

Polistinae biogeography in the Neotropics: history and prospects

Antônio F. Carvalho^{1,2}, Rodolpho S. T. Menezes^{3,4}, Alexandre Somavilla⁵,
Marco A. Costa³, Marco A. Del Lama¹

1 Universidade Federal de São Carlos, Departamento de Genética Evolutiva e Biologia Molecular, Via Washington Luís, Km 235, São Carlos, São Paulo, Brazil **2** The City University of New York, Department of Biology, 160 Convent Avenue, New York, NY, USA **3** Universidade Estadual de Santa Cruz, Rod. Jorge Amado, Km 16, Ilhéus, Bahia, Brazil **4** Department of Entomology, National Museum of Natural History, Smithsonian Institution, 10th St. & Constitution Avenue, NW, 20560, Washington, D.C., USA **5** Instituto Nacional de Pesquisas da Amazônia, Avenida André Araújo, 2936, Aleixo, Manaus, Amazonas, Brazil

Corresponding author: Antônio F. Carvalho (carvalhoaf@ufscar.br)

Academic editor: *W. Pulawski* | Received 15 October 2014 | Accepted 14 December 2014 | Published 18 March 2015

<http://zoobank.org/31A2ECF8-F232-409E-825D-97FBD902914E>

Citation: Carvalho AF, Menezes RST, Somavilla A, Costa MA, Del Lama MA (2015) Polistinae biogeography in the Neotropics: history and prospects. *Journal of Hymenoptera Research* 42: 93–105. doi: 10.3897/JHR.42.8754

Abstract

Discussions regarding Polistinae biogeography in the last two decades rarely associated current patterns of distribution with environmental changes. This well-known and very diverse group of insects is highly endemic in the Neotropics, but environmental factors influencing the enormous biological diversity in the region are not well established. Exploring evidence on the two main hypotheses concerning the origins and early colonization processes of paper wasps we position in favor of the Gondwanan hypothesis and discuss change-promoter processes in the Neotropics whose effects might have altered the distributions and facilitated the speciation of Polistinae in the region. Furthermore, based on recent advances in biogeography, mostly in the integration of ecological and evolutionary information, we highlight directions for future biogeographical research within the group.

Keywords

Biological richness, ecology, evolution, paper wasps, speciation, species distribution

Introduction

It is surprising how young the biogeography of Polistinae is. Many questions remain unsolved or have never been posed for this subfamily. This gap in our knowledge is partially due to the absence of discussions linking variations (e.g., morphological, molecular and physiological) with historical processes. Exciting themes such as colonization routes, population genetics and phylogeography have not been featured in discussions of paper wasps' biology, thereby seriously limiting our ability to draw evolutionary conclusions. Furthermore, many recent advances in science have not been applied to the study of these insects. For example, it is not known how distributions of Polistinae species have changed during the Late Cenozoic or if existed and where refuges were located for forest-dwelling species during periods of extreme cold (i.e., the ice ages). These issues have already been explored and explanations have been proposed for some amphibians (Carnaval et al. 2009), birds (Batalha-Filho et al. 2012; Maldonado-Coelho 2012), ants (Resende et al. 2010) and plants (Pinheiro et al. 2013). Also, population relationships and historical demography are unknown for the subfamily Polistinae.

Compared with Africa, Europe and Asia, regions where paper wasps are abundant, an endemism of nearly 70% (~630 species) is recorded in the Americas (Richards 1978, Jeanne 1991, Silveira 2008) and most of the species are restricted to the Neotropics. In fact, these insects constitute a well-represented group in the Neotropical region, both in terms of abundance and richness. In addition, differences regarding both nest and body morphological traits and behavioral strategies (e.g., necrophilia, cyclic oligogyny) indicate that the region is the main hotspot for Polistinae or, using the words of O. W. Richards, is “the metropolis of social wasps” (Evans and West-Eberhard 1970).

Despite this richness, biogeographic studies related to Polistinae are not common. In fact, discussions regarding the origins and distribution patterns of this subfamily were not discussed by almost two decades; the last study on this subject before Silva and Noll (2014) was published by Carpenter (1996). However, factors related to the current distribution and success of paper wasps are typically associated with environmental conditions (e.g., Dejean et al. 2011). In addition, the historical reasons regarding the irradiation of these insects in the Neotropics – i.e., the explosion of species richness, likely during the Cenozoic – have not been discussed.

