BIODIVERSITY AND SYSTEMATICS OF THE BLATTODEA OF THE GUIANA SHIELD

by

DOMINIC ANTHONY EVANGELISTA

A dissertation submitted to the Graduate School of

Rutgers, The State University of New Jersey

in partial fulfillment of the requirements for the degree of

Doctor of Biological Sciences written under the direction of

Jessica Lee Ware Ph.D. and approved by

_____

_____

_____

_____

_____.

Newark, New Jersey, United States of America

Rutgers, The State University of New Jersey

May, 2016

DISSERTATION ABSTRACT

Biodiversity and systematics of the Blattodea of the Guiana Shield

by Dominic Anthony Evangelista

Dissertation Director:

Jessica Lee Ware

Cockroaches are a moderately diverse but understudied insect order with the majority of their diversity present in the tropics. Recent works have made great strides in improving our understanding of the cockroach faunas of Brazil, Ecuador, Argentina, and Colombia. However, the subcontinent-sized landmass known as the Guiana Shield (itself containing three countries and parts of another two) has been largely ignored by cockroach systematists and taxonomists for over 20 years. The first goal of this dissertation research is to update the current understanding of the cockroach fauna in the Guiana Shield. Once this has been accomplished through synthesis of existing data and collection of new data from the field, we describe the diversity at multiple scales using perspectives that are more widely applicable to our understanding of ecology and systematics. This includes: exploring the relationship between dispersal ability and the evolution of geographic ranges (regional scale), the effect of species delimitation on estimates of species richness within a community of cockroaches (local/community scale), and the effect of specific landscape variables on species distributions (local/species scale). The major finding of this dissertation include: 3 descriptions of new species; 18 new species records including 1 genus entirely new to the Guiana Shield; the

understanding that different approaches to identification can yield huge (~25%) discrepancy in estimated richness; that savannas limit the distributions of cockroach taxa but patterns of flooding do not; and that flight ability may affect how geographical ranges evolve, with better flying taxa having ranges more clustered in space. We also provide minor ethological and ecological insights from side projects or field observations.

PREFACE

How to cite this dissertation

In reference to information from the introduction, chapter 4 or conclusions of this dissertation please this document appropriately as in:

Evangelista, D. A. (2016). Biodiversity and Systematics of the Blattodea of the Guiana Shield. Biological Sciences, Rutgers, The State University of New Jersey. PhD.

In reference to taxon records or descriptions from chapter 1 please consult the two sources below and cite appropriately.

Evangelista, D. A., et al. (2015). "The Blattodea s.s. (Insecta, Dictyoptera) of the Guiana Shield." Zookeys 475: 37-87.

Evangelista, D. A., et al. (in press, 2016). "New and enigmatic cockroaches (Insecta: Dictyoptera: Blattodea) of Guyana." The Journal of Natural History.

However, if citing pooled data from chapter 1 (e.g. checklist, entire regional faunas, information from figures 1-30 to 1-34 or tables 1-7 to 1-8) please cite this dissertation.

In reference to anything from chapter 2 please cite:

Evangelista, D. A., et al. (2014). "Species richness estimates of Blattodea s.s. (Insecta: Dictyoptera) from northern Guyana vary depending upon methods of species delimitation." Systematic Entomology 39: 150-158.

In reference to anything from chapter 3 please search for the peer-reviewed form and cite that document. If no peer-reviewed form exists at the time of reference please cite this dissertation.

Notes on taxonomic priority

There are some species descriptions and new records written in this dissertation. However, these were prepared specifically for submission to various academic, peer reviewed journals. They are also in the scope of this thesis, so I include them here. To avoid taxonomic confusion, any description printed here should simply be considered a reproduction over the peer-reviewed versions of these descriptions. In the event that there are any discrepancies among these descriptions, the peer-reviewed versions should take priority. Two descriptions (*Xestoblatta berenbaumae* and *Calhypnorna* sp.) are published prior to the time of this writing and two more (*Dendroblatta litura* and *Dasyblatta warei*) are submitted. The two published descriptions should be cited appropriately (see above). The two submitted descriptions should be cited appropriately as well, assuming they were published after the release of this dissertation. If the descriptions of *Dendroblatta litura* and *Dasyblatta warei* are not published elsewhere they should not be considered valid species from this dissertation.

Video and media

A recorded presentation of this dissertation is available at:

https://www.youtube.com/watch?v=L4wBfyHFX3Y

ACKNOWLEDGMENTS

The people who contributed to this research are numerous. Many, if not most, are inevitably forgotten here by no one's fault other than my own. Nonetheless, I will make the best attempt to list everyone.

First I would like to thank all the people that contributed directly to this research through data collection, providing of facilities, or other support. Thank you to the reliable and intelligent undergraduate students of Rutgers University, particularly those on the Newark campus. Special thanks to: Pia Colon, Kimberly Chan, Ian Biazzo, Laila Abbas, Irene Shaji, Megan Wilson, Dan Troast, Tarik Hussein, Danny Bishara, Lucianni Lantigua, Folake Olamiju, James Pimentel, Zainab Poonawalla, Kayla Kaplan, Kimberly Guzman, Molly Duda, Alana Lai, Erik Gamarra, Ciara Mae Mendoza, and Erdine Sylvain. Thank you to those amazing people that assisted with field work. I would wholeheartedly thank: Oswin Ambrose, Susan George, Megan Wilson, Ian Biazzo and Joseph Evangelista. Also, Godfrey Bourne, Joyce Wade, Abigail, Shaneeza, Sheri-Ann Ashanti, Celina, Diane McTurk, Gerard Periera, Salvador DeCaires, Andrea DeCaires, Wazeed Manjour and his family. Thank you to other organizations who helped as well: the Entomological Society of America, Karanambu Trust, CEIBA, Peddie School, Genewiz, Macrogen, NYU genomics facility, Rutgers Libraries, Pensoft publishing and Rutgers University. Thank you to my department administration who assisted in many capacities, particularly: Shandell Rivera, Edward Bonder, Karen Roach, Maty Nieves, Sheronda Martin and

Neermala Gazze. Important thanks to my funding sources without whom this research would not exist: Rutgers University, NSF, Entomological Society of America, Experiment.com and, most of all, May Berenbaum.

