REVIEW

Evolutionary Developmental Biology (Evo-Devo) Research in Latin America

JOURNAL OF EXPERIMENTAL ZOOLOGY
PART B
MOLECULAR AND DEVELOPMENTAL EVOLUTION

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ABSTRACT Famous for its blind cavefish and Darwin's finches, Latin America is home to some of the richest biodiversity hotspots of our planet. The Latin American fauna and flora inspired and captivated naturalists from the nineteenth and twentieth centuries, including such notable pioneers such as Fritz Müller, Florentino Ameghino, and Léon Croizat who made a significant contribution to the

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Received 24 March 2016; Revised 16 June 2016; Accepted 20 June 2016
DOI: 10.1002/jez.b.22687
Published online in Wiley Online Library (wileyonlinelibrary.com).

study of embryology and evolutionary thinking. But, what are the historical and present contributions of the Latin American scientific community to Evo-Devo? Here, we provide the first comprehensive overview of the Evo-Devo laboratories based in Latin America and describe current lines of research based on endemic species, focusing on body plans and patterning, systematics, physiology, computational modeling approaches, ecology, and domestication. Literature searches reveal that Evo-Devo in Latin America is still in its early days; while showing encouraging indicators of productivity, it has not stabilized yet, because it relies on few and sparsely distributed laboratories. Coping with the rapid changes in national scientific policies and contributing to solve social and health issues specific to each region are among the main challenges faced by Latin American researchers. The 2015 inaugural meeting of the Pan-American Society for Evolutionary Developmental Biology played a pivotal role in bringing together Latin American researchers eager to initiate and consolidate regional and worldwide collaborative networks. Such networks will undoubtedly advance research on the extremely high genetic and phenotypic biodiversity of Latin America, bound to be an almost infinite source of amazement and fascinating findings for the Evo-Devo community. *J. Exp. Zool. (Mol. Dev. Evol.) 00:1–36, 2016.*

How to cite this article: Marcellini S, González FA, Sarrazin AF, Pabón-Mora N, Benítez M, Piñeyro-Nelson A, Rezende GL, Maldonado E, Schneider PN, Grizante MB, Da Fonseca RN, Vergara-Silva F, Suaza-Gaviria V, Zumajo-Cardona C, Zattara EE, Casasa S, Suárez-Baron H, Brown FD. 2016. Evolutionary developmental biology (Evo-Devo) research in latin america. J. Exp. Zool. (Mol. Dev. Evol.) 00:1–36.

J. Exp. Zool. (Mol. Dev. Evol.) 00:1–36, 2016

"Evolutionism in general from mollusks and birds to mammals: what, finally, Empedocles said and Aristotle wrote" title in Léon Croizat's *Space, Time, Form* ('64:481)

INTRODUCTION

Evolution and development are two fields in biology that were considered to be associated and complementary to each other since their conception. Just 4 years after publication of Darwin's *opus magna*, Fritz Müller proposed what came to be the first Evo-Devo explanation of von Baer's laws of embryology, which soon became further expanded in Ernst Haeckel's biogenetic law (von Baer, 1828; Darwin, 1859; Haeckel, 1866; Müller, 1869). At the end of the nineteenth century, the philosophical rift between naturalism and experimentalism split these twin fields apart. As a result, evolutionary biology and developmental biology remained mostly isolated from each other until the second half of the twentieth century, when foundational developmental genetic experiments started rebuilding bridges between the development and evolution of form and function (Raff and Kaufman, '83). The pioneering works of Richard Goldschmidt and Stephen Jay Gould (Goldschmidt, '40; Gould, '77a, '77b) eventually led to 1981's Dahlem Workshop on Evolution and Development, which set out an agenda to "pry open the black box [of development]" (Haag and Lenski, 2011) and became an early milestone of modern Evo-Devo. Since then, a number of highly influential books (e.g., Raff and Kaufman, '83; Gerhart and Kirschner, '97; Carroll et al., 2005) have inspired researchers to combine evolutionary and developmental approaches. Evo-Devo has proven to be a dynamic, multidisciplinary and hotly debated field (Gilbert et al., '96; Sommer, 2009; Parsons and Albertson, 2013; Wray et al., 2014; Moczek et al., 2015; Pieretti et al., 2015; Roux et al., 2015). It has fostered the establishment of several specialized journals (e.g., *Evolution & Development*; *Evo-Devo*; *Development, Genes, and Evolution*; *Journal of Experimental Zoology, Part B: Molecular and Developmental Evolution*), journal sections (e.g., Evolution of Developmental Control in Developmental Biology; Evolutionary Developmental Biology in *Frontiers in Ecology and Evolution*; Evolutionary Developmental Biology in *Neotropical Biodiversity*), and scientific societies (Euro Evo-Devo and PanAm Evo-Devo). Hence, the number of articles that mention "Evo-Devo" or equivalent terms and synonyms per year has been increasing steadily since the mid-1990s (Fig. 1A). In Latin America, Evo-Devo is only starting to emerge when compared to scientific output in the rest of the world (Fig. 1A), but also displays a pronounced and steady growth in its use as a concept in the scientific literature (Fig. 1B). As part of the Latin American community, we took advantage of the inaugural meeting of the PanAmerican Society for Evo-Devo (August 5–9, 2015, in Berkeley, CA) to organize a workshop aimed at discussing the current challenges of Evo-Devo in Latin America (Lesoway, 2016; Specht, 2016). One of the issues identified in this workshop was the lack of visibility of Latin American research. In this review, we sought to highlight the work of forerunners of Evo-Devo research in Latin America and to comment

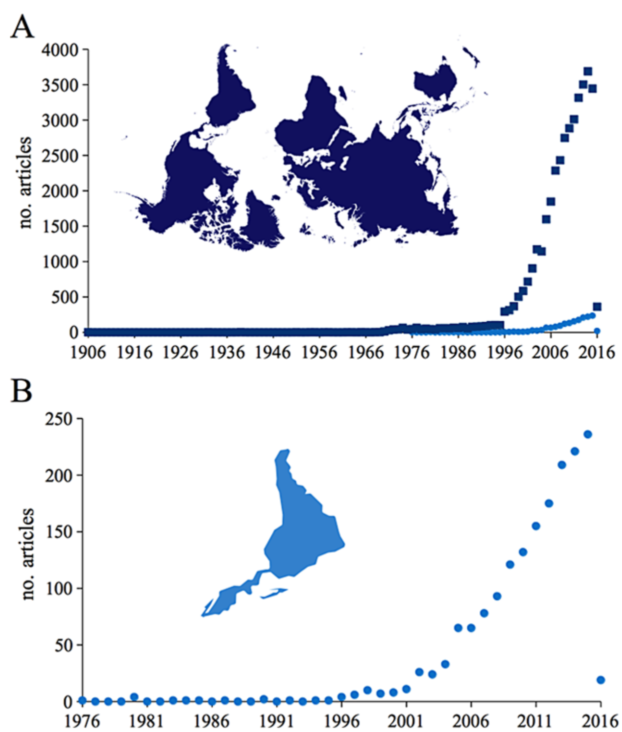

Figure 1. Usage of the word "Evo-Devo" (and all its synonyms in English, Spanish, or Portuguese) expands rapidly in the world scientific literature in the mid-1990s, and only 5 years later in Latin America. (A) Number of articles that use "Evo-Devo" or equivalent terms in the world (dark blue squares) and in Latin America (light blue circles); (B) number of articles that use "Evo-Devo" or equivalent terms in Latin America only (light blue circles). Synonyms used in the Scopus database search (1906–2016): "evo-devo" or "evodevo" or "evolutionary developmental biology" or "evolution and development" or "evolution & development" or "biología del desarrollo evolutiva" or "biologia del desarrollo evolutiva" or "biología evolutiva del desarrollo" or "biología evolutiva del desarrollo" or "biologia do desenvolvimento evolutiva" or "biologia evolutiva do desenvolvimento". South-up maps or upside down maps, as proposed by Uruguayan artist Joaquín Torres García (1874–1949) or Argentinean cartoonist Quino (1932–present).

on cutting-edge Evo-Devo research carried out by several groups in the region. It is clear that the great and unique biodiversity in Latin America contributes to understanding fundamental principles of evolution, Evo-Devo, or Ecological Evo-Devo (Eco-Evo-Devo); thus, researchers from this region are best poised to address many important and interesting questions in the field.

LATIN AMERICA: A LIVING LABORATORY FOR EVO-DEVO RESEARCH

One can only marvel at the staggering biodiversity of Latin America. Three of five leading biodiversity hotspots (Tropical Andes, Brazil's Atlantic Forest, and Caribbean) are located in this region, which together holds nearly 12% of the world's endemic plant species (Myers et al., 2000). This is not surprising knowing that the Neotropics are estimated to house about 100,000 plant species (Stoll, 2012). Furthermore, in a single hectare of the Western Amazon over 300 species of trees can be found, the same number of species found in the whole of Eastern North America (Wade, 2015). If Mesoamerica is included into the biodiversity hotspots mentioned above, these four regions alone serve as shelter to 15% of the world's endemic vertebrate species (Myers et al., 2000). The Neotropics are estimated to have 40% (approximately 4000) of bird species in the world (Stotz et al., '96). Similarly, South America alone contains a third (approximately 1700) of all anuran species, with nearly 96% of these being endemic to the region (Duellman, '99; www.amphibiaweb.org).

Present-day diversity is the result of millions of years of biologic, oceanographic, geologic, and climatologic changes. Present day diversity in the Neotropics is proposed to have been generated by events dating back to the early Miocene (15–23 Mya) when the Caribbean sea poured into South American northwestern regions forming an enormous marine estuary about the size of Bolivia or Colombia (approximately 1,100,000 km^2), a tangle of saltwater, freshwater, and terrestrial habitats that prompted speciation (hence, pink dolphins and stingrays inhabit the Amazon river). The uplifting of the Andes (10–65 Mya) accelerated speciation events as it generated environmental altitudinal clines, mountaintops (known as Páramos) (Madriñan et al., 2013), and isolated valleys, trapping precipitation, and inducing the formation of lakes and rivers (Wade, 2015). Between 14 and 3.5 Mya, South and North America joined as the Isthmus of Panama arose from the seas when the Central American volcanic arc collided with South America. Through this narrow strip of land armadillos, opossums, capybaras, giant sloths, porcupines, and terror birds crossed from south to north, whereas horses, parrots, peccaries, rabbits, deer, llamas, bears, cougars, and saber-toothed cats migrated from north to south (Carrillo et al., 2014). In fact, South American porcupines can be found in Alaska today as a result of this large-scale event of migration and radiation (Wood, '50). Many plants, insects, fungi, and freshwater fish crossed both sides as well (Stone, 2013). Although the timing of closure of the isthmus remains contentious, the rich biodiversity in Central and South America serve as evidence for the explosive adaptive radiation that followed this event (Bacon et al., 2015; Stone, 2013).