Many unanswered questions regarding the biogeography of these interesting insects can be posed: (1) what evidence exists supporting the biogeographical hypotheses on the origins of Polistinae and colonization of the New World?, (2) what are the primary ecological and environmental constraints shifting the distributions of the wasps and promoting changes in the Neotropics that make it “the metropolis of social wasps”? and (3) how did these wasps proceed while colonizing the New World? In this work we focus on the first two questions; the later is the theme of another ongoing study. In order to address these questions, we provide a brief review of the two main hypotheses regarding Polistinae biogeography (i.e., the Beringian and Gondwanan hypotheses) and associate historical processes such as climatic-vegetational changes, orogeny and

global temperature oscillations with the promotion of changes in Polistinae diversity and distribution in the Neotropics. In the last section of the text, we highlight some perspectives that are, in our opinion, critical for a deeper understanding of Polistinae biogeography. We maintain that these perspectives will drive future knowledge in this field. If we are able to influence ecological and evolutionary integrative discussions about these wasps, our goals in this work will certainly be achieved.

Biogeographical hypotheses: origins of Polistinae and colonization of the Neotropics

Early biogeographical hypotheses stated that paper wasps originated in the tropics based on the high diversity of such insects in the region (Wheeler 1922, Richards and Richards 1951). The sympatric and restricted occurrence in the oriental tropics of the three social subfamilies of Vespidae (Stenogastrinae, Vespinae and Polistinae) and the presence of ancestral forms in nest architecture (West-Eberhard 1969) and basal morphological traits (Van der Vecht 1965) support assumptions that the Vespinae/Polistinae split likely occurred in southeastern Asia (Van der Vecht 1965, Richards 1971). According to these assumptions, the dispersion of paper wasps into the New World occurred twice through the Bering Strait in the Middle Tertiary and the current distribution therein was likely reached after the last ice age (Richards 1978).

Carpenter (1981) criticized the relation between center of diversity and center of origin and suggested that the distribution pattern of paper wasps is “widely Gondwanan.” It was also suggested by Carpenter (1993) that the separation between Africa and South America in the Early Cretaceous (120–100 million years ago; Mya) was an important event in the evolutionary history of the group. Carpenter (1996) also reviewed the two main hypotheses of Polistinae biogeography and performed Component Analyses for *Polistes* Latreille subgenera. Area cladograms presented in that work supported the Gondwanan distribution of subgenera and rejected the expected dispersion through the Bering Strait (as defended by Van der Vecht 1965, Richards 1971, 1978).

Other data also support the Gondwanan distribution of paper wasps and we reviewed some of these studies, focusing on paleontological, phylogenetic and divergence time evidence.

Fossil records

There are few data related to the paleodistribution of paper wasps based on fossil records. Despite this fact, important evidence that permits inferences about the biogeographic hypotheses was obtained by Brown (1941a) with a specimen from the Upper Cretaceous: a wasp nest comb of *Brownichnus favosites* (previously treated as genus *Celliforma*) from Utah, United States. The specimen shows traits comparable to papery nests, just like those of *Polistes*. This finding defined the presence of social behavior in

insects earlier than that predicted in that time, from the Eocene to the Cretaceous, but Brown (1941a) was unable to determine the relationships of the specimen with today's social wasps.

After some discussions regarding the classification of such a comb in Bequaert and Carpenter (1941) and Brown (1941b), Wenzel (1990) confirmed that the comb is indeed from a social wasp. Despite the fact that Wenzel (1990) has not been conclusive about the relationships of *B. favosites* with present-day groups, the author advocated that the comb is certainly from a Vespinae or a Polistinae. Moreover, he defended that if *B. favosites* is an ancient *Polistes*, the vicariance hypothesis (i.e., Gondwanan) “should remain intact.”

Phylogeny

Phylogenetic inferences have provided important information about the evolutionary history of Polistinae. Carpenter (1991) carried out the first cladistic analysis of the relationships among the genera of subfamily based on morphological and nest architecture characters. This analysis placed the cosmopolitan Polistini as the sister group to the other tribes. Ropalidiini (Old World), Mischocyttarini and Epiponini were grouped in a polytomy. Wenzel and Carpenter (1994) solved the polytomy by placing Mischocyttarini as an intermediate group and Ropalidiini and Epiponini as more derived groups. Pickett and Carpenter (2010), however, reviewed several molecular and morphological characters of Vespidae and placed Ropalidiini as the most basal group, followed by Mischocyttarini and Polistini + Epiponini as sister tribes.