In addition to those that contributed through data collection, funding, facilities and support many others contributed through other means. As such, I would also like to acknowledge the contributions of people that generally contributed to my completion of this dissertation. Thank you to my committee: Dan Bunker, Kimberly Russell, Gareth Russell, and Klaus Klass. High thanks to mentors as well: Karl Kjer, Robin Rice, Esteban Gutierrez, Sonia M. Lopes, Lyle Bus, Gavin Svennson, Benjamin Wipfler, George Beccaloni, Marie Djernaes and others. Thank you to my mother, father and brother for their unwavering support. Thanks as well to my aunts, uncles and grandparents. Thank you to my colleagues: Sarah Kornbluth, Caroline Devan, Nidhi Dharithreesan, Tony Cullen, Megan Litwhiler, Kimberly Plank, Julian Rondon-Rivera, Richard Mariani and others. Thank you to teachers and mentors: Gareth Russell, Kimberly Russell, Douglas Morrison, and Lion Gardiner. A huge heartfelt thank you to Ivonne Huaman as well.

Thank you to my fellow lab members, whose contribution is both immeasurable and indescribable: Melissa Sanchez-Herrera, Manpreet Kohli, Nicole Sroczinski, Jayshree Patel, William Kuhn, Dan Troast, Megan Wilson, Merlijn Jocque and Phil Barden.

Finally, thank you to my adviser, Jessica Lee Ware, for unparalleled mentorship and support.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Cockroaches (order: Blattodea) have the second most species of any polyneopteran insect group (~7200 described species; Beccaloni & Eggleton 2011). Despite the fact that we broadly generalize them as pests, the vast majority of these species never come into contact with humans (but see: Arruda et al. 2001; El-Sherbini & El-Sherbini 2011; Evangelista et al. 2013; Lemos et al. 2006; Maumholts et al. 1997; Peterson & Cobb 2009; von Beeren et al. 2015). In fact, a wide variety of research on Blattodea concerns understanding the nature and origins of their diversity (e.g. Djernaes et al. 2014; Grandcolas 1998; Legendre et al. 2015; Nalepa et al. 2001; Pellens & Grandcolas 2003; Schal 1982; Schauer et al. 2014; Ware et al. 2008) and not their pestiferous nature. The main goal of this dissertation is to explore the biodiversity of a regional cockroach fauna.

Cockroaches are distributed across all continents but mainly inhabit the tropical regions (Beccaloni 2014; Bell *et al.* 2007; Princis 1963; Figure I - 1). In tropical rainforests canopies, Blattodea (when either including or excluding termites) are thought to be the number one group contributing to insect biomass (Basset 2001). This suggests they are important food items for insectivores and likely perform significant ecosystem services by devouring dead matter (their presumed diets).

Coming to a better understanding of cockroach biology provides us with insights into the origins of their diversity and the ecosystem services they provide. These are lofty goals, but begin with the simple step of cataloging and describing species. Recent catalogues for new world cockroaches have been produced for Brazil (Pellens & Grandcolas 2008), Ecuador (Vidlička 2013), Colombia (Velez 2008), Argentina (Crespo *et al.* 2010) and various Caribbean islands (Gutierrez 1995; Gutierrez & Fisk 1998;

Gutierrez & Perez-Gelabert 2000; Lu *et al.* 2014). These are by no means complete lists. New species will continue to be catalogued in these regions for decades or centuries if the motivation and funding to do such research continues. Yet having even incomplete lists facilitates future research and can inform conservation practices.

Unlike the neotropical regions listed above, the cockroach fauna of the Guiana Shield has not been catalogued recently (see chapter 1). The last attempt was in 1975 (Bonfils 1975) but new species have been recorded since (e.g. Grandcolas 1990;1992;1993a; Grandcolas 1993b). The Guiana Shield is a massive area of South America. Guyana, Suriname, French Guiana and parts of Brazil and Venezuela all compose the Guiana Shield (see figure I – 2; a small part of Colombia is also sometimes included in the Shield; Alexander *et al.* 2005). The region is primarily rainforest, but also includes expansive wetlands, savannas, mountains, and waterways. The rainforests themselves are diverse as there are 20 distinct forest types recognized (Huber *et al.* 1995).

Chapter 1 of this dissertation provides the newest checklist of cockroaches of the Guiana Shield. In addition to simply naming and listing the biodiversity of regions, as we do in a checklist, we also want to investigate higher level questions regarding the spatial organization of species. We approach this in chapter 1 but expand on the topic more in other parts of this dissertation.