Naturalists from different parts of the world have recognized the biodiversity in Latin America as central to biological discovery. In their youths, Humboldt, Darwin, Wallace, Bates,

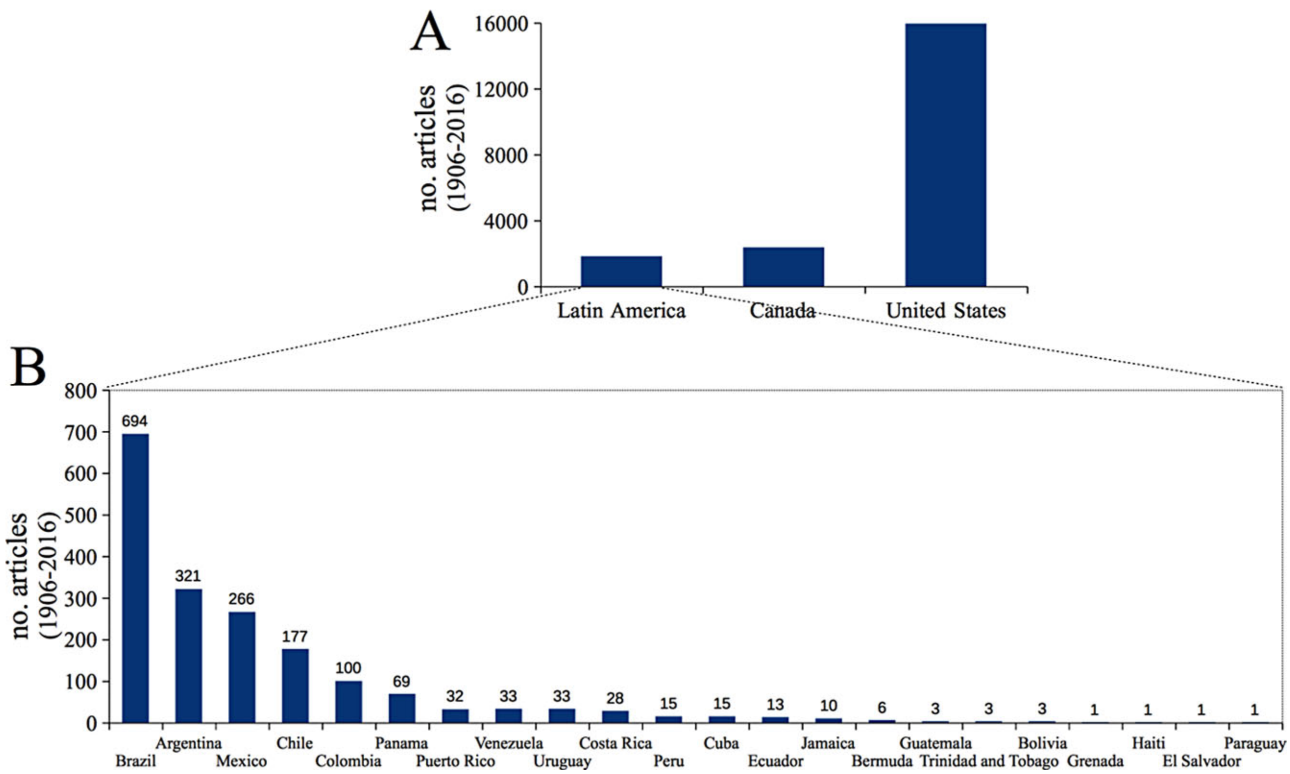

Figure 2. Usage of the word "Evo-Devo" (and all its synonyms in English, Spanish, or Portuguese) in the scientific literature of all Latin American countries parallels that of Canada, but is eight times lower than in the United States. (A) Number of articles that mention "Evo-Devo" or equivalent terms is dominated by the United States in the Pan-American region. (B) In Latin America, the term is used predominantly by the scientific regional powerhorses: Brazil, Mexico, Argentina, and Chile. Synonyms used in the Scopus database search (1906–2016) are the same as described in Figure 1.

and Spruce were awed by the diversity of shapes, colors, and behaviors of the organisms they observed. As a result, natural history observations made in this region of the world helped to shape many central ideas of evolutionary biology. From Darwin's early observations to modern biological analyses, biodiversity in Latin America has played a central role for our understanding of intra- and interspecific variation (Grant and Grant, 2006.; Gross et al., 2009; Yoshizawa et al., 2012; Lamichhaney et al., 2015). It continues to provide a "living laboratory" to observe natural selection and mimicry in action and to untangle interesting biogeographic patterns. Modern tools to address large-scale biological studies in largely unexplored diversity or unique ecosystems of Latin American open up new possibilities to uncover novel evolutionary and developmental principles.

But what is the contribution of the Latin American scientific community to Evo-Devo? An increase in papers mentioning "Evo-Devo" or equivalent terms in articles published by authors from Latin American institutions occurred just recently, around 2003 (Fig. 1B). The number of articles related to the evolution of developmental processes from the whole Latin American community is far lower than that of the United States and slightly inferior to that of Canada (Fig. 2A); within Latin America, most articles are from Brazil, Argentina, Mexico, and Chile (Fig. 2B). As no keyword searches can efficiently and exhaustively retrieve Evo-Devo articles, we reasoned that recent work published in four journals overtly dedicated to Evo-Devo could be used as a proxy to compare the activity of Evo-Devo laboratories among Pan-American countries (Fig. 3). Again, this analysis shows that total Latin American production is considerably lower than that of the United States and a bit lower than that of Canada (Fig. 3A). For instance, the United States alone contributed to almost 30% of Evo-Devo articles, whereas Latin America accounted for 3% of articles published in these journals (Fig. 3B). However, normalizing these results to the number of articles published per country in all disciplines of biology indexed in PubMed during the same period reveals similar relative productivities for North America (around three articles published in these four journals per 10,000 biology articles) and Latin America (between 0.9 and

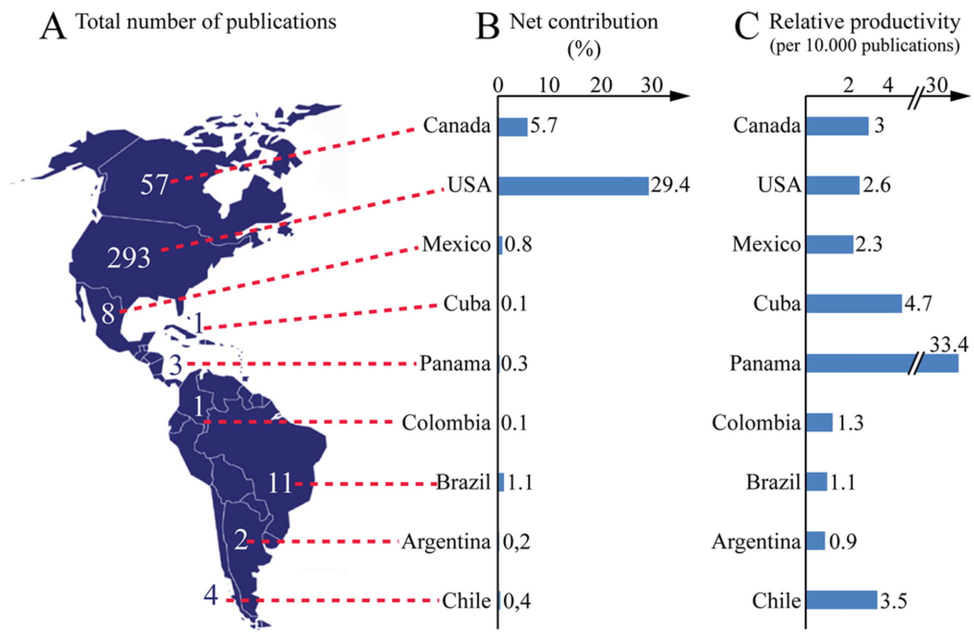

Figure 3. Recent contribution of Pan-American researchers to four journals overtly dedicated to Evo-Devo: *Dev Genes Evol*, *Evol Dev*, *EvoDevo*, and *J Exp Zool B Mol Dev Evol*. Only the 2010–2015 period was considered for this analysis. (A) Total number of publications by country; (B) net contribution of each country to these four journals; (C) number of publications in these four journals per 10.000 publications referenced in PubMed, for each country. Note that the high relative productivity observed for Panama is an artifact resulting from the particularly low total number of publications generated in this country. Source: PubMed, NCBI.

4.7 articles published in these four journals per 10,000 biology articles, depending on the country) (Fig. 3C). While this suggests that the proportional importance of the field in Latin America is on par with that of North America, the absolute number of research groups in each Latin American country (Table 1) is low enough that the disappearance of a single group can significantly impact countrywide productivity of Evo-Devo research. Clearly, Evo-Devo is still in its early days in Latin America; while showing encouraging indicators of productivity, it remains fragile as it relies on few laboratories in each country. Furthermore, this isolation limits opportunities for productive training and collaboration. Such a recent and incipient development of Evo-Devo in Latin America stands in contrast to the notable historical importance of long-standing ideas of evolution in the region.

THE DAWN OF EVOLUTIONARY DEVELOPMENTAL BIOLOGY IN LATIN AMERICA: MÜLLER'S *FÜR DARWIN*, AMEGINHO'S *FILOGENIA*, AND CROIZAT'S *SPACE, TIME AND FORM*

Evo-Devo is a historical discipline that requires a great deal of consilience, the convergence of evidence from independent sources, thus depending on the generation of a common groundwork of explanatory facts and fact-based theories across disciplines (Wilson, '98). Suggestions recently brought up by Latin American philosophers that may help explain the origins of consilience are as follows: (1) Evolutionary developmental biology as a historical discipline has been oriented to study remote causes of specific evolutionary processes highly influenced by models of variation established by Darwinism (Caponi, 2011), and (2) Evo-Devo offers apparently opposite explanations as a result of the distinction among internal/external factors and the relative importance of variation in individuals or populations when examining roles that should be attributed to structure or function, to genes or the environment, to self-regulation or natural selection (Andrade, 2007). Individual disciplines, for example, developmental biology, molecular genetics, comparative morphology, and phylogenetic systematics, have together generated substantial knowledge to allow for consilience required for a successful Evo-Devo program (Edgar and Chinga, 2015).

During most of the twentieth century in Latin America, clerical institutions dominated the teaching of natural sciences; hence college and university education was influenced by theology and religion, as well as philosophical positivism (for Colombian and Mexican historical perspectives on these issues, see Restrepo and Becerra, '95; Argueta Villamar, 2009; Ruiz Gutierrez et al., 2015). From the start of the twentieth century, biologists arduously described many species and studied the diversity of life forms in the region. Trapped in such descriptive approaches, biology

Table 1. A nonexhaustive list of Evo-Devo scientists that have established their own research groups in Latin America

Name	Affiliation	Research interests	Articles related to Evo-Devo[1]
Abdala, Virginia	Universidad Nacional de Tucumán (Argentina)	Tetrapod musculoskeletal development and evolution	– Musculoskeletal anatomical changes that accompany limb reduction in lizards (Abdala et al., 2015) – Life in the slow lane: the effect of reduced mobility on tadpole limb development (Abdala and Ponssa, 2012)
Aboitiz, Francisco	Pontificia Universidad Católica de Chile (Chile)	Evolution and developmental changes in brain connectivity patterns	– Olfaction, navigation, and the origin of isocortex (Aboitiz and Montiel, 2015) – Genetic and developmental homology in amniote brains. Toward conciliating radical views of brain evolution (Aboitiz, 2011)
Álvarez-Buylla, Elena	Universidad Nacional Autónoma de México (Mexico)	MADS-box genes, morphological evolution of plants, bio-mathematical modeling of gene regulatory network dynamics	– Molecular evolution constraints in the floral organ specification gene regulatory network module across 18 angiosperm genomes (Davila-Velderrain et al., 2014) – When ABC becomes ACB (Garay-Arroyo et al., 2012)
Alves, Marccus	Universidade Federal de Pernambuco (Brazil)	Morphological evolution of plants	– Occurrence and evolutionary inferences about Kranz anatomy in Cyperaceae (Poales) (Martins et al., 2015) – Comparative study of ovule and fruit development in species of Hypolytrum and Rhynchospora (Cyperaceae, Poales). Plant Systematics and Evolution (Coan et al., 2008)
Andrade, Eugenio	Universidad Nacional de Colombia (Colombia)	Molecular evolution, biological theory, phylosophy	– La ontogenia del pensamiento evolutivo (Andrade, 2011) – The role of animal behavior in evolution. Consideration from developmental systems' theory and biosemiotics (Toscano and Andrade, 2015)
Benítez, Mariana*	Universidad Nacional Autónoma de México (Mexico)	Eco-evo-devo	– Development of cell differentiation in the transition to multicellularity: a dynamical modeling approach (Van Cauwelaert et al., 2015) – Dynamics of cell-fate determination and patterning in the vascular bundles of *Arabidopsis thaliana* (Benítez and Hejátko, 2013)
Berois, Nibia	Universidad de la República (Uruguay)	Evo-devo of annual fishes	– Annual Fishes: Life History Strategy, Diversity, and Evolution (Berois et al., 2015) – Annual fish: developmental adaptations for an extreme environment (Berois et al., 2012)
Bitner-Mathé, Blanche	Universidade Federal do Rio de Janeiro (Brazil)	Phenotypic plasticity in drosophilids	– Genetic variability and phenotypic plasticity of metric thoracic traits in an invasive drosophilid in America (Bitner-Mathé and David, 2015) – Cellular basis of morphological variation and temperature-related plasticity in *Drosophila melanogaster* strains with divergent wing shapes (Torquato et al., 2014)