The evolutionary history of *Polistes* has been the most thoroughly studied by phylogenetic assessments. We reviewed five of the main studies (Carpenter 1996, Zhu et al. 2000, Arévalo et al. 2004, Pickett and Wenzel 2004, Pickett et al. 2006) and noted that the Old World subgenera are invariably those at the base of the trees and that the New World subgenera are derived. We consider this settlement as a strong evidence for a more recent colonization in the western tropics. Likewise, considering that Mischocyttarini and Epiponini only occur in the Neotropics, and that no fossils of these groups were recorded outside of this region [following the suggestion of Carpenter and Grimaldi (1997) in not considering the misidentifications of two *Polybia* Lepeletier found in Burnham (1978) from England] and if genus *Paleopolistes* from France is not an Epiponini (Perrard & Carpenter, 2014) we are tempted to give credit to the hypothesis that both tribes arose in the New World after the separation of Africa and South America (120 Mya).

Divergence time estimates

Ezenwa et al. (1998) raised assumptions that even though the oldest known paper wasp fossil dates from the Cretaceous (Brown 1941a), the Vespinae/Polistinae split likely

occurred in the Middle Jurassic (about 175 Mya) and the four tribes arose between 175 and 80 Mya. These assumptions, although not tested empirically, strengthen the hypothesis of a possible colonization of the Americas in a Gondwanan scenario due the exclusivity of Mischocyttarini and Epiponini in this region.

Based on these data, we tend to give credence to the Gondwanan hypothesis as a reasonable and convincing assumption able to explain the origins and colonization processes of the worldwide Polistinae distribution, as well as early colonization routes.

The life in the metropolis

Distinct from other regions of the globe, the Neotropics are composed of large, humid forests that have undergone several changes (Hoorn et al. 2010). These forests harbor most of the paper wasp fauna in the region (Richards 1978). The causes for the high biodiversity levels in these rainforests have been recurrently associated with environmental changes and hypotheses regarding extrinsic processes (non-genetic mechanisms) that facilitate speciation in the biota, mostly in the Amazonian region, have also been explored in previous studies. Haffer (1997, 2008) provided extensive reviews concerning these hypotheses and argued that several of them are relevant to speciation processes in different geological periods of the Cenozoic.

Although environmental processes have not been commonly explored to explain the diversity of paper wasps in the Neotropics, historical and recurrent events have certainly provided evolutionary scenarios for adaptive irradiation of this group in the region. Richards (1978) recognized that climate and vegetation changes in South America have mixed the distribution of paper wasps during the geologically recent past of Brazil. Dejean et al. (2011) associated the fluctuation of species richness to climatic phenomena such as El Niño and La Niña in French Guiana. However, empirical analyses and theoretical assumptions regarding environmental factors able to induce putative alterations in populations of paper wasps have not been sufficiently discussed. Here, we provide a quick review of the main hypotheses concerning speciation processes in the Neotropics. We aim to highlight the major environmental events that we consider to have been involved in the Neotropical irradiation of Polistinae during the Cenozoic. Other proposals can be found in the reviews of Haffer (1997, 2008), including the Gradient, Canopy-density and Museum hypotheses; we opted not to include these hypotheses in this work because the arguments used to explain speciation processes are less general in these hypotheses than in those presented here.

Climatic-vegetational changes: the Refuge hypothesis

The Refuge hypothesis predicts the occurrence of putative forest refuges – regions where forests remain unaltered irrespective of global temperature oscillations – during the Cenozoic and before, i.e., more than 60 Mya (Haffer 1997, 2008). Even so, Haffer (1969)

proposed initially that climatic-vegetational changes during the Pleistocene (1.8–0.1 Mya) were the main causes for novelties and speciation processes to arise in the Amazonian rainforest. This idea suffered criticisms (e.g., Bush and Oliveira 2006) and was not supported by many studies that contested the short timespan for speciation events predicted initially by the author since most of the Neotropical groups likely arose before the Pleistocene (e.g., Zink and Slowinski 1995, Costa 2003, Geurgas et al. 2008).

Haffer modified his earlier ideas based mainly on Bennett's (1990) assumptions regarding the influences of Milankovitch cycles on communities over a time scale of 20–100 thousand years, or ky. These cycles, caused by alterations in the Earth's orbit, would have affected population structures and caused disruptive events in the Neotropical communities and might be the main factors responsible for oscillating the climate of the planet due to its influence on glacial/interglacial cycles (see Bennett (1990) for complete explanations on the Milankovitch cycles). In summary, the Refuge hypothesis (Haffer 1997, 2008) is particularly based on the effects of dry/humid periods of the Cenozoic on the speciation events in the Amazonian rainforest.

Some refuges have also been proposed for the Brazilian Atlantic Forest (e.g., Carnaval and Moritz 2008, Carnaval et al. 2009), suggesting that these areas might have indeed served as stable forest patches for many forest-dwelling taxa throughout climatic-vegetational changes. Moreover, because each species has its own ecological niche, idiosyncratic responses to alterations as well as different distribution of refuges are expected for different species.