On the widest spatial scale we can address questions about what biological features determine individual species distributions (e.g. Arribas *et al.* 2012; Buden 2010; Gutierrez & Menendez 1997) or what geographic processes compose regional faunas (Cook *et al.* 2015; Warren *et al.* 2014). The distinct features of the Guiana Shield likely act as dispersal filters or range edges for many species. Savannas and waterways are both known to be

boundaries for dispersal (Hayes & Sewlal 2004; Naka 2011; Wallace 1852). Therefore, one would expect the Rupununi/Roraima savannas and the hundreds of waterways in the Guianas to coincide with range edges for many species. Yet, these would correspond only to animals that do not have the power or stamina to disperse across them (Lester *et al.* 2007; Rundle *et al.* 2007b). We address part of this issue in Chapter 4.

Although regional faunas are interesting subjects for questions about broad biogeographical processes, local ecological communities are more tangible and practical study systems for understanding ecological dynamics (e.g. Jocque & Field 2014; Panizzo 2011; Paoletti *et al.* 1991; Petermann *et al.* 2014). Despite the fact that they are tractable, they are still subject to error when taxonomists have not fully catalogued species or when identification tools are inaccessible to non-experts (e.g. Ensing *et al.* 2012; but see Vinarski & Kramarenko 2015). In chapter 2 we describe the community composition of cockroaches from two areas in Guyana while addressing how differing perspectives on how to delimit species can affect ecological indices (i.e. richness and diversity).

Integrating these two approaches we can address questions about how the same processes that affect regional faunas (biotic or abiotic dispersal limitation) organize species in local ecological assemblages (Banks-Leite *et al.* 2011; Watanabe *et al.* 2010). By studying how individual species, or populations, respond to specific parts of landscapes, we can perhaps come to a better understanding of how assemblages come together at increasingly large spatial scales, as well as make predictions about population level evolution. Chapter 3 of this thesis addresses this with regard to cockroach assemblages in the Rupununi savannas.

In all, this thesis will provide new insights into a little studied fauna from the perspective of taxonomy, biogeography, molecular systematics, and ecology. We also provide minor ethological and ecological insights from side projects or field observations.

Works cited

Alexander, E.E., Bassett, Y., Charles, E., De Dijn, B.P.E., Forget, P.-M., Hammond, D.S., Hounter, N.C., Pons, T.L., Rijkers, T., Rose, S.A. & Springate, N.D. (2005) Tropical Forests of the Guiana Shield: Ancient Forests in a Modern World. CABI Publishing, Cambridge, MA, 535 pp.

Arribas, P., Velasco, J., Abellán, P., Sánchez-Fernández, D., Andújar, C., Calosi, P., Millán, A., Ribera, I. & Bilton, D.T. (2012) Dispersal ability rather than ecological tolerance drives differences in range size between lentic and lotic water beetles (Coleoptera: Hydrophilidae). Journal of Biogeography, 39, 984-994.

Arruda, L.K., Vailes, L.D., Ferriani, V.P., Santos, A.B., Pomes, A. & Chapman, M.D. (2001) Cockroach allergens and asthma. Journal of Allergy and Clinical Immunology, 107, 419-28.

Banks-Leite, C., Ewers, R.M., Kapos, V., Martensen, A.C. & Metzger, J.P. (2011) Comparing species and measures of landscape structure as indicators of conservation importance. Journal of Applied Ecology, 48, 706-714.

Basset, Y. (2001) Invertebrates in the Canopy of Tropical Rain Forests How Much Do We Really Know? Plant Ecology, 153, 87-107.

Beccaloni, G. (2014) Cockroach Species File Online. Version 5.0/5.0. World Wide Web electronic publication, World Wide Web electronic publication

Beccaloni, G. & Eggleton, P. (2011) Taxonomy of Blattodea. Zootaxa, 3148, 199-200.

Bell, W.J., Roth, L.M. & Nalepa, C. (2007) Cockroaches: Ecology, Behavior and Natural History. Johns Hopkins University Press, Baltimore,pp.

Bonfils, J. (1975) Blattoptera [Orthopteroidea] récoltés en Guyane Française par la mission du muséum national d'histoire naturelle. Annales de la Société entomologique de France Medecine, 11, 29-62.

Buden, D.W. (2010) Pantala flavescens(Insecta: Odonata) Rides West Winds into Ngulu Atoll, Micronesia: Evidence of Seasonality and Wind-Assisted Dispersal. Pacific Science, 64, 141-143.

Cook, L.G., Hardy, N.B. & Crisp, M.D. (2015) Three explanations for biodiversity hotspots: small range size, geographical overlap and time for species accumulation. An Australian case study. New Phytol, 207, 390-400.

Crespo, F.A., Valverde, A.d.C. & Iglesias, M.S. (2010) Catalogue of Blattaria (Insecta) from Argentina. Zootaxa, 2726, 1-33.

Djernaes, M., Klass, K.D. & Eggleton, P. (2014) Identifying possible sister groups of Cryptocercidae+Isoptera: A combined molecular and morphological phylogeny of Dictyoptera. Molecular Phylogenetics and Evolution,

El-Sherbini, G.T. & El-Sherbini, E.T. (2011) The role of cockroaches and flies in mechanical transmission of medical important parasites. Journal of Entomology and Nematology, 3, 98-104.

Ensing, D.J., Moffa, C.E. & Pithera, J. (2012) Taxonomic identification errors generate misleading ecological niche model predictions of an invasive hawkweed. Botany, 91, 137-147.

Evangelista, D.A., Buss, L. & Ware, J.L. (2013) Using DNA Barcodes to Confirm the Presence of a New Invasive Cockroach Pest in New York City. Journal of Economic Entomology, 106, 2275-2279.

Grandcolas, P. (1990) Descriptions de nouvelles Zetoborinae guyanaises avec quelques remarques sur la sous-famille. Bulleting of the Entomological Society of France, 95, 241-246.