(*Continued*)

Table 1. Continued

Name	Affiliation	Research interests	Articles related to Evo-Devo[1]
Bitondi, Márcia	Universidade de São Paulo (Brazil)	Development of honey bees	– Dimorphic ovary differentiation in honeybee (*Apis mellifera*) larvae involves caste-specific expression of homologs of Ark and Buffy cell death genes (Dallacqua and Bitondi, 2014) – Genes involved in thoracic exoskeleton formation during the pupal-to-adult molt in a social insect model, *Apis mellifera* (Soares et al., 2013)
Boege, Karina	Universidad Nacional Autónoma de México (Mexico)	Plant–animal interactions	– Plant defence as a complex and changing phenotype throughout ontogeny (Ochoa-López et al., 2015) – Induced responses to competition and herbivory: natural selection on multitrait phenotypic plasticity (Boege, 2010)
Borojevic, Radovan	Universidade Federal do Rio de Janeiro (Brazil)	Characterization of embryonic development of several sponges	– Primmorphs generated from dissociated cells of the sponge Suberites domuncula: a model system for studies of cell proliferation and cell death (Custodio et al., '98) – Retinoic acid acts as a morphogen in freshwater sponges (Imsiecke et al., '94)
Bortolini, María Cátira	Universidade Federal do Rio Grande do Sul (Brazil)	Genetic diversity	– Origins and evolvability of the PAX family (Paixao-Cortes et al., 2015) – Evolutionary history of chordate PAX genes: dynamics of change in a complex gene family (Paixao-Cortes et al., 2013)
Brante, Antonio	Universidad Católica de la Santísima Concepción (Chile)	Evolution of development and reproductive strategies in marine invertebrates	– A new case of poecilogony from South America and the implications of nurse eggs, capsule structure, and maternal brooding behavior on the development of different larval types (Oyarzún and Brante, 2015) – Genetic variation of the shell morphology in *Acanthina monodon* (Gastropoda) in habitats with different wave exposure conditions (Solas et al., 2013)
Brown, Federico*	Universidade de São Paulo (Brazil)	Invertebrate evo-devo (tunicates, nematodes, flatworms)	– Evolution of flatworm central nervous systems: insights from polyclads (Quiroga et al., 2015) – [Evolutionary developmental biology of] Tunicata (Stolfi and Brown, 2015)
Chaparro, Oscar	Universidad Austral de Chile (Chile)	Molluskan eco-evo-devo	– Impact of short-term salinity stress on larval development of the marine gastropod *Crepipatella fecunda* (Calyptraeidae) (Montory et al., 2014) – Comparing biochemical changes and energetic costs in gastropods with different developmental modes: *Crepipatella dilatata* and *C. fecunda* (Chaparro et al., 2012)
Chiapella, Jorge	Universidad Nacional de Córdoba (Argentina)	Morphological and molecular phylogeny in Plants	– Disentangling the *Tillandsia capillaris* complex: phylogenetic relationships and taxon boundaries in Andean populations (Castello et al., 2016) – Molecular phylogeny of Gymnocalycium (Cactaceae): assessment of alternative infrageneric systems, a new subgenus, and trends in the evolution of the genus (Demaio et al., 2011)

(*Continued*)

Table 1. Continued

Name	Affiliation	Research interests	Articles related to Evo-Devo[1]
Collin, Rachel*	Smithsonian Tropical Research Institute (Panama)	Snails, life cycles, reproduction, evolution of life histories	– The development of viable and nutritive embryos in the direct developing gastropod *Crepidula navicella* (Lesoway et al., 2014) – The effects of experimentally induced adelphophagy in gastropod embryos (Thomsen et al., 2014)
Concha, Miguel	Universidad de Chile (Chile)	Neural development and brain asymmetry	– Evolutionary plasticity of habenular asymmetry with a conserved efferent connectivity pattern (Villalón et al., 2012) – Zebrafish and medaka: model organisms for a comparative developmental approach of brain asymmetry (Signore et al., 2009)
de Menezes, Nanuza Luiza	Universidade de São Paulo (Brazil)	Plant anatomy and development	– Cytogenetics and cytotaxonomy of Velloziaceae (de Melo et al., '97) – Evolution of the anther in the family Velloziaceae (de Menezes, '88)
Delgado, Jean-Paul	Universidad de Antioquia (Colombia)	Limb regeneration in salamanders	– Maintaining Plethodontid salamanders in the laboratory for regeneration studies (Arenas et al., 2015) – The aneurogenic limb identifies developmental cell interactions underlying vertebrate limb regeneration (Kumar et al., 2011)
del Pino, Eugenia	Pontificia Universidad Católica del Ecuador (Ecuador)	Comparative development of amphibians	– Developmental diversity of amphibians (Elinson and del Pino, 2012) – Variation in the schedules of somite and neural development in frogs (Sáenz Ponce et al., 2012)
Dornelas, Marcelo	Universidade Estadual de Campinas (Brazil)	Plant reproduction and evolution	– A genomic approach to study anthocyanin synthesis and flower pigmentation in passion flowers (Aizza and Dornelas, 2011) – Rapid touch-stimulated movement in the androgynophore of Passiflora flowers (subgen. Decaloba; Sect. Xerogona) an adaptation to enhance cross-pollination? (Scorza and Dornelas, 2014)
Espinosa-Soto, Carlos*	Universidad Autónoma de San Luis de Potosí (Mexico)	Gene regulatory circuits	– Tetramer formation in Arabidopsis MADS domain proteins: analysis of a protein–protein interaction network (Espinosa-Soto et al., 2014) – Phenotypic plasticity can facilitate adaptive evolution in gene regulatory circuits (Espinosa-Soto et al., 2011)
Fabrezi, Marissa	Instituto de Bio y Geociencias (Argentina)	Anuran morphology variation	– Developmental changes and novelties in ceratophryid frogs (Fabrezi et al., 2016) – Heterochrony in growth and development in anurans from the Chaco of South America (Fabrezi, 2011)
Fanara, Juan José	Universidad de Buenos Aires (Argentina)	Genetic basis of phenotypic traits in Drosophila	– Genetic architecture of olfactory behavior in Drosophila melanogaster: differences and similarities across development (Lavagnino et al., 2013) – Evolution of male genitalia: environmental and genetic factors affect genital morphology in two Drosophila sibling species and their hybrids (Soto et al., 2007)

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Table 1. Continued

Name	Affiliation	Research interests	Articles related to Evo-Devo[1]
Fernández, Daniel	Centro Austral de Investigaciones Científicas (Argentina)	Evolution and diversification of Antarctic and sub-Antarctic fishes	– Ancient climate change, antifreeze, and the evolutionary diversification of Antarctic fishes (Near et al., 2012) – Temperature effects on growing, feeding, and swimming energetics in the Patagonian blennie *Eleginops maclovinus* (Pisces: Perciformes) (Vanella et al., 2012)
Fernández, Miriam	Pontificia Universidad Católica de Chile (Chile)	Eco-evo-devo in marine invertebrates	– Correlated evolution between mode of larval development and habitat in muricid gastropods (Pappalardo et al., 2014) – Mode of larval development as a key factor to explain contrasting effects of temperature on species richness across oceans (Pappalardo and Fernández, 2014)
Flores, Augusto	Universidade de São Paulo (Brazil)	Marine invertebrates ecology	– Conspecific cues affect stage-specific molting frequency, survival, and claw morphology of early juvenile stages of the shore crab *Carcinus maenas* (Duarte et al., 2014) – Uneven abundance of the invasive sun coral over habitat patches of different orientation: an outcome of larval or later benthic processes? (Mizrahi et al., 2014)
Frankel, Nicolas*	Universidad de Buenos Aires (Argentina)	Genetic basis of morphological evolution	– Parental age influences developmental stability of the progeny in Drosophila (Colines et al., 2015) – Multiple layers of complexity in cis-regulatory regions of developmental genes (Frankel, 2012)
Gallardo, Carlos	Universidad Austral de Chile (Chile)	Evolution of life cycles in closely related species of slipper limpets	– Egg-laying behaviour and intracapsular development of *Argobuccinum pustulosum* (Gastropoda: Ranellidae) in temperate waters at the South coast of Chile (Gallardo et al., 2012) – Morphological analysis of two sympatric ecotypes and predator-induced phenotypic plasticity in *Acanthina monodon* (Gastropoda: Muricidae) (Sepúlveda et al., 2012)
García-Arraras, José Enrique	Universidad de Puerto Rico (Puerto Rico)	Sea cucumber regeneration	– Postembryonic organogenesis of the digestive tube: why does it occur in worms and sea cucumbers but fail in humans? (Mashanov et al., 2014a) – Heterogeneous generation of new cells in the adult echinoderm nervous system (Mashanov et al., 2015)
Godoy-Herrera, Raul	Universidad de Chile (Chile)	Larval development in *D. melanogaster*	– The neuro-ecology of *Drosophila* pupation behavior (del Pino et al., 2014) – Chemical cues influence pupation behavior of *Drosophila simulans* and *Drosophila buzzatii* in nature and in the laboratory (Beltramí et al., 2012)
González, Favio	Universidad Nacional de Colombia (Colombia)	Leaf, flower, and fruit development in angiosperms	– Flower development and perianth identity candidate genes in the basal angiosperm *Aristolochia fimbriata* (Piperales: Aristolochiaceae) (Pabón-Mora et al., 2015) – Flower and fruit characters in the early-divergent lamiid family Metteniusaceae, with particular reference to the evolution of pseudomonomery (Gonzalez and Rudall, 2010)

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Name	Affiliation	Research interests	Articles related to Evo-Devo[1]
Hasson, Esteban	Universidad de Buenos Aires (Argentina)	Evolutionary genetics of host plant choice in *Drosophila*	– Positive selection in nucleoporins challenges constraints on early expressed genes in *Drosophila* development (Mensch et al., 2013) – Evolutionary genomics of genes involved in olfactory behavior in the *Drosophila melanogaster* species group (Lavagnino et al., 2012)
Hartfelder, Klaus	Universidade de São Paulo (Brazil)	Bee development, developmental endocrinology	– Insights into the dynamics of hind leg development in honey bee (*Apis mellifera* L.) queen and worker larvae—a morphology/differential gene expression analysis (Santos and Hartfelder, 2015) – Development and evolution of caste dimorphism in honeybees—a modeling approach (Leimar et al., 2012)
Irles, Paula*	Pontificia Universidad Católica de Chile (Chile)	Ovary development and evolution in insects	– The notch pathway regulates both the proliferation and differentiation of follicular cells in the panoistic ovary of *Blattella germanica* (Irles et al., 2016) – Unlike in *Drosophila* meroistic ovaries, Hippo represses notch in *Blattella germanica* panoistic ovaries, triggering the mitosis-endocycle switch in the follicular cells (Irles and Piulachs, 2014)
Kohlsdorf, Tiana*	Universidade de São Paulo (Brazil)	Tetrapod development and evolution	– Molecular evolution of HoxA13 and the multiple origins of limbless morphologies in amphibians and reptiles (Singarete et al., 2015) – Musculoskeletal anatomical changes that accompany limb reduction in lizards (Abdala et al., 2015)
Lanna, Emilio*	Universidade Federal da Bahia (Brazil)	Sponge development and evolution	– Environmental effects on the reproduction and fecundity of the introduced calcareous sponge *Paraleucilla magna* in Rio de Janeiro, Brazil (Lanna et al., 2015) – Evo-devo of non-bilaterian animals (Lanna, 2015)
Mashanov, Vladimir	Universidad de Puerto Rico (Puerto Rico)	Neural and visceral regeneration in echinoderms	– Myc regulates programmed cell death and radial glia dedifferentiation after neural injury in an echinoderm (Mashanov et al., 2015) – Transcriptomic changes during regeneration of the central nervous system in an echinoderm (Mashanov et al., 2014b)
Maldonado, Ernesto*	Universidad Nacional Autónoma de México (Mexico)	Eco-evo-devo in zebrafish, cavefish and coral reefs animals	– Spatial mapping in perpetual darkness: EvoDevo of behavior in *Astyanax mexicanus* cavefish (Santacruz et al., 2015) – The zebrafish scarb2a insertional mutant reveals a novel function for the Scarb2a/Limp2b receptor in notochord development (Diaz-Tellez et al., 2016)
Maldonado, Sara	Universidad de Buenos Aires (Argentina)	Plant and seed development and evolution	– Programmed cell death in seeds of angiosperms (Lopez-Fernandez and Maldonado, 2015) – Analogous reserve distribution and tissue characteristics in quinoa and grass seeds suggest convergent evolution (Burrieza et al., 2014)

