* (53 specimens) is distributed in Argentina (Buenos Aires, Catamarca, Córdoba, Corrientes, Chaco, Entre Ríos, Jujuy, La Rioja, Mendoza, Misiones, Neuquén, Salta, San Juan, San Luis, Santa Fe, Santiago del Estero, and Tucumán), Bolivia (Chulumaní, Río Bermejo, Río Negro, and Tarija), Brazil (Encruzilhada and Río Prado), Paraguay (Asunción, Departamento de San Pedro Carumbe, Río Negro, and Villa Rica), and Uruguay (Montevideo, Peñarol, Piriapolis, Cerro Largo, and Cuchilla de Melo). *Epicauta cavernosa* (19 specimens) is distributed in Argentina (Buenos Aires, Córdoba, San Luis, Mendoza, and San Luis) and Uruguay (Maldonado, Cerro Pelado, Cerro Largo, Cuchilla de Melo, Fraile Muerto, Punta del Este, and Chuy). *Epicauta dilatipennis* (two specimens) is endemic to Argentina and is distributed in Misiones and Santiago del Estero. *Epicauta fulvicornis* (ten specimens) is endemic to Argentina and is distributed in Chaco, Corrientes, Entre Ríos, Formosa, La Rioja, and Santa Fe. *Epicauta koheleri* (11 specimens) is distributed in Argentina (Mendoza, Neuquén, and Río Negro) and Bolivia (Coroico-Nor Yungas, La Paz, and Chulumaní). *Epicauta lizeri* (five specimens) is endemic to Argentina and is distributed in Catamarca, Salta, and Tucumán. *Epicauta minutepunctata* (15 specimens) is endemic to Argentina and is distributed in Jujuy, Salta, San Luis, and Tucumán. *Epicauta nigropunctata* (12 specimens) is distributed in Argentina (Chaco and Misiones) and Bolivia (Chulumaní and Coroico). *Epicauta pluvialis* (17 specimens) is endemic to Argentina and is distributed in Chubut and Mendoza.

Based on the overlap of 20 individual tracks, four generalized tracks were identified. These tracks were constituted by a different number of species, and two of them are located in the Nearctic region and Mexican transition zone, herein called tracks "A" and "B" (Fig 3a, b). Two other tracks are located in the Neotropical region, herein called tracks "C" and "D" (Fig 4c, d).

The generalized track "A" (Fig 3a) is supported by the individual tracks of *E. abeona*, *E. andersoni*, *E. apache*, *E. jeffersi*, *E. maculata*, *E. ocellata*, *E. pardalis*, and *E. phoenix*. This track is distributed from southern Guatemala, along Mexico (Chiapas, Oaxaca, Puebla, Morelos, Estado de México, Michoacán, Guanajuato, north of Jalisco, through Zacatecas, Durango, and east of Chihuahua) to south–central Texas, where it branches in one generalized track distributed along northwest of the Río Grande, entering USA through southwest New Mexico and continuing through Arizona state, and in one track distributed in Texas, New Mexico, Colorado, Nebraska, South Dakota, North Dakota, and southeastern Saskatchewan through the Great Plains, at sea level.

The generalized track "B" (Fig 3b) is supported by three individual tracks of *E. magnomaculata*, *E. normalis*, and *E. ventralis*. This track is distributed from southeast Saskatchewan (Canada) through northwestern USA, to north Montana, Idaho, and north Oregon. This track branches forming a track that is distributed along eastern Oregon, through eastern California state, and along Sierra Nevada, and another track that is distributed through central Idaho, northwestern Wyoming, west of Colorado state, and through southeastern Arizona, biogeographic provinces usually over 450 m up to about 1,900 m bsl.

The generalized track "C" (Fig 4c) is supported by four individual tracks: *E. dilatipennis*, *E. koheleri*, *E. minutepunctata*, and *E. nigropunctata*. This generalized track is located between 15° and 35°S in Argentina, Bolivia, and Paraguay. It is directed from south to north, beginning in the southeast of Rio Negro and upwardly through south of provinces La Pampa and San Luis, east of Catamarca, Tucumán, Salta, and Jujuy; crossing Bolivia by southwest of Potosi, Oruro, and La Paz. In Bolivia (La Paz), this track is directed to the southwest through Cochabamba, continuing to Chuquisaca and Tarija, then entering Argentina by northeast of Salta, passing by the north of Formosa, and crossing Paraguay in the south of and returning to Argentina through north of Misiones.