Grandcolas, P. (1992) Paradicta n. gen. et Neorhicnoda n. gen., deux nouvaeux genres de Blaberinae (Dict., Blattaria, Blaberidae). Bulleting of the Entomological Society of France, 97, 7-15.

Grandcolas, P. (1993a) L'Ecologie de la Repartition de Thanatophyllum akinetum en Guyane Francaise (Insecta, Blattaria). Biogeographica, 69, 73-86.

Grandcolas, P. (1993b) Le genre Paramuzoa Roth, 1973: sa repartition et un cas de xylophagie chez les Nyctiborinae (Dictyoptera, Blattaria). Bulletin de la Société Entomologique de France, 98, 131-138.

Grandcolas, P. (1998) The Evolutionary Interplay of Social Behavior, Resource Use and Anti-Predator Behavior in Zetoborinae+Blaberinae+Gyninae+Diplopterinae Cockroaches: A Phylogenetic Analysis. Cladistics, 14, 117–127.

Gutierrez, D. & Menendez, R. (1997) Patterns in the distribution, abundance and body size of carabid beetles (Coleoptera: Caraboidea) in relation to dispersal ability. Journal of Biogeography, 24, 903-914.

Gutierrez, E. (1995) Annotated Checklist of Cuban Cockroaches. Transactions of the American Entomological Society, 121, 65-85.

Gutierrez, E. & Fisk, F. (1998) Annotated Checklist of Puerto Rican Cockroaches. 124, 3/4, 333-354.

Gutierrez, E. & Perez-Gelabert, D. (2000) Annotated Checklist of Hispaniolan Cockroaches. Transactions of the American Entomological Society, 126, 433-446.

Hayes, F.E. & Sewlal, J.-A.N. (2004) The Amazon River as a dispersal barrier to passerine birds: effects of river width, habitat and taxonomy. Journal of Biogeography, 31, 1809-1818.

Huber, O., Gharbarran, G. & Funk, V. (1995) Vegetation Map of Guyana. University of Guyana, Georgetown, Center for the Study of Biological Diversity

Jocque, M. & Field, R. (2014) Aquatic invertebrate communities in tank bromeliads: how well do classic ecological patterns apply? Hydrobiologia,

Legendre, F., Nel, A., Svenson, G.J., Robillard, T., Pellens, R. & Grandcolas, P. (2015) Phylogeny of Dictyoptera: Dating the Origin of Cockroaches, Praying Mantises and Termites with Molecular Data and Controlled Fossil Evidence. PloS One, 10, e0130127.

Lemos, A., Lemos, J.A., Prado, M.A., Pimenta, F.C., Gir, E., Silva, H.M. & Silva, M.R.R. (2006) Cockroaches as carriers of fungi of medical importance. Mycoses, 49, 23-25.

Lester, S.E., Ruttenberg, B.I., Gaines, S.D. & Kinlan, B.P. (2007) The relationship between dispersal ability and geographic range size. Ecol Lett, 10, 745-58.

Lu, W., Valentine, B.D., Perez-Gelabert, D.E. & Gutiérrez, E. (2014) Ecology and Diversity of Cockroaches (Dictyoptera: Blattaria) from the Virgin Islands. Insecta Mundi, 0349, 1-32.

Maumholts, M.A., Parish, L.C., Witkowski, J.A. & Nutting, W.B. (1997) The medical importance of cockroaches. International Journal of Dermatology, 36, 90-96.

Naka, L.N. (2011) Avian distribution patterns in the Guiana Shield: implications for the delimitation of Amazonian areas of endemism. Journal of Biogeography, 38, 681-696.

Nalepa, C., Bignell, D.E. & Bandi, C. (2001) Detritivory, coprophagy, and the evolution of digestive mutualisms in Dictyoptera. Insectes Sociaux, 48, 194-201.

Panizzo, J.U. (2011) Physical factors influencing macro-invertebrate assemblages in epiphytic bromeliads in the rainforest of Belize. In: Department of International Environment and Development Studies. Vol. Masters. Norwegian University of Life Sciences

Paoletti, M.G., Taylor, R.A.J., Stinner, B.R., Stinner, D.H. & Benzing, D.H. (1991) Diversity of Soil Fauna in the Canopy and Forest Floor of a Venezuelan Cloud Forest. Journal of Tropical Ecology, 7, 373-383.

Pellens, R. & Grandcolas, P. (2003) Living in Atlantic forest fragments: life habits, behaviour, and colony structure of the cockroachMonastria biguttata(Dictyoptera, Blaberidae, Blaberinae) in Espirito Santo, Brazil. Canadian Journal of Zoology, 81, 1929-1937.

Pellens, R. & Grandcolas, P. (2008) Catalogue of Blattaria (Insecta) From Brazil. Zootaxa, 1709, 1-109.

Petermann, J.S., Farjalla, V.F., Jocque, M., Kratina, P., MacDonald, A.A.M., Marino, N.A.C., Omena, P.M.d., Piccoli, G.C.O., Richardson, B.A., Richardson, M.J., Romero, G.Q., Videla, M. & Srivastava, D.S. (2014) Dominant predators mediate the impact of habitat size on trophic structure in bromeliad invertebrate communities. Ecology, ?,

Peterson, W. & Cobb, K. (2009) First Record of the Turkestan Cockroach, Blatta lateralis (Walker), in Georgia (USA). Journal of Entomological Sciences, 44, 415-416.

Princis, K. (1963) Orthopterum Catalogus. W. Junk, 's-Gravenhage, The Netherlands,pp.