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Table 1. Continued

Name	Affiliation	Research interests	Articles related to Evo-Devo[1]
Manriquez, Patricio	Centro de Estudios Avanzados en Zonas Áridas (Chile)	Eco-evo-devo in marine invertebrates	– Ocean acidification disrupts prey responses to predator cues but not net prey shell growth in *Concholepas concholepas* (loco) (Mánriquez et al., 2013) – Adaptive shell color plasticity during the early ontogeny of an intertidal keystone snail (Mánriquez et al., 2009)
Marcellini, Sylvain*	Universidad de Concepción (Chile)	Vertebrate skeletal development, bone and cartilage-specific regulatory networks	– Molecular footprinting of skeletal tissues in the catshark *Scyliorhinus canicula* and the clawed frog *Xenopus tropicalis* identifies conserved and derived features of vertebrate calcification (Enault et al., 2015) – Evolution of the vertebrate bone matrix: an expression analysis of the network forming collagen paralogues in amphibian osteoblasts (Aldea et al., 2013)
Marques-Souza, Henrique*	Universidade Estadual de Campinas (Brazil)	Mouse stem cells and gene regulatory networks	– De novo transcriptome assembly and analysis to identify potential gene targets for RNAi-mediated control of the tomato leafminer (*Tuta absoluta*) (Camargo et al., 2015)
Marroig, Gabriel	Universidade de São Paulo (Brazil)	Evolution of modularity in mammalian skull	– Directional selection can drive the evolution of modularity in complex traits (Melo and Marroig, 2015) – Skull modularity in neotropical marsupials and monkeys: size variation and evolutionary constraint and flexibility (Shirai and Marroig, 2010)
Martínez, Maximiliano*	Universidad Nacional Autónoma de México (Mexico)	Phylosophy of Evo-Devo and complex systems	– Multilevel causation and the extended synthesis (Martínez and Esposito, 2014) – Constreñimientos, variación evolutiva y planos corporales (Martínez and Andrade, 2014)
Mendoza, Luis	Universidad Nacional Autónoma de México (Mexico)	Modeling and simulation of biological networks	– Building qualitative models of plant regulatory networks with SQUAD (Weinstein and Mendoza, 2012) – The *Arabidopsis thaliana* flower organ specification gene regulatory network determines a robust differentiation process (Sánchez-Corrales et al., 2010)
Monteiro, Leandro	Universidade Estadual do Norte Fluminense (Brazil)	Vertebrate morphology evolution and diversification	– Evolutionary patterns and processes in the radiation of phyllostomid bats (Monteiro and Nogueira, 2011) – Evolutionary integration and morphological diversification in complex morphological structures: mandible shape divergence in spiny rats (Rodentia, Echimyidae) (Monteiro et al., 2005)
Montiel, Juan*	Universidad Diego Portales (Chile)	Brain development and evolution	– From sauropsids to mammals and back: new approaches to comparative cortical development (Montiel et al., 2016) – Maternal-fetal unit interactions and eutherian neocortical development and evolution (Montiel et al., 2013)
Mora-Osejo, Luis Eduardo	Universidad Nacional de Colombia (Colombia)	Comparative plant morphology	– Estudios morfológicos, autoecológicos y sistemáticos en angiospermas (Mora-Osejo, '87) – Estudios ecológicos del Páramo y del Bosque Altoandino-Cordillera Oriental de Colombia (Mora-Osejo and Sturm, '94)

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Name	Affiliation	Research interests	Articles related to Evo-Devo[1]
Negreiros-Fransozo, María Lucia	Universidade Stadual Paulista (Brazil)	Systematics and development of crustaceans	– Morphological analysis of the female reproductive system of *Stenorhynchus seticornis* (Brachyura: Inachoididae) and comparisons with other Majoidea (Antunes et al., 2016) – First zoeal stage of *Cataleptodius parvulus* (Fabricius, 1793) and *Xanthodius denticulatus* (White, 1848) (Decapoda: Brachyura): larval evidences and systematic position (Barros-Alves et al., 2013)
Nery, Mariana*	Universidade Estadual de Campinas (Brazil)	Gene and molecular evolution	– Increased rate of hair keratin gene loss in the cetacean lineage (Nery et al., 2014) – Genomic organization and differential signature of positive selection in the alpha and beta globin gene clusters in two cetacean species (Nery et al., 2013)
Nespolo, Roberto	Universidad Austral de Chile (Chile)	Evolution of life histories, bioenergetics, ecophysiology and quantitative genetic	– Testing the aerobic model for the evolution of endothermy: implications of using present correlations to infer past evolution (Nespolo and Roff, 2014) – Thermoregulatory capacities and torpor in the South American marsupial, *Dromiciops gliroides* (Cortés et al., 2014)
Nunes da Fonseca, Rodrigo*	Universidade Federal do Rio de Janeiro (Brazil)	Arthropod evo-devo	– Toll signals regulate dorsal-ventral patterning and anterior-posterior placement of the embryo in the hemipteran *Rhodnius prolixus* (Berni et al., 2014) – Evolution of extracelular Dpp modulators in insects: the role of tolloid and twisted-gastrulation in dorsoventral patterning of the Tribolium embryo (da Fonseca et al., 2010)
Núñez-Farfán, Juan	Universidad Nacional Autónoma de México (Mexico)	Evolution of plant defense	– Adaptive divergence in resistance to herbivores in *Datura stramonium* (Castillo et al., 2015) – Phylogenetic correlations among chemical and physical plant defenses change with ontogeny (Karinho-Betancourt et al., 2015)
Olson, Mark	Universidad Nacional Autónoma de México (Mexico)	Plant morphological evolution in dry tropical habitats, evolutionary theory	– Convergent vessel diameter-stem diameter scaling across five clades of New- and Old- World eudicots from desert to rain forest (Olson et al., 2013) – Ontogenetic modulation of branch size, shape, and biomechanics produces diversity across habitats in the *Bursera simaruba* clade of tropical trees (Rosell et al., 2012)
Opazo, Juan*	Universidad Austral de Chile (Chile)	Evolution of genomes	– How to make a dolphin: molecular signature of positive selection in Cetacean genome (Nery et al., 2013) – Whole-genome duplication and the functional diversification of teleost fish hemoglobins (Opazo et al., 2013)
Oyarzún, Fernanda	Universidad de Concepción (Chile)	Ecology and development of larval stages in marine invertebrates	– A new case of poecilogony from South America and the implications of nurse eggs, capsule structure, and maternal brooding behavior on the development of different larval types (Oyarzún and Brante, 2015) – The effects of nurse eggs and sibling interactions on the larval development of the poecilogonous annelid *Boccardia proboscidea* (Spionidae) (Oyarzún and Brante, 2014)

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Table 1. Continued

Name	Affiliation	Research interests	Articles related to Evo-Devo[1]
Pabón-Mora, Natalia*	Universidad de Antioquia (Colombia)	Plant evo-devo	– Flower development and perianth identity candidate genes in the basal angiosperm *Aristolochia fimbriata* (Piperales: Aristolochiaceae) (Pabón-Mora et al., 2015) – Analysis of the CYC/TB1 class of TCP transcription factors in basal angiosperms and magnoliids (Horn et al., 2014)
Paulino, Juliana	Universidade de São Paulo (Brazil)	Floral morphology and development	– Comparative development of rare cases of a polycarpellate gynoecium in an otherwise monocarpellate family, Leguminosae (Paulino et al., 2014) – Floral developmental morphology of three Indigofera species (Leguminosae) and its systematic significance within Papilionoideae (Paulino et al., 2011)
Perez, Oscar*	Pontificia Universidad Católica del Ecuador (Ecuador)	Comparative development of amphibians	– The morphology of prehatching embryos of *Caecilia orientalis* (Amphibia: Gymnophiona: Caeciliidae (Perez et al., 2009) – Comparative analysis of Xenopus VegT, the meso-endodermal determinant, identifies an unusual conserved sequence (Perez et al., 2007)
Piñeyro-Nelson, Alma*	Universidad Autónoma Metropolitana (Mexico)	Developmental molecular genetics and plant evolution	– The role of transcriptional regulation in the evolution of plant phenotype: a dynamic systems approach (Rodríguez-Mega et al., 2015) – When ABC becomes ACB (Garay-Arroyo et al., 2012)
Pozner, Raúl	Instituto de Botánica Darwinion (Argentina)	Systematics and morphology of angiosperms	– Evolutionary origin of the Asteraceae capitulum: Insights from Calyceraceae (Pozner et al., 2012) – Multiple origins of congested inflorescences in Cyperus s.s. (Cyperaceae): developmental and structural evidence (Guarise et al., 2012)
Quinzio, Silvia	Universidad Nacional de Salta (Argentina)	Morphological diversity in anuran tadpoles	– The lateral line system in anuran tadpoles: neuromast morphology, arrangement, and innervation (Quinzio and Fabrezi, 2014) – Ontogenetic and structural variation of mineralizations and ossifications in the integument within Ceratophryid frogs (Anura, Ceratophrydae) (Quinzio and Fabrezi, 2012)
Rezende, Gustavo*	Universiade Estadual do Norte Fluminense (Brazil)	Evolution of the resistance to desiccation in insect eggs	– Physical features and chitin content of eggs from the mosquito vectors *Aedes aegypti*, *Anopheles aquasalis* and *Culex quinquefasciatus*: connection with distinct levels of resistance to desiccation (Farnesi et al., 2015) – Serosal cuticle formation and distinct degrees of desiccation resistance in embryos of the mosquito vectors *Aedes aegypti, Anopheles aquasalis* and *Culex quinquefasciatus* (Vargas et al., 2014)
Rodrigues, Miguel	Universidade de São Paulo (Brazil)	Taxonomy and evolution of neotropical amphibians and reptiles	– Digit evolution in gymnophthalmid lizards (Roscito et al., 2014) – Embryonic development of the fossorial gymnophthalmid lizards *Nothobachia ablephara* and *Calyptommatus sinebrachiatus* (Roscito and Rodrigues, 2012)

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Table 1. Continued

Name	Affiliation	Research interests	Articles related to Evo-Devo[1]
Rubinstein, Marcelo	Instituto de Investigaciones en Ingeniería Genética y Biología Molecular (Argentina)	Regulatory landscape evolution, exaptation of repetitive elements	– Evolution of transcriptional enhancers and animal diversity (Rubinstein and de Souza, 2013) – Convergent evolution of two mammalian neuronal enhancers by sequential exaptation of unrelated retroposons (Franchini et al., 2011)
Sarrazin, Andres*	Pontificia Universidad Católica de Valparaíso (Chile)	Segmentation in arthropods, gene regulatory networks and body plan evolution	– A *Tribolium castaneum* whole embryo culture protocol for studying the molecular mechanisms and morphogenetic movements involved in insect development (Macaya et al., 2016) – A segmentation clock with two-segment periodicity in insects (Sarrazin et al., 2012)
Sajo, Maria das Graças	Universidade Estadual Paulista (Brazil)	Morphological evolution of plants	– Developmental morphology of a dimorphic grass inflorescence: the Brazilian *Bamboo eremitis* (Poaceae) (Graca Sajo et al., 2015) – Morphology, development and homologies of the perianth and floral nectaries in *Croton* and *Astraea* (Euphorbiaceae-Malpighiales) (De-Paula et al., 2011)
Schizas, Nikolaos	Universidad de Puerto Rico (Puerto Rico)	Molecular evolution of marine invertebrates	– The evolution of euhermaphroditism in caridean shrimps: a molecular perspective of sexual systems and systematics (Fiedler et al., 2010) – Phenotypic plasticity or speciation? A case from a clonal marine organism (Prada et al., 2008)
Schneider, Igor*	Universidade Federal do Pará (Brazil)	Amazonian fish evo-devo, including the four eyed fish, tetrapod evolution	– Molecular mechanisms underlying the exceptional adaptations of batoid fins (Nakamura et al., 2015) – The origin of the tetrapod limb: from expeditions to enhancers (Schneider and Shubin, 2013)
Schneider, Patricia	Universidade Federal do Pará (Brazil)	Vertebrate development and patterning	– A putative RA-like region in the brain of the scale-backed antbird, *Willisornis poecilinotus* (Furnariides, Suboscines, Passeriformes, Thamnophilidae) (De Lima et al., 2015) – Differential role of Axin RGS domain function in Wnt signaling during anteroposterior patterning and maternal axis formation (Schneider et al., 2012)
Simões, Zilá Luz	Universidade de São Paulo (Brazil)	Bee development and endocrinology	– MicroRNA signatures characterizing caste-independent ovarian activity in queen and worker honeybees (*Apis mellifera* L.) (Macedo et al., 2016) – Juvenile hormone biosynthesis gene expression in the corpora allata of honey bee (*Apis mellifera* L.) female castes (Bomtorin et al., 2014)
Vargas, Alexander*	Universidad de Chile (Chile)	Paleontology, digit evolution, vertebrate homologies, origins of novelty	– Bird embryos uncover homology and evolution of the dinosaur ankle (Ossa-Fuentes et al., 2015) – New developmental evidence clarifies the evolution of wrist bones in the dinosaur-bird transition (Botelho et al., 2014)