Richards (1978) considered that climatic-vegetational changes could have affected the distribution of species but pointed out that paper wasps had not showed clear evidence for refuge areas. Indeed, there are no empirical data concerning this matter, but distribution of some species denote that the retraction of South American rainforests during dry periods disrupted populations of *Epipona media* Cooper, *Synoeca septentrionalis* Richards and *Angiopolybia pallens* (Lepelletier) (Menezes et al. 2010, 2011, Carvalho et al. 2014).

Phylogeographic analyses carried out with the extinction-threatened ant *Dinoponera lucida* Emery (Resende et al. 2010) and with orchid bees (López-Urbe et al. 2014) indicated that, in fact, different size refuges were important for the creation and maintenance of hymenopterans' diversity in the Neotropical rainforests. For paper wasps, however, there are no studies on this matter.

Paleogeography and River hypotheses

According to these hypotheses, different models are expected to have caused geographic separation and speciation of the animal populations in the Amazonian rainforest that are related to worldwide sea level changes, uplifts of plateaus and flooding of plains. The emergence of islands (Island Model (Emsley 1965, Croizat 1976)), archs (Arch Model (Morell 1996)), lagoons (Lagoon Model (Marroig and Cerqueira 1997)) and rivers (River hypothesis (Sick 1967)) in the Amazonian basin were recog-

nized as historical events that putatively shifted species' distribution ranges, facilitating their differentiation.

Despite Haffer (2008) arguing that some of these inferences are highly speculative and contain several missing links, it is possible that such alterations in the geography of the Amazonian region, if they occurred during the Cenozoic, would have provided a great variety of environments for diversification of paper wasps. Furthermore, it is not surprising that large bodies of water might act as barriers to the flow between disrupted populations of land species. For wasps, that would not be different. Indeed, swarms have great difficulty in dispersing across water (Jeanne 1981). This fact possibly affected the decline of paper wasps in the Caribbean, for example, due to limitations of the chemical trail system, but might not be a very convincing overall explanation since the subfamily is present throughout Southeast Asia, the Philippines, and Australia (Carpenter and Grimaldi 1997), for example.

Mainland species in turn might also have had their distributions altered during landscape changes in the Cenozoic caused by both water barriers and tectonic events. As showed by Silva and Noll (2014), phylogenetics and distribution data call attention to the importance of land bridges connecting the Northern and Southern Hemispheres to the cladogenesis of basal species of genus *Brachygastra* Perty. Unfortunately, although these alterations have influenced substantially the distribution of some land organisms (Croizat 1976, Hershkovitz 1977), it is not possible to our knowledge to quantify precisely how much these changes have contributed to extinction, disruptions and speciation events of paper wasps.

Disturbance-Vicariance hypothesis

This hypothesis regards the influence of cold/warm cycles (not dry/humid, as proposed by the Refuge hypothesis) as selecting Amazonian lineages throughout temperature oscillations during the Pleistocene (Colinvaux 1993, Bush 1994). Invasion, counter-invasion and competitive interactions are seen in this model as events affecting distributions and abundances of species. According to these assumptions, the presence of invading and cold-adapted taxa could have resulted in local extinctions, favoring isolation of genotypes and allopatric speciation of some taxa.

There is a regional focus of this hypothesis on the peripheral areas of the Amazonian rainforest due to the high faunal endemism in such areas. Such regions are recognized by the model as being rich in endemic taxa due to their supposed environmental instability. Indeed, temperature oscillations during the Pleistocene might have influenced the distribution of taxa and genotypes, but speciation events are mostly expected to have occurred before 1.8 Mya (Zink and Slowinski 1995, Costa 2003).

The Quaternary is undoubtedly a short time to explain the huge diversity of paper wasp species in the Neotropics. Both temperature oscillations and the short period, however, are apparently sufficient for population structuring mainly of widely disrupted taxa. Polistinae species might have undergone their distribution to optimal lo-

cations during such changes in the temperature and environmentally related genotypes might have been frequently selected. Such alterations might also have influenced both behavioral and physiologic traits, including feeding habits, defense, nest building, resistance to diseases and predators and adaptive strategies against cold or warm climate. Future researches are undoubtedly needed for accurate detailing.