Rundle, S.D., Bilton, D.T. & Foggo, A. (2007) By wind, wings or water: body size, dispersal and range size in aquatic invertebrates. In: Hildrew, A.G., Raffaelli, D.G. & Edmonds-Brown, R. (Eds.). Cambridge University Press, British Ecological Society, pp.

Schal, C. (1982) Behavioral and Physiological Ecology and Community Structure of Tropical Cockroaches (Dictyoptera: Blattaria). In: Entomology. Vol. PhD. University of Kansas

Schauer, C., Thompson, C. & Brune, A. (2014) Pyrotag sequencing of the gut microbiota of the cockroach Shelfordella lateralis reveals a highly dynamic core but only limited effects of diet on community structure. PloS One, 9, e85861.

Velez, A. (2008) Checklist of Colombian cockroaches (Dictyoptera, Blattaria). Biota Colombiana, 9, 21-38.

Vidlička, Ľ. (2013) Cockroaches (Blattaria) of Ecuador-checklist and history of research. Zootaxa, 5, 401-445.

Vinarski, M.V. & Kramarenko, S.S. (2015) How does the discrepancies among taxonomists affect macroecological patterns? A case study of freshwater snails of Western Siberia. Biodiversity and Conservation,

von Beeren, C., Stoeckle, M.Y., Xia, J., Burke, G. & Kronauer, D.J. (2015) Interbreeding among deeply divergent mitochondrial lineages in the American cockroach (Periplaneta americana). Scientific Reports, 5, 8297.

Wallace, A.R. (1852) On the Monkeys of the Amazon. Alfred Russel Wallace Classic Writings, 3,

Ware, J.L., Litman, J., Klass, K.-D. & Spearman, L.A. (2008) Relationships among the major lineages of Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. Systematic Entomology, 33, 429-450.

Warren, D.L., Cardillo, M., Rosauer, D.F. & Bolnick, D.I. (2014) Mistaking geography for biology: inferring processes from species distributions. Trends Ecol Evol,

Watanabe, K., Monaghan, M.T., Takemon, Y. & Omura, T. (2010) Dispersal ability determines the genetic effects of habitat fragmentation in three species of aquatic insect. Aquatic Conservation: Marine and Freshwater Ecosystems, 20, 574-579.

CHAPTER 1

CHECKLIST OF THE BLATTODEA OF THE GUIANA SHIELD INCLUDING RECORDS AND DESCRIPTIONS

Reproduced from vol. 475 in ZooKeys and the Journal of Natural History (in press)

Abstract

Here we provide a checklist of cockroach species known from areas within the Guiana Shield based on literature records and new field collection. The complete checklist contains 238 species of Blattodea s.s. currently known in the shield. This checklist shows particularly low richness in Guianan Venezuela, Roraima and Amapa Brazil, but this is likely an artifact due to under–sampling. Indeed, based on previously published data and current fieldwork, we believe that most regions of the Guiana Shield are under–sampled for cockroaches. Despite this, French Guiana (151 spp.) and Suriname (136 spp.) rank as the second and sixth most species dense faunas of cockroaches in the neotropics. Out of the 238 species in the checklist 18 are new records for Guyana, 6 are new species records for the Guiana Shield, and 1 is a new generic record for the shield. We report on species in the genera *Lamproblatta*, *Neorhicnoda*, *Eublaberus*, *Epilampra*, *Colapteroblatta*, *Thanatophyllum*, *Anaplecta*, *Anisopygia*, *Dasyblatta*, *Ischnoptera*, *Xestoblatta*, *Nyctibora*, *Chorisoneura*, *Dendroblatta*, *Calhypnorna* and *Euphyllodromia*. Four species are described in detail here (*Calhypnorna* sp., *Xestoblatta berenbaumae*, *Dendroblatta litura*, *Dasyblatta warei*). We also provide photographs, measurements, and some new biological information for our specimens.

Introduction

The Guiana Shield is known for a high diversity of both plant and animal life (Alexander*et al.* 2005). Blattodea (Insecta, Dictyoptera), or cockroaches and termites, as well as most other insects, remain under-sampled relative to their biodiversity in the region. Developing more complete lists of fauna improves our ability to infer biogeographical patterns and make predictions about biodiversity loss. Additionally, keeping current records of regional faunas can assist in documenting introduced and invasive species, something particularly relevant to the study of cockroaches (Evangelista *et al.* 2013; Nickle 1984; Peterson & Cobb 2009).

The cockroach fauna of the entire Guiana Shield has previously been addressed by three works (i.e. Bonfils 1975; Bruijning 1959; Princis 1963). Princis' catalogue (1963) of global cockroach distributions is an important resource to consult for this fauna. However, there were cases (although very few) where Princis was incomplete in his records (pers. obs.; Pellens & Grandcolas 2008). Bruijning's (1959) and Bonfils' (1975) checklists are more manageable than Princis's global catalog given their focused geographic scope, but they are also an incomplete record of the fauna. Regardless, Bonfils' (1975), Bruijning's (1959) and Princis' (1963) work are all now 40 years or more out of date.

The cockroach fauna of sections of the Guiana Shield have been addressed directly by a few sources (e.g., Bonfils 1987; Bruijning ; Hebard 1926; Perez 1988; Rehn 1906; Rocha E Silva Albuquerque & Gurney 1962) as well as peripherally by others sources (e.g., Evangelista *et al.* 2014; Hebard 1921b;1929; Pellens & Grandcolas 2008; Rehn 1928; Velez *et al.* 2006). A few manuscripts have addressed the Blattodean faunas of French

Guiana (Hebard 1926) and Suriname (Bruijning 1959) respectively. The Guianan fauna of relevant parts of Brazil and Venezuela are available from checklists for these respective countries (Bonfils 1987; Pellens and Grandcolas 2008; Perez 1988). However, there is no singular source to be consulted for the blattodean fauna of Guyana (formerly known as British Guyana).