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Table 1. Continued

Name	Affiliation	Research interests	Articles related to Evo-Devo[1]
Vergara-Silva, Francisco*	Universidad Nacional Autónoma de México (Mexico)	History, philosophy, bioethics, biological anthropology, systematics, eco-evo-devo	– Recurrent abnormalities in conifer cones and the evolutionary origins of flower-like structures (Rudall et al., 2011) – Complex patterns of morphogenesis, embryology, and reproduction in *Triuris brevistylis*, a species of Triuridaceae (Pandanales) closely related to *Lacandonia schismatica* (Espinosa-Matías et al., 2012)
West-Eberhard, Mary Jane	Universidad de Costa Rica (Costa Rica)	Developmental plasticity and evolution; sociobiology and behavioral ecology	– Darwin's forgotten idea: the social essence of sexual selection (West-Eberhard, 2014) – Phenotypic accommodation: adaptive innovation due to developmental plasticity (West-Eberhard, 2005)
Xavier-Neto, Jose	Laboratório Nacional de Biociências (Brazil)	Evo-devo of the vertebrate heart, paleontology	– Signaling through retinoic acid receptors in cardiac development: doing the right things at the right times (Xavier-Neto et al., 2015) – The evolutionary origin of cardiac chambers (Simões-Costa et al., 2005)
Zaher, Hussam	Universidade de São Paulo (Brazil)	Phylogeny, evolution, and development of neotropical snakes	– A new snake skull from the Paleocene of Bolivia sheds light on the evolution of macrostomatans (Scanferla et al., 2013) – The anatomy of the upper Cretaceous snake *Najash rionegrina* (Apesteguía and Zaher, 2006), and the evolution of limblessness in snakes (Zaher et al., 2009)

[1]We have highlighted here recent contributions, not necessarily the most relevant/cited articles of each researcher.
*Researchers that have established their laboratories in the last decade.

in Latin America missed the opportunity to build consilience among divergent and emerging fields, except perhaps for certain attempts to bring together embryology and genetics together in a few schools of medicine (Restrepo, 2009). In contrast to the rapid and profound effect of Darwinism on biological thought in North America, evolutionary thinking in Latin America had a slower, more heterogeneous—but still deep—impact. Evolution influenced anthropology (including indigenism), medicine (including eugenics), and psychology (including education) and was often used in nationalistic discourses with direct effects in state policies, for example, agriculture or economics (Glick et al., 2001; McCook, 2002; Novoa, 2010; Novoa and Levine, 2010; Gómez, 2012; Levine and Novoa, 2012). Despite the fact that a translation of Hennig's *Grundzüge einer Theorie der phylogenetischen Systematik* (1950) into Spanish was available two decades later (Hennig, '68). phylogenetic systematics only blossomed in the 1980s after DNA sequencing started to become broadly available. Biological research was mainly focused in descriptive natural history likely due to an implicit necessity to document the large diversity of undescribed organisms. Thus, in Latin America the study of biological patterns/processes and the integration of evolutionary thought in empirical biology were delayed until the second half of the twentieth century. In the following section, we comment on landmarks that are crucial for a historical perspective of Evo-Devo in Latin America.

Müller's (1869) *Für Darwin* and Other Contributions

Fritz Müller (1821–1897) was a German naturalist exiled in the Brazilian island city of Desterro (current Florianópolis). In exile, Müller made important contributions to the knowledge of South American biodiversity. Owing to their common interest in crustaceans, particularly on *Cirripedia*, Fritz Müller and Charles Darwin exchanged extensive correspondence. However, many observations on plants and animals communicated by Müller remained unpublished, or appeared only as part of their correspondence (cf. González and Bello, 2009; West, 2003). Müller also described a new, remarkably large (reaching up to 2.5 m) hemichordate species from Brazil, *Balanoglossus gigas* (1898), rediscovered later (Sawaya, '51). We highlight here important contributions by Müller relevant to the field of Evo-Devo.

One of Darwin's preferred disciplines was embryology. At the time, Darwin played a crucial role in reviving recapitulation, also known as the "biogenetic Law," in Europe. In his *Für*

Darwin (1864), Müller went further in discussing development and evolution. Müller was aware that it was necessary to explain in much more detail the observations made by Darwin on embryology, vestigial organs, and transmutation in his chapter XIII of *The Origin* (1859). Although the full complexity of Müller's arguments remained unaddressed, Darwin commented his findings in the fourth edition of *The Origin* (1866) after reading a preliminary translation of *Für Darwin*. Both Darwin and Müller supported views of recapitulation and dismissed creationist views put forth by influential academics such as Louis Agassiz or Johannes Müller (Ghiselin, '96; Richards, 2008). Müller's book provided, simultaneously, arguments in favor of Darwin's observations and against one of the most outstanding figures at the time, Louis Agassiz. For example, Müller proposed the generally conserved pattern of sequential larval stages in the Crustacea, that is the nauplius and the zoea, as an argument to support Darwin's ideas about the relationship between ontogeny and phylogeny (Ghiselin, '96; Müller, 1869). Müller (1864, 1869) stated that "Descendants therefore reach a new goal, either by deviating sooner or later whilst still on the way toward the form of their parents, or by passing along this course without deviation, but then, instead of standing still, advance still further" and that in the second case "the entire development of the progenitors is also passed through by the descendants, and, therefore, so far as the production of a species depends upon this second mode of progress, **the historical development of the species will be mirrored in its developmental history**" (**boldface**, our emphasis). Thus, Müller rapidly embraced views of recapitulation that went largely unrecognized, and that in some respects resembled those first articulated in the biogenetic law by Haeckel (1866).

Even from Desterro, which coincidentally means exile in Portuguese, Fritz Müller was deeply involved in the birth of evolutionary physiological anatomy, along with Darwin and Anton Dohrn (Ghiselin, '96), as well as in the conception of other important and pioneer studies of evolutionary biology. Müller analyzed and clearly understood and analyzed in situ natural selection, as evidenced by his discovery of *Müllerian mimicry* (Ghiselin, '96), a predator avoidance strategy in which two or more unpalatable, toxic or otherwise dangerous species sharing the same potential predators mimic each other, or by his careful description of the three-way mutualism between scale insects, ants, and orbicules (or *Müllerian bodies*) that form a peculiar cushion immediately below the abaxial portion of the petiole of *Cecropia* trees. A branching notion of species diversification was already used by Müller very early on, as he illustrated one of the first "cladograms," in which he used two characters ("clasp forceps" or the "secondary flagellum") to demonstrate two conflicting relationships among three amphipod species in the genus *Melita* (Müller 1864). In botany, an example of Müller's integrative views on evolution and development was found in a letter sent to Darwin in 1875, in which Müller explained and illustrated the presence of an ancestral character state (i.e., the presence of petals in terminal flowers) in the inflorescence of a Brazilian species of *Gunnera* (Gunneraceae) and communicated the occurrence of broad arrangements of flowers and inflorescences in related *Gunnera* species (González and Bello, 2009). These observations served to complement Darwin's (1868) studies on peloric flowers in garden plants, such as the snapdragon *Antirrhinum*.

Müller also contributed to the general ongoing debate on whether phenotypes were exclusively a result of "inherited" or "acquired" characters by following phenotypic variation across generations of another Latin American species, *Abutilon* (Malvaceae). He argued against heredity and its link to observed variation of characters in consecutive generations, thus challenging the views of August Weismann (see review by West, 2003). For example, in some of the last known letters to Weismann (dated between 1886 and 1888; cf. West, 2003), Müller attributed the de novo appearance of a floral trait in a hybrid species of *Abutilon* that was not present in one of the parental species as co-occurrence of variation, but not as a result of inheritance. In his 1888 letter, Müller considered the co-occurrence of these traits in the hybrid offspring as "acquired, not as inherited characteristics, above all from the fact that most of the time the very rare deviations in the usual structure, which occur once in many thousands if at all, usually appear together in most cases." In the recent literature, however, we find examples that point to a common regulatory network for leaf development and floral organ identity (Ferrandiz et al., 2000; Pabón-Mora et al., 2012), which would explain the co-occurrence of leaf and flower variation of Müller's original observations. In spite of Müller's misinterpretation of genetic inheritance in *Abutilon*, it is worthwhile mentioning that studies by Müller in non-European species contributed significantly to our current understanding of evolutionary theory.

Ameghino's *Filogenia* (1884) and Other Texts

Florentino Ameghino (1854–1911) was an Argentinean self-taught naturalist who, along with his brothers Carlos and Juan, made very important contributions to the development of paleontology in Latin America, his published and unpublished works adding up to 24 volumes of 700–800 pages (Torcelli, '35). He owned a small bookshop in Buenos Aires and used his meager earnings to finance paleontological expeditions lead by his brothers. Indeed, he "had to write the immortal pages of his *Filogenia* while selling cheap goods and paper sheets to earn ten cents" (Torcelli, '13). In *Filogenia* (Ameghino, 1884), his *opus magna*, he recognized the great importance of embryology for understanding animal evolution, devoting two full chapters to it. In one of them, he recognizes the difficulty of doing developmental biology work at that time in Argentina, suggesting instead a methodology that would use "evolutionary laws" to allow paleontologists to infer phylogenies even in the absence of fossils. To such end, he developed analytical tools and used them in his "*procedimiento de seriación,*" becoming a pioneer in both the use of mathematics and the recognition for the need to identify ancestral traits as a first step to determine a transformational character series during evolution. Without knowing it, Ameghino found the recipe to solve Darwin's *abominable mystery of angiosperm evolution*, and anticipated for almost 60 years the foundations of Hennig's ('50) *Paläontologische Methode*. Without the discovery of fossils or vestiges, Ameghino hypothesized the existence of transformation of characters or character states, for example, during the evolution of the foot of Equidae or the skull of hominids (Torcelli, '13). Ameghino was a Lamarckian, a recapitulationist, and an orthogeneticist (i.e., supporter of directional evolution). His views of the natural world were strongly influenced by the rich and endemic South American mammalian paleofauna, along with the fossil remains of the diverse human groups that formerly inhabited the Pampas and Patagonian plains. These materials, along with the evolutionary laws he proposed, led him to the idea of *bestialization*. This concept was an orthogeneticist extension of the Haeckel's "biogenetic law" and proposed the existence of unidirectional trends in both the ontogeny and evolution of organisms that could eventually lead to extinction due to maladaptive trait exageration. He applied bestialization to explain human evolution, proposing that humans shared a common ontogeny to the "antropomorphs," which included the big African and Asian apes, as well as some "smooth skull" fossil primates from Latin America. In Ameghino's view, humans represented a more primitive, early step in an orthogenetic trend that led to other apes and monkeys; a biogeographic corollary of his hypothesis proposed South America as the point of origin of humans (for a review, see Salgado, 2011). While many of his peculiar hypotheses were proven wrong later, Ameghino can no doubt be considered not only among the first Argentinean evolutionists, but also a pioneer of Evo-Devo in Latin America.