Future directions

Since ecological and phylogenetic information can comprise very useful frameworks for raising hypotheses on historical biogeography in scenarios constantly in change, to explore the different impact of variables on the distribution of Polistinae is an important subject to be discussed. Furthermore, the knowledge of environmental and geological constraints that affect distribution of species can help predictions about extrinsic mechanisms shifting large-scale distributional patterns. In addition, to resolve important questions like the causes of some clades disperse to some areas but not to others is the major challenge in historical biogeography (Wiens and Graham 2005) and define the favorable and unfavorable conditions that unbalance population density over time figures as a crucial factor to describe distribution of any group (Haldane 1956). However, understanding how extrinsic factors alter distribution we can determine environmental and ecological constraints that species can tolerate or not and, likewise, which regions these species might occupy by dispersal events.

A very promising group of paper wasps for start this kind of research is that composed by forest-dwelling species. Using data regarding current distribution, one can propose past and present distributions of acceptable conditions for a clade to occur, based on ecological niche modelling, for example (e.g., Hugall et al. 2002, Carnaval et al. 2009). Since the bioclimatic conditions that maintain the distribution of humid forests have changed in the Neotropics during ice ages and since forest-dwelling species depend on forest coverage to nest and forage, the distribution of these wasps has likely responded in a convergent manner to these alterations. Thinking about the biogeographic research of paper wasps in the next years, the formulation of potential paleodistribution models might be considered a cornerstone that will drive population genetics hypotheses, mostly based on phylogeographic frameworks, in studies of these insects.

Specialized literature related to the distribution or phylogenetics is very common for different clades of paper wasps. However, a fine-scale distribution pattern of Neotropical Polistinae could be more precisely understood by reviewing specialized literature; i.e., species by species. Also, tests of hypotheses using these data for making inferences about the ecological and evolutionary causes of the success or failure of Polistinae in colonizing certain regions have been rarely done. For example, the Tropical Niche Conservatism hypothesis (Wiens and Graham 2005) could explain the tendency of paper wasps to inhabit tropical areas instead of temperate regions since the subfamily was originated in a similar environment (i.e., tropical Asia). A strategy for testing such a hypothesis could be based on the integration of physiological responses, such as thermoregulation,

and population relationships in the study of dry-adapted lineages of paper wasps. Since niche conservatism predicts that unaltered lineages are not likely to habit areas characterized by conditions different from fundamental niches, lineages of a clade showing thermoregulatory responses different from their ancestral populations would be expected to be adapted to local climatic alterations as a result of niche expansion.

Many recent studies have shown that integrative approaches linking climatic and phylogeny-based information to explain biogeographical patterns might be very useful for testing explicit hypotheses of causation by particular, mostly environmental, events (Hugall et al. 2002, Waltari et al. 2007, Carnaval et al. 2009). Moreover, recent discussions have drawn attention to the strong connection between evolutionary processes (e.g., ecological specialization) and environmental events such as climatic-vegetational changes in shaping the distribution of organisms over time (Wiens 2004, Hoorn et al. 2010). Quantifying the different impacts of each of these factors in the evolutionary history of Polistinae should be regarded as the main challenge in the future of biogeography and speciation research of the subfamily. The study of biogeographical processes using such wasps as models can also aid in our understanding of significant events that have influenced the distribution, historical demography and extinctions of the Neotropical biota, including the disjunction between Amazonia and Atlantic Forest and the demographic retraction of populations adapted to rainforest conditions during glacial periods, for example.

Despite Ezenwa et al. (1998) have proposed possible periods for the arising of the Polistinae tribes, current techniques are more precise for inferring divergence times. Based on a molecular clock model, which permits dating putative splits between lineages using fossil-calibrated phylogenetic trees, the proposal of the geological periods in which the subfamily Polistinae and its four tribes arose, as well as temporal concentration of speciation events, would be more convincing. Such research could also be conducted to test hypotheses regarding the influence of geological events such as river formation and land uplifts on the separation of lineages since the periods in which these events occurred are known.

In light of the differences regarding life histories, occupied niches, huge diversity, etc., the Neotropical paper wasps represent an interesting group to be used as model in a wide range of studies. However, biogeographic patterns as colonization routes and causes behind alterations on the distribution have not been sufficiently discussed using advanced analyses. We expect that by focusing on some of the challenges presented in this work, the study of biogeography with these wasps will progress in the forthcoming years.

Acknowledgements

This study was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, 2011/13391-2 and BEPE 2013/04317-9) through a Ph.D. scholarship for the first author. Our most sincere thanks are addressed to Ana Carolina Carnaval (The City University of New York, USA), Fernando Noll and Marjorie Silva (UNESP, São

José do Rio Preto, Brazil), Gilberto Santos (UEFS, Feira de Santana, Brazil), Reinaldo Brito and Evandro Moraes (UFSCar, São Carlos, Brazil) and one anonymous reviewer, whose commentaries improved the manuscript.