The generalized track "D" (Fig 4d) is supported by six individual tracks: *E. adspersa*, *E. atomaria*, *E. cavernosa*, *E. fulvicornis*, *E. lizeri*, and *E. pluvialis*. This generalized track is located between 12° and 39°S in Argentina, Bolivia, Paraguay, and Brazil. It runs from east to west beginning in west–central Mendoza, San Luis, Cordoba, Santa Fe, and northwest Entre Ríos where it branches in one generalized track distributed along the north of República Oriental del Uruguay in the Departments of Salto, Rivera, Cerro Largo, Treinta y Tres in the north, and Rocha, Maldonado, and Canelones in the west; and in a track distributed from northwest Entre Ríos and upwards through Corrientes, crossing to Paraguay by Ñeembucu, east of Misiones, Paraguarí, Cordillera, San Pedro, Concepción, and Amambay, then to Brazil through Mato Grosso do Sul to the central–south region of Mato Grosso.

Six nodes were recognized (Fig 3 I and II; Fig 4 III to VI). Two of them are included in the Nearctic Region, node 'I' located in northern USA at the intersection of tracks "A" and "B", and node 'II,' located in southwestern USA at the intersection of the same tracks. These nodes are located in the Grassland and Sonoran biogeographic provinces, respectively (Fig 3 I–II). The other four are included in the Neotropical Region at the intersection of tracks "C" and "D": node 'III' is located in central–south Bolivia close to the border with Argentina. This node is in the Chaco province, comprising southern Bolivia, western Paraguay, southern Brazil, and central–north Argentina (Fitakku 1969, Cabrera & Willink 1980, Willink 1988, Morrone 1999, 2006). Node 'IV' is located in the east of Paraguay close to the border with Argentina. Node 'V' is located in the northwest of Argentina, in Puna province (Cabrera & Willink 1980, Dinerstein *et al* 1995, Morrone 1994, 1999, 2001a, b). Node 'VI' is located in the central–west of Argentina, in the Monte province, and comprises central Argentina between latitudes 24° and 43°S (Cabrera & Willink 1980, Müller 1973, Rivas-Martínez & Navarro 1994, Morrone 2000, 2001a). These last nodes (V and VI) are particularly located in the South American transition zone (Morrone 2001a, b) (Fig 4 III to VI).

Discussion

The geological and climatic processes in the past provide at least partial explanations for the current biogeographical patterns of the *E. maculata* group in America. The geological history of America is particularly uncertain and has been subject to much debate between biologists (Rosen 1976, Pregill 1981, Briggs 1984) and geologists (Donnelly 1985). During the Cenozoic era, North and South America remained geographically isolated for several millions years until they became connected again via the Panama Island Arc (15 mya) and later across the Panama Isthmus in the late Pliocene. Lewis (1966) and Raven & Axelrod (1974) provided another explanation for the current biogeographical patterns in America. They considered that the similarity between the desert in North and South America is due to long distance dispersal, and thus, the semiarid conditions during glacial ages favored a corridor between North and South America. In spite of this dispersal hypothesis, the clear division of the *E. maculata* group in North and Central America and in South America suggests that the separation of these taxa occurred because of the isolation of South America in the Cenozoic. This barrier affects other organisms both from arid and semiarid subtropical areas, like the species of the *E. maculata* group. Thus, it seems that the species of *E. maculata* group could have had a broad and ancient ancestral area of distribution, including North, Central, and South America.

The central and north generalized tracks and southern generalized tracks of the *E. maculata* group here obtained represent an ancestral biota widely distributed in the past. The central and north generalized tracks include the actual Nearctic regions and Mexican transition zones; the other two tracks include the actual Neotropical region and South American transition Zone. According to Craw *et al* (1999), the spatial homology indicative of an ancestral biota should be supported by the presence of a baseline. Thus, it should be noted that the identification of the spatial homology for the geographic areas dealt with requires complex and interdisciplinary analyses. Therefore, the generalized tracks that were constructed by the individuals tracks in this analysis are accepted as representatives of an ancestral biota (primary biogeographic homology), until the baselines that acted in the past can be identified.