Croizat's *Space, Time, Form* (1964)

Léon Croizat (1894–1982) was a French–Italian botanist who worked in Venezuela from 1947 until his death. Croizat raised pivotal questions of evolution and development by the observation of peculiar biological patterns. His largely overlooked book *Space, time, form* (1964) is, perhaps, the first text with explicit notions that integrate evolutionary thought and developmental observations in plants and animals, not to mention the relevant contribution of biogeography to evolutionary patterns. Although the book remains marginal in relevance in the scientific literature, it covers some keystone and up-to-date issues still debated in Evo-Devo today. For example, Croizat ('64) extensively discussed issues related to the concept of the flower versus the inflorescence, the unique importance of evolutionary switches in floral symmetry in Euphorbiaceae, and the structural development and evolution of fruit formation in the *Rhododendron* family (Ericaceae). Croizat discussed extensively the origin of angiosperms and the homology of flowers and floral organs; many of these key questions remain unresolved in plant Evo-Devo today. In zoology, Croizat discussed the issue of feather development, morphology, and function, and compared these structures to putative homologs in fish or lizards; compared cranial structures and teeth development of extant and extinct "subungulates"; discussed the occurrence of paedomorphosis in hominids; and discussed genetic mutations in the light of natural selection, presenting early examples of homeosis, and homeotic mutants in insects (Croizat, '64).

The extraordinary effort of Croizat to reach a biological synthesis has only recently been acknowledged (Nelson and Platnick '81; Williams and Ebach 2008), yet much of his work provides a useful resource for empirical or conceptual research in Evo-Devo. Although technical advancements had occurred since the nineteenth century, Croizat alerted the community that theoretical frameworks in biology had not progressed a great deal and needed serious attention. For example, he noted that botanical concepts established by Goethe (1790), De Candolle (1827), and Van Tieghem (1868) were still under investigation at the time with no clear theoretical breakthrough (Croizat, '64). Croizat anticipated that to expand concepts in evolution it was necessary to take into account the developmental program (or "inherited tendencies") underlying the origin of novel structures, a fundamental aspect of modern Evo-Devo studies. An example of this predicted conceptual expansion is the homology of the dorsal surface of segmented invertebrates with the ventral surface of vertebrates, proposed by Geoffroy St.-Hilaire almost two centuries ago, and ultimately studied and hotly debated by developmental geneticists almost two centuries later (De Robertis and Sasai, '96; Panchen, 2001). Croizat ('64) appealed for more empirical data to help integrate development and evolution, anticipated overhauling homology hypotheses of far-reaching proportions in botany, and recognized two discernible moments in our understanding of evolutionary change: one primarily directional (orthogenetic) and another that involves adaptation or selection. He argued that natural selection could only operate on an extant framework of directional development (or orthogeny) that, in turn, was completely independent of the environment. However, recent evidence suggests that biotic and abiotic factors can influence developmental processes and give rise to diverse forms, which can then be selected upon (Gilbert et al., 2015). The emerging field of Eco-Evo-Devo is, in this sense, an update of Croizat's ideas, since it aims to generate newer evidence for the action of the environment to select phenotypes and its effects in shaping organisms during ontogeny. The integration of environmental/ecological studies to classic questions of evolutionary developmental biology represents a promising contribution to advance evolutionary theory.

PIONEERS OF EVOLUTIONARY AND DEVELOPMENTAL BIOLOGY IN LATIN AMERICA: THE BLENDING OF DISTINCT FIELDS AND EXPERTISE

Evo-Devo may be defined nowadays as an integrative field consisting of at least four different but interconnected research programs addressing the reciprocal influence of evolution and development (sensu Müller, 2007). Formal establishment of the field only occurred in Latin America toward the end of last century, and subsequently increased its presence throughout many countries after the year 2000 (Fig. 1). Most researchers identified their work either as strictly developmental biology or as evolutionary biology, and few articles published before the year 2000 clearly integrated both concepts within the main text of a single article (Fig. 1). To identify the earliest researchers in the region that began to question how developmental mechanisms evolve or how developmental biology can contribute to our understanding of evolutionary processes, we searched for research articles from Latin American authors that included the term "evolution" but also contained the term "development", and found that early research focused in the study of alternative developmental trajectories of frogs with distinct modes of reproduction (Lutz, '47, '48; del Pino and Escobar, '81) and life history evolution in marine mollusks (Gallardo, '73).

Brazilian zoologist Bertha Lutz reported deviations and peculiar modes of development in South American anurans (Lutz, '47). Lutz noted differences in egg size and development of embryonic structures, for example, gill sacs, in tropical and subtropical anuran species adapted to terrestrial development (Lutz, '48), but a clear understanding of the cellular and development mechanisms of oogenesis (i.e., formation of mononucleated and multinucleated oocytes), modes of gastrulation, and early frog embryogenesis only occurred after seminal studies by Eugenia del Pino from Ecuador decades later (del Pino and Humphries, '78; del Pino and Elinson, '83; del Pino, '89; del Pino et al., 2007). Early work by del Pino clearly presented some of the fundamental integrating principles of Evo-Devo. She found that embryos of brooding frogs developed from only a subset of blastomeres, resembling the development of embryonic disks in birds or mammals (del Pino and Elinson, '83). These findings showed convergent patterns of development among distantly related groups of vertebrates resulting from adaptive processes likely related to brooding or egg size. Del Pino's findings occurred in parallel to other seminal Evo-Devo research that raised new questions about the constraints imposed by development and phylogeny, and the adaptive significance of developmental processes and patterns. Her research program on the embryonic development in a diverse group of local frogs is still active and has provided new insights on how variation in developmental processes and patterns arise among closely related groups of animals (Sáenz-Ponce et al., 2012a, b).

Carlos Gallardo from Chile addressed questions about the evolution of animal life cycles (Table 1). In his initial studies, he investigated the evolution and variation of developmental patterns in the abalone *Concholepas concholepas* (Gallardo, '73, '79), the intertidal snail *Nucella crassilabrum* (Gallardo, '79), and slipper limpets *Crepipatella* (previously referred as *Crepidula*) (Gallardo, '77; Gallardo and Garrido, '87). The latter studies allowed him to propose an adaptive significance to the generation of alternative developmental trajectories within egg capsules of closely related or cryptic species of limpets, as observed for species that generate additional nurse eggs or embryos to feed other sibling embryos within the same capsule (Gallardo, '77; Gallardo and Garrido, '87). More recent studies of intracapsular variation of developmental modes in *Crepipatella* spp., as well of the variation of shell thickness in the unicorn snail *Acanthina monodon* (Sepúlveda et al., 2012) have set the stage for further Evo-Devo research to address questions on the evolution of polyphenisms and phenotypic plasticity using mollusks as model systems (West-Eberhard, 2003; Lesoway et al., 2014). Both del Pino and Gallardo's foundational work was soon to be followed by that of a large number of researchers contributing to the construction and consolidation of Evo-Devo research in Latin America (Table 1).

A SELECTION OF EVO-DEVO TOPICS CURRENTLY ADDRESSED BY LATIN AMERICAN RESEARCH GROUPS

The identification of deeply conserved gene networks deployed during the development of a few model organisms has established paradigms that allow us to better understand homology and embryological transformations and to frame new questions regarding developmental evolution. With the advent of high throughput sequencing techniques of genomes and transcriptomes, the Evo-Devo research field has been steadily shifting toward the study of nonmodel local species presenting interesting biological questions. Table 1 shows a nonexhaustive list of present day laboratories that conduct Evo-Devo research in Latin America. A younger generation of researchers with diverse interests and expertise has come together to facilitate new avenues of research with unique questions and laboratory models (Fig. 4).

Evolution of Body Plans, Patterning, and Structures

Plants present a plethora of examples of diversification and adaptation, including developmental phenomena that are well worth investigating using Evo-Devo approaches (Vergara-Silva, 2003). Interesting study topics that take advantage of the diversity of life cycles in plants or specific adaptations include: the alternation of generations in land plants by extending the mitotic phase after the zygote formation to form an embryo; the acquisition of vascular tissue in ferns and seed plants; the acquisition of flowers and in particular carpels in the angiosperms; the occurrence of highly synorganized flowers in the Aristolochiaceae (Figs. 4A, B), Orchidaceae, and Zingiberaceae (Fig. 4E); or the evolution of numerous seed dispersal strategies due to changes


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in fruit shape and dehiscence. Heterotopy can also trigger novel changes in floral shape, like in Neotropical poppies where petals are replaced by stamens (e.g., *Bocconia frutescens;* Figs. 4C,D), or in the mycoheterotrophic, achlorophyllous monocot species from the Lacandon rainforest (Chiapas, Mexico) which bears hermaphroditic "inside-out" flowers with central stamens and lateral carpels (Álvarez-Buylla et al., 2010; Rudall et al., 2016; Figs. 4F,G). Novelty can also arise by loss or reduction, as occurs for the tiny unisexual flowers of hemiparasitic plants (e.g., Viscaceae). Carpellate flowers of these species sometimes lack ovules and exhibit a remnant structure called the *mamelon*, where gametogenesis occurs (Fig. 4H).

Assessment of the genetic basis of novelty in plants has been dominated by studies in flower development, as one of the first developmental genetic models was the ABCE model of floral organ identity based on homeotic mutants of *Arabidopsis thaliana* (Pelaz et al., 2000). The model explained the interactions between four classes of transcription factors (A, B, C, and E) involved in controlling the identity of the canonical floral organs, the sepals (A+E class genes), the petals (A+B+E class genes), the stamens (B+C+E class genes), and the carpels (C+E class genes) (Coen and Meyerowitz, '91). Comparative studies in nonmodel species point to conserved functions of B and C class genes in stamen and carpel identity, but a more flexible recruitment of genes in sepal and petal identity (Litt & Kramer 2010; Pabón-Mora et al., 2012, 2013, 2015). Conversely, functional characterization in nonmodel plants has shown that the least conserved is the A-function. There is growing evidence of the role of A-class genes in other processes that include leaf morphogenesis, inflorescence architecture and fruit development and the recruitment of other MADS-box transcription factors contributing to perianth identity (e.g., *AGAMOUS-like6*; Pabón-Mora et al., 2013, 2015, Wang et al., 2016). We therefore must now move beyond the genes involved in the ABCE model and indeed beyond "organ identity" alone to explain floral variation in angiosperms, and particularly changes in perianth, whose diversity correlates with pollinator preferences (Pabón-Mora et al., 2012, 2015; Specht and Howarth, 2015; Almeida et al., 2015a,b).