References

- Arévalo E, Zhu Y, Carpenter JM, Strassmann JE (2004) The phylogeny of the social wasp subfamily Polistinae: evidence from microsatellite flanking sequences, mitochondrial COI sequence, and morphological characters. *BioMed Central Evolutionary Biology* 4: 8. doi: 10.1186/1471-2148-4-8
- Batalha-Filho H, Cabanne GS, Miyaki CY (2012) Phylogeography of an Atlantic forest passerine reveals demographic stability through the last glacial maximum. *Molecular Phylogenetics and Evolution* 65: 892–902. doi: 10.1016/j.ympev.2012.08.010
- Bequaert JC, Carpenter JM (1941) The antiquity of social insects. *Psyche* 48: 50–55. doi: 10.1155/1941/64162
- Bennett KD (1990) Milankovitch cycles and their effects on species in ecological and evolutionary time. *Paleobiology* 16: 11–21.
- Brown RW (1941a) The comb of a wasp nest from the Upper Cretaceous of Utah. *American Journal of Science* 239: 54–56. doi: 10.2475/ajs.239.1.54
- Brown RW (1941b) Concerning the antiquity of social insects. *Psyche* 48: 105–110. doi: 10.1155/1941/76070
- Burnham L (1978) Survey of social insects in the fossil record. *Psyche* 85: 85–134. doi: 10.1155/1978/80816
- Bush MB (1994) Amazonian speciation: a necessarily complex model. *Journal of Biogeography* 21: 5–17. doi: 10.2307/2845600
- Bush MB, Oliveira PE (2006) The rise and fall of the Refugial Hypothesis of Amazonian Speciation: a paleoecological perspective. *Biota Neotropica* 6, 17 pp.
- Carnaval AC, Hickerson MJ, Haddad CFB, Rodrigues MT, Moritz C (2009) Stability predicts genetic diversity in the Brazilian Atlantic Forest Hotspot. *Science* 323: 785–789. doi: 10.1126/science.1166955
- Carnaval AC, Moritz C (2008) Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic forest. *Journal of Biogeography* 35: 1187–1201. doi: 10.1111/j.1365-2699.2007.01870.x
- Carpenter JM (1981) The phylogenetic relationships and natural classification of the Vespoidea (Hymenoptera). *Systematic Entomology* 7: 11–38. doi: 10.1111/j.1365-3113.1982.tb00124.x
- Carpenter JM (1991) Phylogenetic relationships and the origin of social behavior in the Vespidae. In: Ross KG, Matthews RW (Eds) *The social biology of wasps*. Cornell University, Ithaca, 7–32.
- Carpenter JM (1993) Biogeographic patterns in the Vespidae (Hymenoptera): two views of Africa and South America. In: Goldblatt P (Ed.) *Biological relationships between Africa and South America*. Yale University, New Haven, 139–155.
- Carpenter JM (1996) Phylogeny and biogeography of *Polistes*. In: Turillazzi S, West-Eberhard MJ (Eds) *Natural history and evolution of paper wasps*. Oxford University, New York, 18–57.