Although the Guiana Shield is among the world's hotspots for known cockroach biodiversity, Guyana is fairly poorly sampled given it size. Recently, two resources have become available, greatly expediting the speed at which Guianan species can be diagnosed. First is the "Cockroach Species File" online database, which provides easy access to taxonomic names and citations for taxa (Beccaloni 2014). Second is the "Global Cockroach Library", a digital folder shared among taxonomists with the goal of accumulating all taxonomic works on cockroaches (George Beccaloni, pers. comm.).

Lastly, the most current phylogenies of Blattodea all show that termites (Termitoidae) are nested within Blattodea (Djernaes et al. 2012; 2014; Inward et al. 2007; Ware et al. 2008). Given that this has only been recently adopted by systematists, there are few taxonomic treatments considering both termites and cockroaches simultaneously. Since each insect group requires very different morphological and organismal expertise this is understandable. Using these resources to analyze specimens collected on a series of expeditions (2011-2015), we are adding taxon records to the Guyanese fauna of cockroaches, excluding termites.

Methods

Checklist

The checklist was initially compiled by synthesizing range data from the published literature. Searches for taxonomic records included some combination of the following locality names: British Guiana, Suriname, French Guiana, Guyane, Guiana or Guyana. Five additional sources were consulted (Bonfils 1987; Pellens & Grandcolas 2008; Perez 1988; Rocha E Silva Albuquerque & Gurney 1962) for the taxa of the following states: Amazonas Venezuela, Bolivar Venezuela, Delta Amacuro Venezuela, Roraima Brazil and Amapa Brazil. The states of Para and Amazonas in Brazil were omitted because the majority of these states do not fall within the borders of the Guiana Shield. The recently published checklist of the cockroaches of Brazil (Pellens & Grandcolas 2008) sufficiently covered the fauna of these states. We treated ranges specified by Princis (1963) as circumtropical, neotropical, or cosmopolitan as a presence for each region, even without a specific record for that region. Additional records were added based on specimens collected by the Ware lab in the field.

The validity of all taxonomic names was verified on the Cockroach Species File (CSF) online database (Beccaloni 2014). All synonymous names were changed to their valid name in the final checklist. All invalid higher taxa were given proper names in accordance with the most current taxonomy (Beccaloni & Eggleton 2011; 2013).

Specimen collection

Specimens were collected from a variety of expeditions to Guyana in 2011-2014. The specific methods for these collections are reported in Chapter 2 (also see: Evangelista *et al.* 2014; Evangelista*et al.* 2015). Specimens were also collected during an additional trip in 2014-2015 at Iwokrama Forest and Karanambu Ecolodge, both of which are in the

North Rupununi region of Guyana. Specific collection information (locality and GPS, collection date, collectors and ecological information) is given with each record.

New records and descriptions

Species that were collected and could be identified are presented here. We report all collection information and some morphological information for each specimen as well as currently known geographic distribution as described on the Cockroach Species File database (Beccaloni 2014). All morphological measurements were done using Infinity software. For new species, we provide descriptions of gross morphology and male genitalia. The genitalia were dissected in accordance with the method of Roth (1969), whereby the genitalia are removed from the specimen by making a lateral incision along the subgenital plate, separating the genitalia from the remainder of the body and placing them in a KOH (10% by mass) solution until cleared (approx. 8 hours). Cleared genitalia were kept in a micro-vial with 70% ethanol after examination. We also include some notes on potential evolutionary relationships of some genera by referencing the cytochrome oxidase I (COI) gene tree published by the first and last author (Evangelista *et al.* 2014).

All specimens were processed in the lab at Rutgers University in Newark. Voucher numbers and labels were provided to them and they were added to an ongoing database of Guianan cockroaches we collected.The collection was identified using published species descriptions and keys. Traits used to identify specific taxa are indicated in the results section.

Specimens were measured manually using a ruler with .25 mm precision. The cockroaches were kept in 70% ethanol at the time of the completion of this study. 70%

ethanol provides sufficient preservation of genetic material and allows the specimen to remain truer to life (undeformed and flexible). Unless otherwise stated, all specimens reported here will ultimately be stored at the AMNH or the Center for Biodiversity at the University of Guyana.

The classification used in this paper is based on Beccaloni and Eggleton (2013) and Beccaloni (2014). All references to internal genital morphology follow McKittrick (1964) unless otherwise noted.

We imported the checklist data into Mathematica 9.1 (Wolfram Research 2012) to calculate the endemism rates of the faunas of each region. We calculated this as the proportion of species in a given region not present in any other region of the shield. We also calculated faunal similarity rates (inverse of endemism) among each region.

Results

Records and descriptions of cockroaches from Guyana

Here we report information on some of the specimens from our field collection. Those species listed here that are new records for Guyana are denoted by a "+" in the checklist (Table 1 - 1). Morphological measurements for all specimens are given in Table 1 – 2, 1 – 3, 1 – 4, 1 – 5, & 1 – 6.