Structural homologies are not always easy to identify in organisms, given the extreme morphological and anatomical modification that they can exhibit across large evolutionary distances. Ontogenetic studies are important for assessing homologous structures in modular organisms. In each module, the same reference points can be used to assess correspondence and homology despite extreme metamorphosis. For instance, meristematic origin, identity, polarity, and position are additive criteria to pinpoint leaf homologs despite their reduction or extreme variation in shape, color, or size, along one or different axes, whether vegetative or reproductive. Another example of extreme body shape transformation that has been studied using nonmodel organisms is the convergent evolution of snakelike forms in Neotropical Squamata (lizards, snakes, and amphisbaenians), which involve limb reduction or loss along with an increase in the number of trunk vertebrae. Comparative anatomical and molecular studies suggest that convergent forms do not necessarily involve the same evolutionary changes in

Figure 4. Examples of emerging model systems for Evo-Devo studies in Latin America. (A–B) *Aristolochia fimbriata* and *A. ringens* flowers having petaloid sepals, lacking petals, and exhibiting fusion between stamens and stigmas (C–D) Petalless poppy flowers in preanthesis (C) and anthesis (D) of *Bocconia frutescens*, growing in the wild in Colombia. (E) *Costus* sp. (Costaceae). The labellum, formed from the fusion of five laminar staminodes, dominates the floral display and has markings and conical epidermal cells typically associated with petals in other lineages of flowering plants. Thus, in Costaceae, the stamens are responsible for floral display and pollinator signaling. (F–G) *Lacandonia schismatica* is a mycoheterotrophic, achlorophylous monocot from the Lacandon rainforest (Chiapas, Mexico) harboring hermaphroditic "inside-out" flowers with central stamens and lateral carpels. (H) Longitudinal section of *Phoradendron nervosum* female flower, a common American hemiparasite, showing the tepals covering the carpels. Ovules do not develop, and the female gametophyte forms in the reddish blue lower area called the mamelon. (I–L) The threatened Caribbean cnidarian species *Acropora palmata* (Elkhorn Coral) collected off the eastern coast of Mexico; a fully grown individual (I), dividing blastula cells (J), gastrulating embryos (K), and planula larvae (L). (M) The solitary ascidian *Herdmania pallida* in late gastrula just before blastopore closure; a classic example of a bilateral and determinate embryo used for teaching and research at CEBIMAR, São Paulo. (N) The ribbon worm *Lineus bonaerensis*—a junior synonym of *Lineus (= Ramphogordius) sanguineus* is reported in the intertidal of the Atlantic coast of Argentina, Uruguay, and Southern Brazil; it is a top predator capable of clonal reproduction and exhibiting amazing regenerative capabilities. (O–P) *Aedes aegypti* (O) is the vector of yellow fever, dengue, zika, and chikungunya viruses and *Culex quiquefasciatus* (P) is the vector of the filariasis nematode and the St. Louis encephalitis, Western equine encephalitis and West Nile viruses; remarkably, of these two species, only the *Aedes aegypti* embryos are resistant to desiccation. (Q) Four-eyed fish *Anableps anableps* from Venezuela and Brazil. (R) Skeletal preparation of the toad *Rhinella spinulosa*, sampled in Chile. This species inhabits the Andean slopes of Argentina, Chile, Bolivia, and Peru from 0 to 5100 m above sea level. Photo credits: A–D: Natalia Pabón-Mora; E: Chelsea Specht; F and G: Juan Pablo Abascal; H: Vanessa Suaza-Gaviria. I–L: Guillermo Jordan and Griselda Avila; M: Alvaro Migotto and Ana Perticarrari de Osório; N: Eduardo Zattara; O and P: Gustavo Rezende; Q: Patricia Schneider; and R: Sylvain Marcellini.

developmental processes and genetic pathways (Waters, 2013; Roscito et al., 2014; Singarete et al., 2015). Changes in the anatomy of the musculoskeletal system associated with limbless morphologies and epigenetic effects of reduced mobility on limb development have also been studied for anurans (Abdala and Ponssa, 2012; Abdala et al., 2015). Whether there are evolutionary changes that simultaneously affect the limb and vertebrae modules simultaneously remains an open question.

Comparative Development and Systematics

While essential for understanding developmental evolution, the integration of ontogeny and phylogeny has been a challenging task for many years, as the connection between these two fields requires a fair comparison between observations at a developmental timescale and hypotheses at an evolutionary timescale. Developmental series are often recorded as consecutive events with a particular timing, resulting in qualitative and quantitative phenotypic changes. Advances in microscopy techniques have allowed for incredibly detailed descriptions of comparative developmental processes at the cellular level; in parallel, a growing molecular-genetics toolkit has enabled the identification of some of the underlying molecular factors regulating such processes. Advances in techniques for phylogenetic comparative analyses and the development of more comprehensive statistical models capable of analyzing large data sets obtained from genomic and transcriptomic sequence data have allowed more rigorous testing of hypotheses of ancestry and relationships among lineages (Blaimer et al., 2015). The extremes of the tree of life are still problematic, as both deep nodes separating major ancient groups and shallow nodes identifying very recent speciation events remain hard to resolve (Phillippe et al., 2011). Despite these limitations, modern comparative biology relies on the construction of robust phylogenetic frameworks from which to analyze developmental changes and thus determine common ancestry and homology of form and function (Minelli, 2009). In this section, we highlight how Evo-Devo studies that integrate both developmental observations and gene or organismic evolution have improved our understanding of morphological variation in nonmodel plant and animal systems.

Plant Evo-Devo: Traditional techniques for chemical or morphological analyses have been successfully combined with computational methods in ancestral character estimation to investigate the evolution of plant defenses (Karinho-Betancourt et al., 2015), tree architecture (Rosell et al., 2012), floral diversification (Gonzalez and Rudall, 2010; Pozner et al., 2012; Bull-Herenu and Classen-Bockhoff, 2013; Cardoso-Gustavson et al., 2014; Paulino et al., 2014; Almeida et al., 2015a, b), vascular variants (Pace et al., 2009, 2011), and seed anatomy (Sousa-Baena and de Menezes, 2014). On the other hand, many of the molecular techniques developed in the model plant *A. thaliana* are now being used on a broader comparative framework to assess functional evolution of gene lineages. This effort has resulted in the transfer of genetic information from model systems to a diversity of organismal studies, offering novel insights into the molecular evolution and gene regulatory network involved in the development and diversification of organs such as leaves (Sousa-Baena et al., 2014), flowers (Pabon-Mora et al., 2013; Davila-Velderrain et al., 2014; Almeida et al., 2015a, b), fruits (Pabon-Mora et al., 2014), seeds (Lopez-Fernandez and Maldonado, 2015), and conifer cones (Vazquez-Lobo et al., 2007; Englund et al., 2011; Carlsbecker et al., 2013). Understanding the evolution of gene regulatory networks in plant development has shed light to a series of commonalities among plant and animal systems (Hernandez-Hernandez et al., 2012; Moczek et al., 2015), which currently allow us to expand Evo-Devo approaches across different biological systems under the same theoretical framework.

Animal Evo-Devo: Evolutionary and developmental questions in both invertebrates and vertebrates have been addressed using comparative morphological approaches with ancestral trait reconstruction. Studies related to the evolution of life history traits include studies of egg size in relation to direct or indirect development in marine invertebrates (Collin, 2012), evolution of larval development in relation to habitats and patterns of distribution in muricid gastropods (Pappalardo et al., 2014), evolution of adelphophagic larvae in marine gastropods (Thomsen et al., 2014), gonad development and evolution of viviparity in fish (Martínez et al., 2014), and evolution of terrestrial reproduction in frogs (Pereira et al., 2015). Studies related to heterochrony, allometry, and modularity include geographic variations of body size adapted to local climate or habitat in gymnophthalmid lizards (Grizante et al., 2012), evolution of larval and juvenile development and allometry in secondary sexual characters of crabs (Flores et al., '98; Flores and Negreiros-Fransozo, '99; Negreiros-Fransozo et al., 2003), digit length ratios, locomotor performance, and sexual dimorphism in iguanian lizards (Gomes and Kohlsdorf, 2011), modulatory gene network regulation of tooth number in mammalian dentition (Line, 2003), variation of cranial shape and structure number in mammals (Monteiro et al., 2005; Shirai and Marroig, 2010; Giannini, 2014; Koyabu et al., 2014), muscle identity and attachments during human digit evolution and development (Diogo et al., 2015), or mammalian cortical development and brain size evolution (Montiel et al., 2013, 2016). Studies related to evolutionary novelties or losses include evolution of transparent eyelids in lizards (Guerra-Fuentes et al., 2014), evolution of jaw abductor muscles, tooth variation, and limblessness in snakes (Zaher, '94; Zaher and Prudente, '99; Zaher and Rieppel, '99; Apesteguía and Zaher 2006; Zaher et al., 2009), evolution of limb bone elements in turtles (Fabrezi et al., 2009), or loss of digits and limb reduction in gymnophthalmid lizards (Roscito and Rodrigues, 2012; Roscito et al., 2014). Separate but often complementary lines of research take advantage of the growing wealth of genomic data to explore the molecular evolution of different gene families and their role in morphological and physiological adaptation, such as evolution of *Hox* genes and the origins of limbless morphologies in amphibians and reptiles (Singarete et al., 2015), origin and evolvability in PAX genes involved in embryonic development and organogenesis (Paixao-Cortes et al., 2013, 2015), nonvertebrate origins of retinoic acid involved in vertebrate development and homeostasis (Simoes-Costa et al., 2008), genes involved in olfactory behaviors (Lavagnino et al., 2012) or in hybrid incompatibility (Mensch et al., 2013) in flies, hemoglobin diversification in teleost fish (Opazo et al., 2013), and comparative genomics of cetaceans (Nery et al., 2013).

Mathematical and Computational Modeling Approaches to Evo-Devo

Morphogenesis and phenotypic change in plants, animals, and other multicellular systems involve changes in time and space of developmental processes and gene regulatory dynamics. These changes can be studied with the help of mathematical models (Álvarez-Buylla et al., 2008; Caballero et al., 2012). Models allow for simplification and quantification of the processes under study and provide a formal framework to understand and predict developmental processes at a mechanistic and dynamic level. The recent emergence of powerful computational tools has enabled the implementation of some of these models, which in turn has allowed researchers to exhaustively explore parameter values, perform in silico experiments, test hypotheses, and render new predictions—often unforeseen or counterintuitive—that can in turn guide further experimental work (Prusinkiewicz and Runions, 2012; Hay-Mele et al., 2015). It is important to keep in mind some of the possible pitfalls of mathematical and computational modeling, such as the imposition of models upon actual study systems (reification) and the use of mathematical and computational tools to "animate" developmental and evolutionary processes, rather than to understand them.

The Latin American community has a robust tradition in the development of different types of mathematical and computational models for the study of development. At the genetic and biochemical level, there is a strong school of network modeling that has largely contributed to understanding how the collective activity of genes and other factors can lead to cell-fate determination and to the balance between proliferation and differentiation in different developmental systems (Alvarez-Buylla et al., 2007; Azpeitia et al., 2010; Weinstein and Mendoza, 2012). These gene network models have shown that different cell fates can be attained during the development of multicellular organisms when the intracellular networks, in interaction with local cues (e.g., ligands or morphogen gradients), reach one of their potential steady states. This echoes Kauffman's proposal that cell types are dynamical attractors of gene networks (Kauffman, '69) and has provided a way to study Waddington's epigenetic landscapes in particular developmental models (e.g., Alvarez-Buylla et al., 2008).

Gene network models, which provide a valuable framework to postulate precise mechanisms and events underlying phenotypic change, have been developed mostly from a qualitative view, but have also included large data sets from model genetic organisms and experimental evidence to build and validate the models and postulate their role in evolution of form (Espinosa-Soto, 2004; Alvarez-Buylla et al., 2008; Hernández-Lemus, 2013). Indeed, one of the conclusions of these modeling efforts is that even qualitative gene regulatory network models are able to reproduce the overall regulatory logic of some differentiation and developmental events, suggesting that the global dynamic of these processes largely depends on the network architecture and nature of the interactions, rather than on particular kinetic details.

At the organismic scale, Latin American groups have contributed to the integral study of patterning and morphogenetic processes in which diverse biological, chemical, physical, and even environmental factors are involved. Importantly, many of these efforts have provided conceptual, methodological, and technical tools to couple genetic/biochemical factors with physicochemical processes at the multicellular level (Cocho et al., '87; Caballero et al., 2012; Swat et al., 2012; Barrio et al., 2013). From these mathematical models, it is now clear that, besides biochemical signals or morphogens, physical factors like mechanical fields play a central role in the establishment of spatial-dependent information and in morphogenesis in general. Elena Álvarez-Buylla has been fundamental in training a new generation of scholars in the biomathematical field, to interpret morphogenetic data with an Evo-Devo approach. Such studies have opened new avenues in the study of multicausal mechanisms in plant and animal systems.

Organismal evolution is restricted, affected, and driven by processes occurring at different scales. To address evolution from a comprehensive Evo-Devo view, it is therefore necessary to develop computational approaches able to integrate molecular, cellular, and environmental subprocesses, among others. With the advent of new theoretical and technological approaches from the computational and mathematical fields, multiscale models that study the interaction of these subprocesses have recently been developed (García and Azpeitia, 2014). Developing models that enable the coupling of different spatiotemporal scales has improved our understanding of major evolutionary transitions (Miramontes, 2014; Mora Van Cauwelaert et al., 2015) and may help to elucidate the complex relations between ecological, sociocultural, and developmental processes in evolution (Casanueva and Martínez, 2014; Martínez and Esposito, 2014). These complex interactions could benefit from theoretical platforms elaborated by historians or philosophers of biology interested in Evo-Devo (for instance, see Abrantes, 2011).