- Carpenter JM, Grimaldi DA (1997) Social Wasps in Amber. *American Museum Novitates* 3203: 7 pp.
- Carvalho AF, Santos GMM, Menezes RST, Costa MA (2014) Genetic diversity of *Angiopolybia pallens* (Lepeletier) (Hymenoptera, Vespidae, Polistinae) explained by the disjunction of South American rainforests. *Genetics and Molecular Research* 13: 89–94. doi: 10.4238/2014.January.8.7
- Colinvaux P (1993) Pleistocene biogeography and diversity in tropical forests of South America. Biological relationships between Africa and South America. Yale University, New Haven, 473–499.
- Costa LP (2003) The historical bridge between the Amazon and the Atlantic forest of Brazil: a study of molecular phylogeography with small mammals. *Journal of Biogeography* 30: 71–86. doi: 10.1046/j.1365-2699.2003.00792.x
- Croizat L (1976) Biogeografía analítica y sintética (“Panbiogeografía”) de las Américas. Biblioteca de la Academia de Ciencias Físicas, Matemáticas y Naturales, Caracas, 1–890.
- Dejean A, Céréghino R, Carpenter JM, Corbara B, Hérault B, Rossi V, Leponce M, Orivel J, Bonal D (2011) Climate change impact on Neotropical social wasps. *PLoS ONE* 6: e27004. doi: 10.1371/journal.pone.0027004
- Emsley MG (1965) Speciation in *Heliconius* (Lep. Nymphalidae): Morphology and geographic distribution. *Zoologica* 50: 191–254.
- Evans HE, West-Eberhard MJ (1970) The wasps. University of Michigan, Ann Arbor, 1–265.
- Ezenwa VO, Peters JM, Zhu Y, Arévalo E, Hastings MD, Seppa P, Pedersen JS, Zacchi F, Queller DC, Strassmann JE (1998) Ancient conservation of trinucleotide microsatellite loci in polistine wasps. *Molecular Phylogenetics and Evolution* 10: 168–177. doi: 10.1006/mpev.1998.0528
- Geurgas SR, Rodrigues MT, Moritz C (2008) The genus *Coleodactylus* (Sphaerodactylinae, Gekkota) revisited: a molecular phylogenetic perspective. *Molecular Phylogenetics and Evolution* 49: 92–101. doi: 10.1016/j.ympev.2008.05.043
- Haffer J (1969) Speciation in Amazonian forest birds. *Science* 165: 131–137. doi: 10.1126/science.165.3889.131
- Haffer J (1997) Alternative models of vertebrate speciation in Amazonia: an overview. *Biodiversity and Conservation* 6: 451–476. doi: 10.1023/A:1018320925954
- Haffer J (2008) Hypotheses to explain the origin of species in Amazonia. *Brazilian Journal of Biology* 68(Supplement 4): 917–947. doi: 10.1590/S1519-69842008000500003
- Haldane JBS (1956) The relationship between density regulation and natural selection. *Proceedings of the Royal Society of London B* 145: 306–308. doi: 10.1098/rspb.1956.0039
- Hernandez PA, Graham CH, Master LL, Albert DL (2006) The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography* 29: 773–785. doi: 10.1111/j.1472-4642.2008.00482.x
- Hershkovitz P (1977) Living New World monkeys (Platyrrhini). University of Chicago, Chicago.
- Hoorn C, Wesselingh FP, ter Steege H et al. (2010) Amazonia through time: Andean Uplift, Climate Change, Landscape Evolution, and Biodiversity. *Science* 330: 927–931. doi: 10.1126/science.1194585
- Hugall A, Moritz C, Moussalli A, Stanisci J (2002) Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosiphia*

- bellendenkerensis* (Brazier 1875). Proceedings of the National Academy of Sciences USA 99: 6112–6117. doi: 10.1073/pnas.092538699
- Jeanne RL (1981) Chemical communication during swarm emigration in the social wasp *Polybia sericea* (Olivier). Animal Behaviour 29: 102–113. doi: 10.1016/S0003-3472(81)80157-1
- Jeanne RL (1991) The swarm-founding Polistinae. In: Ross KG, Matthews RW (Eds) The social biology of wasps. Cornell University, Ithaca, 191–231.
- López-Urbe MM, Zamudio KR, Cardoso CF, Danforth BN (2014) Climate, physiological tolerance and sex-biased dispersal shape genetic structure of Neotropical orchid bees. Molecular Ecology 23: 1874–1890. doi: 10.1111/mec.12689
- Maldonado-Coelho M (2012) Climatic oscillations shape the phylogeographical structure of Atlantic Forest fire-eye antbirds (Aves: Thamnophilidae). Biological Journal of the Linnean Society 105: 900–924. doi: 10.1111/j.1095-8312.2011.01823.x
- Marroig G, Cerqueira R (1997) Plio–Pleistocene South American history and the Amazon Lagoon hypothesis: a piece in the puzzle of Amazonian diversification. Journal of Comparative Biology 2: 103–119.
- Menezes RST, Carvalho AF, Raw A, Costa MA (2010) *Epipona media* Cooper (Hymenoptera: Vespidae), a social wasp new to the Brazilian Atlantic Forest. Neotropical Entomology 39: 1046–1047. doi: 10.1590/S1519-566X2010000600031
- Menezes RST, Andena SR, Carvalho AF, Costa MA (2011) First records of *Synoecca septentrionalis* Richards, 1978 (Hymenoptera, Vespidae, Epiponini) in the Brazilian Atlantic Rain Forest. ZooKeys 151: 75–78. doi: 10.3897/zookeys.151.1882
- Morell V (1996) Amazonian diversity: a river doesn't run through it. Special news report. Science 273: 1496–1497. doi: 10.1126/science.273.5281.1496b
- Perrard A, Nel A, Carpenter JM (2014) A new paper wasp from Late Eocene of France (Hymenoptera: Vespidae: Polistinae). Zootaxa 3753: 542–548. doi: 10.11646/zootaxa.3753.6.2
- Pickett KM, Wenzel JW (2004) Phylogenetic analysis of the New World *Polistes* (Hymenoptera: Vespidae, Polistinae) using morphology and molecules. Journal of the Kansas Entomological Society 77: 742–760. doi: 10.2317/E-18.1
- Pickett KM, Carpenter JM (2010) Simultaneous analysis and the origin of eusociality in the Vespidae (Insecta: Hymenoptera). Arthropod Systematics and Phylogeny 68: 3–33.
- Pickett KM, Carpenter JM, Wheeler WC (2006) Systematics of *Polistes* (Hymenoptera: Vespidae), with a phylogenetic consideration of Hamilton's haplodiploidy hypothesis. Annales Zoologici Fennici 43: 390–406.
- Pinheiro F, Cozzolino S, Barros F, Gouveia TMZM, Suzuki RM, Fay MF, Palma-Silva C (2013) Phylogeographic structure and outbreeding depression reveal early stages of reproductive isolation in the Neotropical orchid *Epidendrum denticulatum*. Evolution 67: 2024–2039. doi: 10.1111/evo.12085
- Resende HC, Yotoko KSC, DeLapie JHC, Costa MA, Campiolo S, Tavares MG, Campos LAO, Fernandes-Salomão TM (2010) Pliocene and Pleistocene events shaping the genetic diversity within the central corridor of the Brazilian Atlantic Forest. Biological Journal of the Linnean Society 101: 949–960. doi: 10.1111/j.1095-8312.2010.01534.x