The generalized tracks located in North–Central America ("A" and "B") are represented by 13 species (*E. abeona*, *E. andersoni*, *E. apache*, *E. horni*, *E. jeffersi*, *E. maculata*, *E. magnomaculata*, *E. normalis*, *E. ocellata*, *E. pardalis*, *E. phoenix*, *E. proscripta*, and *E. ventralis*) and correspond to the Nearctic, the Mexican transition zone, and Neotropical region (Udvary 1975, Morrone *et al* 1999). Track "A" partially coincides or completely matches with several other tracks identified for plant species (Katinas *et al* 2004), mammals (Lomolino & Smith 2001, Escalante *et al* 2004), and several insect groups (Rosas *et al* 2011, Márquez & Morrone 2003, Abrahamovich *et al* 2004)". No matching tracks were found for the generalized track "B". The intersection of these tracks (A–B) forms two nodes: Node 'I' is located by the limit of the Canadian taiga and Grassland provinces, and node 'II' is located in the Sonoran province, both from Nearctic region (Udvary 1975, Morrone 2006). The presences of these two tracks ("A" and "B") suggest that the geological and climatic processes that happened in the past have restricted the dispersal and favored speciation in two different areas in this part of continent. The geological and climatic processes in the past provide at least partial explanations for the current biogeographical patterns in North and Central America. Major historical events in this area include orogenic processes such as the uplifting of the Rocky Mountains, the Sierra Madre, and the western Cordillera (Graham 1999). The uplifting of the Rocky Mountain, together with the uplifting of the Sierra Madre Occidental in the early Tertiary, remarkably changed the biota in western North America, creating a barrier between eastern and western North America. From the late Oligocene (25 mya) throughout the Pliocene, new orogeny gave rise to the present western Cordilleran System, including major deformation and uplift of the Rocky Mountains, Sierra Nevada, Sierra Madre Occidental, and Sierra Madre Oriental (Axelrod and Raven 1985, Wing 1987, Graham 1993). These changes resulted in the cooler and drier climates that brought about the development of grasslands in central North America.

The generalized tracks located in South America ("C" and "D") are represented by 11 species (*E. adspersa*, *E. atomaria*, *E. cavernosa*, *E. dilatipennis*, *E. fulvicornis*, *E. koheleri*, *E. lizeri*, *E. minutepunctata*, *E. nigropunctata*, *E. pluvialis*, and *E. rubella*) and correspond to the Neotropical and South American transition zone (Morrone *et al* 1999). Track "C" coincidentally or completely matches with several other tracks such as those in Candela & Morrone (2003), López Ruf *et al* (2006), and Flores & Pizarro-Ayara (2006). The track "D" coincides with the generalized tracks '2 and 3' of López Ruf *et al* (2006) and partially coincides with Southern Mesoamerican generalized track of Abrahamovich *et al* (2004) for insects species, and partially coincides with generalized track '2' of Candela & Morrone (2003) for mammals species. The intersections of these tracks forms four nodes: Node 'III' is located in the Chaco province that comprises southern Bolivia, western Paraguay, southern Brazil, and central–north Argentina (Cabrera & Willink 1980, Dinerstein *et al* 1995, Morrone 2000, 2001a, b, Müller 1973, Rivas-Martínez and Navarro 1994); node 'IV' is located in the Parana Forest province that comprise southeastern Brazil, northeastern Argentina, and eastern Paraguay (Cabrera & Willink 1980, Dinerstein *et al* 1995, Morrone 2006), and the other two nodes (nodes 'V and VI') are located in the South American transition zone that extends along the highlands of the Andes between western Venezuela, northern Chile, and central–west Argentina (Morrone 2004). The presences of these two tracks ("C" and "D") support the hypothesis that South America is an area where numerous biotic interrelationships have occurred. This may be because of the isolation of portions of land due to marine ingressions covering large areas in this region during the Neogene (Cenozoic) and/or because of physiographic changes due to different orogenies that caused major climate changes (Barreda *et al* 2007). The four nodes that have been established in South America indicate that this group of species, as well as the rest of the biota of this region, has had a complex history where Neotropical elements have converged. One possible explanation is that the changes in the biota of South America originated due to cyclical shifts of Antarctic and Neotropical biota in the Cenozoic.

The *E. maculata* group has its greatest diversity in the northern and southern parts of South America. The cladogram of the group (Campos-Soldini & Roig-Juñent In Press) shows a southern–northern direction of evolutionary change, suggesting a Neotropical origin of their ancestors. The four nodes here obtained support this hypothesis and suggest that this genus, possibly like the rest of the biota of this region, has had a complex history. We believe that the ancestors of the *E. maculata* group probably expanded their ranges from South to Central and North America. This group was able to grow and diversify in different regions, possibly following different pathways. They are found in semiarid and arid zones of America that have undergone extensive anthropogenic changes. They are often abundant in low-lying roadsides habitats adjacent to grazing areas and croplands. These results constitute a preliminary contribution to the understanding of the distribution patterns of the *E. maculata* group under an evolutionary biography. Future biogeographic analyzes including other species groups of *Epicauta* will enable a deeper understanding of the evolution of the biota of America.

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