Latin American researchers have produced some pioneering advances toward understanding the dynamic and self-organized nature of developmental processes (Cocho, '99; Varela et al., '74). Moreover, long-standing organizational and educational efforts have created a critical mass of researchers, groups, and institutions actively developing diverse mathematical and computational models in Evo-Devo. Undoubtedly, our community will continue contributing to worldwide efforts aiming at modeling evolutionary processes from genetic, molecular, cellular, developmental, physiological, behavioral, and ecological perspectives and tackle some of the most challenging issues in Evo-Devo.

Evo-Devo Studies on Domesticated Crops in Latin America

A topic of research that is increasingly present in the contemporary scientific literature addresses the evolutionary processes underlying domestication of plants and animals (for an analysis and discussion of these emerging topics, see Piperno, 2011; Moczek et al., 2015). Central and South America harbor areas that have been considered the centers of origin of domesticated plants, a concept that was originally articulated by Vavilov ('26). Based on current knowledge, two centers of origin fall within Latin America: the Mesoamerican and the Andean area(s). In these regions, maize, beans, tomato, amaranth, papaya, avocado, potato, manioc, yams, and quinoa, to name only a few crops, were domesticated between 10,000 and 6,000 years before present (Piperno, 2011). While these areas were originally defined based on botanical and agronomical evidence, the role of humans on moving and diversifying the domesticated plants was acknowledged (Vavilov, '26). In later years, the explicit incorporation of archeological, ethnobotanical, and ethnolinguistic studies, as well as detailed genetic analyses of crops and their wild relatives, have painted a much more nuanced picture of the process of domestication and its bearing on societal/cultural evolution (Piperno, 2011). These studies have not only refined the narrative and increased the evidence used to assert the origin of particular crop plants, but have also emphasized that while domestication occurred sometime in the past (in some cases with independent domestication events of the same species such as *Phaeseolus* sp. and *Cucurbita* sp.; Piperno, 2011), the process of crop diversification, which can include the incorporation of wild germplasm into native cultivars as well as their acclimation to changing agroecological conditions is a current, ongoing phenomenon practiced by peasants and farmers in what has been termed autoctonous genetic improvement (AGI; Turrent et al., 2009). AGI as a process that maintains and recreates the landrace varieties that harbor an important part of the phenotypic, genetic, and epigenetic diversity of a particular plant species. This is a key aspect of in situ conservation, which can be further utilized for professional genetic improvement. Furthermore, while landraces can occupy distinct and restricted ecological niches, as a whole they can cover important parts of the agricultural landscape, commingling with their wild relatives and hybrid counterparts, with whom they can readily interbreed (for a review of documented cases, see Ellstrand et al., 2013). Cultivated plants are embedded in a complex biological patchwork further complicated by the fact that many are staple crops, with the cultural, social, and economic importance that this status entails (Dyer et al., 2009). The acknowledgment of the highly integrated and often complex relationships that underlie the dynamic maintenance of the genetic diversity of domesticated crops by the farmers that live off them—who under certain circumstances chose to harbor particular varieties because these are well suited to particular agronomic conditions, whereas in other cases they sow them for specific organoleptic, symbolic, and/or religious purposes—is at the heart of the ongoing controversy pertaining the introduction of genetically modified cultivars of plants that were domesticated or diversified in Latin America (Acevedo Gasman, 2009). In this context, the notion of coexistence without gene flow from genetically modified cultivars into their conventional counterparts and wild relatives has been strongly put into question, more so after transgene flow has already been documented for species such as maize and cotton (Dyer et al., 2009; Piñeyro-Nelson et al., 2009; Wegier et al., 2011). Transgenes that are introduced into novel genomic contexts could persist across generations with unforeseen consequences at the developmental and evolutionary levels. Furthermore, current patents and intellectual property laws associated with many recombinant constructs introduced into commercial cultivars directly imperil ancestral agronomical practices, such as seed exchange and communal plantings, two phenomena that actively maintain and structure genetic diversity (Álvarez-Buylla and Piñeyro-Nelson, 2013). Thus, the introduction of genetically modified cultivars in the region could affect overall abundance, distribution, and Eco-Evo-Devo dynamics of native varieties of Latin American crops and affect agronomical practices, including AGI efforts.

PERSPECTIVES

Despite the relatively low investment of Latin American countries in science and technology, interest and research in Evo-Devo is on the rise in this part of the world. Many new research groups were established in the past decade, leading to the formation of a new generation of scientists interested in addressing questions of relevance to the international community while maintaining a marked Latin American perspective. Interdisciplinary interactions of Evo-Devo researchers should be encouraged, and more broadly extended to researchers in other academic fields, such as social sciences and humanities, or history and philosophy. We argue that Latin American Evo-Devo must continue to develop and expand, mainly by attracting young principal investigators (PIs) and helping them to start their own original line of research and propose that a variety of complementary strategies will help in reaching this goal. First, current Evo-Devo labs must keep inspiring students to engage in this discipline by proposing exciting thesis projects on a wide variety of species and topics, and by establishing dynamic networks of collaborations with colleagues within Latin America as well as with other regions. Collaborations will

Table 2. Resources for EvoDevo in Latin America

Type	Name	URL
Developmental biology scientific societies	Latin American Society for Developmental Biology (LASDB)	http://lasdbbiology.ning.com/
	Sociedad Mexicana de Biologia del Desarrollo	http://www.smbd.org.mx/
	Sociedade Brasileira de Biologia do Desenvolvimento	
	Sociedad Colombiana de Biología del Desarrollo	http://www.colsdb.org/
	Sociedad Chilena de Reproducción y Desarrollo	http://www.schrd.cl/
Evolutionary biology scientific societies	ColEvol	http://www.colevol.co/
	Sociedad Chilena de Evolución	http://socevol.cl/
Journals	*Neotropical Biodiversity*	http://www.tandfonline.com/loi/tneo20#.Vr-9yRjiEgU
	Genetics and Molecular Biology	http://www.gmb.org.br/
	Gayana	http://www.gayana.cl/es/index.php
Books	*Emergencia de las formas vivas: aspectos dinámicos de la biología evolutiva* by Lorena Caballero (2008)	http://scifunam.fisica.unam.mx/mir/copit/TS0004ES/TS0004ES.pdf
	La ontogenia del pensamiento evolutivo by Eugenio Andrade (2011)	http://www.uneditorial.com/la-ontogenia-del-pensamiento-evolutivo-hacia-una-interpretacion-semiotica-de-la-naturaleza-tapa-dura-biologia.html#.Vr_BRxjiEgU
	Evolución: El Curso de la Vida by Milton H. Gallardo Narcisi (2011)	http://www.medicapanamericana.com/Libros/Libro/4369/Evolucion.html
	Requiem por el centauro: aproximación epistemiológica a la biología evolucionaria del desarrollo by Gustavo Caponi (2012)	http://www.scientiaestudia.org.br/associac/gustavocaponi/index.asp
	Cazadores de monstrous. Monstruos esperanzados y sistemas complejos: evolución y autoorganización by Álvaro Chaos Cador (2014)	http://publicaciones.uacm.edu.mx/monstruos.html
	Introducción a La Biología Evolutiva by Marco A. Méndez and José Navarro B. (2014)	http://www.scribd.com/doc/240808617/Mendez-y-Navarro-2014-Introduccion-a-La-Biologia-Evolutiva#scribd
Blogs	Evolução & Desenvolvimento – Sobre genes, embriões, fósseis e evolução	https://evodevobr.wordpress.com/
	Evolucionismo - I think	http://evolucionismo.org/

accelerate the training of students in Evo-Devo, provide access to cutting edge imaging, molecular, computing, and sequencing technologies, which remain scarcely available in Latin America, and facilitate the access to native species with interesting evolutionary questions for international colleagues. Research networks can also coordinate the generation, acquisition, and use of common resources and core facilities. Until the number of Latin American Evo-Devo researchers reaches the critical mass needed to hold regional Evo-Devo meetings, it is our responsibility to improve our visibility by actively getting involved in the PanAm Evo-Devo, Latin American Society for Developmental Biology (LASDB), European Society for Evolutionary Developmental Biology (Euro Evo Devo or EED), and other societies (Table 2). In addition, current efforts to edit or publish books, create Evo-Devo friendly journals and maintain blogs related to our discipline must be increased (Table 2). Startup funds are crucial to implement laboratories and animal facilities to study local species whose biology and etiology are poorly understood. Finally, Evo-Devo PIs will have to adapt to survive the rapid changes in scientific policies that result from the strong swings that are commonplace during governmental transitions in Latin American countries, as well as embrace the increasing regional bias toward research and development (R&D). Latin American universities and governmental institutions must discourage brain drain phenomena by adopting long-term strategies that contribute to support basic science in general, and more specifically the Evo-Devo field (Fraser, 2014; Miranda, 2014); in turn, researchers could start to adopt distinct Evo-Devo approaches to address societal needs (Moczek et al., 2015). Evolutionary developmental biologists must now find clever ways to apply their passion to socially, economically, medically, and environmentally relevant issues (Losos et al., 2013). Given that heterologous assays with closely related model species are known to be a powerful tool to reveal the functional evolution of genes of interest (Kramer, 2015), such assays, along with transgenesis, mutagenesis and expression protocols could be adapted to regional crop or pest species of medical and economic importance that can easily be raised in the lab. Furthermore, given the multidisciplinary nature of many Evo-Devo studies, insights gained in areas such as Eco-Evo-Devo or crop Evo-Devo can help to increase awareness regarding the uniqueness and frailty of the region's biodiversity, hopefully influencing national policies toward increased conservation efforts and scientifically sound management practices. Much more than a simple "trick" to attract funding, this strategy is a social responsibility of Evo-Devo researchers working in Latin America, a continent that hosts a large fraction of the world's biodiversity, and that is currently threatened by climate change, overexploitation of natural resources, and the spread of many neglected tropical diseases. Hence, Latin America provides a unique and exciting opportunity to combine applied and basic research while exploring how new developmental trajectories have evolved in myriads of endemic species that have never been studied before.

Nowadays, Latin America remains a place of discovery. The importance of the region's biodiversity has also increased during the past decade as Evo-Devo started shifting away from comparisons among the deeply divergent traditional model systems of developmental biology and embraced case studies sampling larger sets of closely related species scattered across the diversity of life. Never before could genomics, transcriptomics, experimental embryology, and genome editing technologies be applied to so many species, and not just model organisms (Chen et al., 2014). Thus, scientific progress now allows us to study unique biological questions in "strange" organisms: What are the physiological and stem cell features that give cnidarians, ascidians, nemerteans, and other marine organisms their impressive ability to regenerate and reproduce clonally (Figs. 4I–N)? What are the differences among mosquitoes that make them vectors of different disease agents (Figs. 4O and P)? How did "electrocytes" (i.e., specialized cells that produce 600 V) evolve in electric eels? How do Hoatzin chicks develop reminiscent claws in their forewings? How did curare vines and *Bothrops insularis* evolve to produce such powerful venom? How does the transparent abdominal skin of glass frogs develop? What are the adaptations to perpetual darkness of cave-dwelling *Speleonectes*, the only known venomous crustacean in the world? How did split eyes evolve to allow vision above (the eye upper half) and below (the eye bottom half) the water surface in the *Anableps* fishes (Fig. 4Q)? These questions, among many others reviewed in this article, are only a minute sample of the exciting topics inspired by Latin America, a continent whose thriving biodiversity represents endless forms most beautiful and most wonderful that are a source of inspiration and opportunities for the Evo-Devo community.

ACKNOWLEDGMENTS

We would like to acknowledge the PanAm Evo-Devo Society, Ehab Abouheif (former President), and Karen Sears (current President), for supporting the workshop "Latin American Challenges in Evo-Devo" and encouraging the writing of this article. We also thank Eugenia del Pino and two anonymous reviewers for valuable comments on the manuscript and Denisse Galarza for her help with the references. We are grateful to Gunter Wagner for the opportunity to write this article and for supporting the publication of a special issue of Evo-Devo in Latin America in the *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*. We apologize to the many research groups and citations that were not included due to space constraints. We acknowledge financial support from FONDECYT 1151196 to SM, FONDECYT 1130824 to AFS, UNAM-DGAPA-PAPIIT IA200714 to MB, CONACYT Fronteras en la Ciencia Project-2 to EM, CNPq 201369/2014-1 to MBG, FAPERJ E-26/102.250/2013 and CNPq 306292/2014-9 to RNdF, and FAPESP 2015/50164-5 to FDB.

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