- Richards OW, Richards MJ (1951) Observations on the social wasps of South America (Hymenoptera, Vespidae). *Transactions of the Royal Entomological Society of London* 102: 1–170. doi: 10.1111/j.1365-2311.1951.tb01241.x
- Richards OW (1971) The biology of the social wasps (Hymenoptera, Vespidae). *Biological Reviews* 46: 483–528. doi: 10.1111/j.1469-185X.1971.tb01054.x
- Richards OW (1978) The social wasps of the Americas excluding the Vespinae. *British Museum Natural History*, London.
- Sick H (1967) Rios e enchentes na Amazônia como obstáculo para a avifauna. *Atas Simpósio sobre a Biota amazônica* 5: 495–520.
- Silva M, Noll FB (2014) Biogeography of the social wasp genus *Brachygastra* (Hymenoptera: Vespidae: Polistinae). *Journal of Biogeography*: 1–10. Article first published online: 22 SEP 2014. doi: 10.1111/jbi.12417
- Silveira OT (2008) Phylogeny of wasps of the genus *Mischocyttarus* de Saussure (Hymenoptera, Vespidae, Polistinae). *Revista Brasileira de Entomologia* 52: 510–549. doi: 10.1590/S0085-56262008000400004
- Van der Vecht J (1965) The geographical distribution of the social wasps (Hymenoptera, Vespidae). *Proceedings of the XII International Congress of Entomology*: 440–441.
- Waltari E, Hijmans RJ, Peterson AT, Nyári ÁS, Perkins SL, Guralnick RP (2007) Locating Pleistocene Refugia: Comparing Phylogeographic and Ecological Niche Model Predictions. *PLoS ONE* 7: e563. doi: 10.1371/journal.pone.0000563
- Wenzel JW (1990) A social wasp's nest from the Cretaceous period, Utah, USA, and its biogeographical significance. *Psyche* 97: 21–29. doi: 10.1155/1990/24696
- Wenzel JW, Carpenter JM (1994) Comparing methods: adaptive traits and tests of adaptation. In: Eggleton P, Vane-Wright R (Eds) *Phylogenetics and Ecology*. London Academic Press, London, 79–101.
- West-Eberhard MJ (1969) The Social Biology of Polistine Wasps. *Miscellaneous publications, Museum of Zoology, University of Michigan* 140: 1–101.
- Wheeler WM (1922) Social life among the insects. *Lecture II. Part 2. Wasps solitary and social.* *The Scientific Monthly* 15: 119–131.
- Wiens JJ (2004) Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution* 58: 193–197. doi: 10.1111/j.0014-3820.2004.tb01586.x
- Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology and Systematics* 36: 519–539. doi: 10.1146/annurev.ecolsys.36.102803.095431
- Zhu Y, Queller D, Strassmann JE (2000) A phylogenetic perspective on sequence evolution in microsatellite loci. *Journal of Molecular Evolution* 50: 324–338. doi: 10.1007/s002399910036
- Zink RM, Slowinski JB (1995) Evidence from molecular systematics for decreased avian diversification in the Pleistocene Epoch. *Proceedings of the National Academy of Sciences USA*, 92: 5832–5835. doi: 10.1073/pnas.92.13.5832