Results

Blattoidea Latreille, 1810

Lamproblattidae McKittrick, 1964

Lamproblatta Hebard, 1919

Lamproblatta ancistroides Rehn, 1930 (Figure 1-1 & 1-2)

2 adult males, 1 adult female

Voucher numbers: DEIWO0279, DEIWO0422, DEIWO0470

Collection locality: Turtle Mountain, Iwokrama Forest, Guyana

GPS:4° 43' N, 58° 43' W

Collection date: 20 - 23 December 2014

Collectors: D. Evangelista, M. Davis, M. Johnney, M. Carter, O. Ambrose

Morphological identification: These specimens were identified to genus by the valvate subgenital plate in the female and lack of wings. The specimen was further identified to species as follows: it differs from *L. mimetes* in the relatively narrower inter-stylar region (Rehn 1930); it shows less acute productions on the lateral tergites, and wider supra-anal plate than in *L. albipalpus* Hebard, 1919; it is larger than *L. albipalpus* Hebard, 1919 and *L. meridionalis* (Bruner, 1906); the female is larger than in *L. romani* Rehn, 1930. All measurements can be found in Table 1 – 2. In all other ways, this species agrees with the description of *L. ancistroides* Rehn, 1930.

Collection/ecological information: Although we only report three individuals here this species was numerous in our collection (43 total adults). Most specimens were collected by hand on low lying vegetation at night. A few other individuals were collected in pitfall traps baited with beer.

Known geographical distribution: Guyana (Iwokrama forest; new record), Colombia, Venezuela

Blaberoidea Saussure, 1864

Blaberidae Saussure, 1864

Blaberinae Saussure, 1864

Eublaberus Hebard, 1920

Eublaberus distanti (Kirby, 1903)

Materials. *Adult* ♂

Voucher number: DEKBO0843

Collection locale: Karanambu Ranch, Rupununi, Guyana.

GPS: 3° 45' 2.2" N, 59° 18' 31.2"W.

Date: 7 – June – 2013.

Collectors. Dominic A. Evangelista, Oswin Ambrose, Susan George, and Megan M. Wilson.

Collection/ecological information. This specimen was collected in the bathroom of one of the cabins at the camp of Karanambu Ranch.

Known geographic distribution. Guatemala, Costa Rica, Panama, Colombia, Trinidad and Tobago, French Guiana, Suriname, Guyana and Brazil

Eublaberus marajoara Rocha E Silva Albuquerque, 1972 (Figure 1 – 3)

1 female

Voucher number: DEKBO1034

Collection locality: Karanambu EcoLodge, Rupununi, Guyana

GPS: 3º 45’ N, 59º 18’ W

Collection date: 17-29 June 2013

Collectors: O. Ambrose, M. Wilson & D. Evangelista

Collection/ecological information: This specimen was found in one of the benabs at the tourist lodge.

Morphological identification: This specimen was identified by the coloration of the pronotum, wings and head.

Known geographical distribution: Guyana (Rupununi savanna region; new record), Brazil (Amazonas, Para, Mato Grosso)

Neorhicnoda Grandcolas, 1992

Neorhicnoda maronensis (Hebard, 1921)

Materials. *Adult* ♂ Figure 1 - 4

Voucher number: DECBA0615

GenBank accession number: KF155090

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W.

Date: 02 – January – 2012.

Collectors. Dominic A. Evangelista, Ian Biazzo, Joseph A. Evangelista, Paul Frandsen, William R. Kuhn, and Jessica L. Ware.

Collection/ecological information. This specimen was caught in a pitfall trap baited with beer in an uplands secondary forest.

Morphological identification. This specimen agrees with the description of the male genitalia in Grandcolas (1992).

Known geographic distribution. Guyana (new record), Suriname, and French Guiana

Epilamprinae Brunner von Wattenwyl, 1865

Colapteroblatta Hebard, 1919

Colapteroblatta surinama (Saussure, 1868)

Materials. *Adult* ♂ Figure 1 - 5 E

Voucher number: DECBA0703

GenBank accession number: KF155029

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W.

Date: 05 – August – 2011.

Collectors: Dominic A. Evangelista, Ian Biazzo, Manpreet K. Kohli, Melissa Sanchez-Herrera, Nicole Sroczinski, and Jessica L. Ware.

Collection/ecological information. This specimen was collected in an uplands secondary forest from within a rotting vine.

Morphological identification. This specimen was identified using Roth and Gutierrez (1998).

Adult ♀ Figure 1 - 2 D

Voucher number: DECBA1810

GenBank accession number: KF155126

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W.

Date: 20 – August – 2011.

Collectors. Dominic Evangelista and William R. Kuhn.

Collection/ecological information. This specimen was collected in an uplands secondary forest from within an arboreal bromeliad.

Morphological identification. This specimen was identified using Roth and Gutierrez (1998).

Juvenile Figure 1 - 2 A–C

Voucher number: DECBA1811

GenBank accession number: KF155112

Collection locale: CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W

Date: 17 – August – 2013.

Collectors. Dominic Evangelista and William R. Kuhn.

Collection/ecological information. This specimen was collected on vegetation in an uplands secondary forest.

Morphological identification. This specimen was associated to its adult morph using barcodes in Evangelista et al. (2014). The overall coloration of the juvenile specimens of this species is more similar to that of *C. darlingtoni* Roth & Gutiérrez, 1998 and *C. rehni* Roth & Gutiérrez, 1998 than to that of the adults of its own species (see Figure 1 - 5).

Genetic information and evolutionary placement. All three specimens have nearly identical cytochrome oxidase I (COI) haplotypes but their position could not be determined relative to other cockroach species with the data evaluated by Evangelista et al. (2014).

Known geographic distribution. Guyana, Suriname

Epilampra Burmeister, 1938

Epilampra colorata Rocha E Silva Albuquerque & Gurney, 1962 (Figure 1 – 6)

2 adult male, 1 adult female, 1 adult unknown, 2 juveniles

Voucher numbers: DEIWO0190, DECBA0213, DECBA1102, DECBA0501, DEKBO1219, DECBA0807

Collection Locality: Iwokrama Research Station, Iwokrama, Guyana (IWO), GPS: 4º40’ N 58º41’ W; CEIBA Biological station, Madewini Guyana (CBA), GPS: 6º29’ N 58º13’ W; and Karanambu EcoLodge, North Rupununi, Guyana, (KBO)

Collection date: 19 - 29 December 2014

Collectors: D. Evangelista, M. Davis, M. Johnney, M. Carter, O. Ambrose

Collection/ecological information: All specimens were collected by hand. No ecological information is known.

Morphological identification: We identified this species by comparing pronotal and facial coloration as well as allometry and total size (Rocha E Silva Albuquerque & Gurney 1962).

Genetic information and evolutionary placement: The barcode tree of Evangelista et al. (2014) groups a number of individuals into one clade (Voucher and GenBank accession numbers: DECBA1102 - KF155086, DECBA0213 - KF155038, DECBA0501 - KF155098, DECBA0807 - KF155077). The individuals include two juveniles, an adult male and an adult female that we now know are of the same species, due to the phylogenetic data. We include a photographs of one of these juveniles (DECBA0501; Figure 1-6 A, B).

Known geographic distribution: Guyana (new record), Brazil (Amapa)

Epilampra opaca Walker, 1868

Materials. *Adult* ♂ Figure 1 - 7 B

Voucher number: DECBA1845

GenBank accession number: KF155125

Collection locale. CEIBA Biological Station, Madewini, Guyana

GPS: 6º 29’ N 58º 13’ W.

Date: 18 – August – 2012.

Collectors. Dominic A. Evangelista and William R. Kuhn.

Adult ♀

Voucher number: DECBA1847

GenBank accession number: KF155124

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29” N 58º 13” W.

Date: 5 – August – 2011.

Collectors. Dominic A. Evangelista, Ian Biazzo, Manpreet K. Kohli, Melissa Sanchez-Herrera, Nicole Sroczinski and Jessica L. Ware.

Collection/ecological information. The adult male (DECBA1845) was collected at a light trap. Adult female (DECBA1847) was collected by hand in the leaf litter by a small pond. Most late instar individuals of this species were also collected at the edge of this pond and some were collected in pitfall traps baited with beer. Early instar individuals of this species were collected from within bromeliads.

Genetic information. The two adult specimens reported here, as well as three juvenile individuals (Voucher and accession numbers: DEDSM0141- KF155097, DECBA1706 - KF155089, DECBA0205 - KF155088) have identical COI barcodes and are sister to each other on the tree. However, other individuals (similar to *E. opaca*) included in the analysis (Voucher and accession number’s: DECBA0214 - KF155018, DECBA0216 - KF155017, DECBA0606 - KF155013, DECBA1101 - KF155016, DECBA0605 - KF155012, DECBA0608 - KF155015) are more genetically diverse and are only supported as monophyletic by 63% bootstrap support.

Morphological identification. There is a great deal of intraspecific variation in the morphology of this species. Early instar nymphs are difficult to associate to later instar nymphs, all of which are entirely unrecognizable from the adults (Figure 1 - 7 A-C). Furthermore, there is variation within instars, where some later instar nymphs will appear to have a medially divided subgenital plate and others do not. This trait was not found to correlate with genetic differences (Evangelista et al. 2014).

The external morphology of this species provides little assistance in its identification, as most descriptions of it emphasize coloration that is both subtle and variable. However, the allometry of our specimens (Table 1 - 2) agree with those of Bruijning (1959). A definitive identification was made by comparison of genital morphology using Roth (1970b), particularly in the shape of the prepuce.

Known geographic distribution. Venezuela (unverified), Guyana, Suriname, French Guiana and Brazil

History and synonymy. Walker (1868) first described both *E. opaca* Walker, 1868 and *E. substrigata* Walker, 1868. Hebard (1926) noted that *E. opaca* Walker, 1868 has a highly variable morphology and may be synonymous with a few other *Epilampra* (e.g. *E. conferta* Walker, 1868 syn. *stigmosa* Giglio-Tos, 1898, *E. maculicollis* (Serville, 1838)). This variability is evident in the work published by Roth (1970b), which shows a great deal of variation in the genital morphology, in particular for L2d. Although it is not clear if anyone before Roth (1970) examined the genitalia of these two species, both Shelford (1910) and Princis (1963) considered them to be synonyms. Roth's (1970) photos show that, although each species is intraspecifically variable, both are distinct and separable by the shape of

L2d and the prepuce. Roth himself acknowledged this and considered the species as being separate. Although we have not examined any *E. substrigata* Walker, 1868, we agree with Roth's interpretation of the morphology and follow from his precedence in considering these separate (see Roth 1970 for the opinions of Princis and Gurney on the status of these two species).

Epilampra sodalis Walker, 1868

Materials. *Adult* ♂ Figure 1 - 8 A

Voucher number: DECBA0401

GenBank accession number: KF155063

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29' N 58º 13' W.

Date: 31 – July to 6 – August – 2011.

Collectors. Dominic A. Evangelista, Ian Biazzo, Manpreet K. Kohli, Melissa Sanchez-Herrera, Nicole Sroczinski, and Jessica L. Ware.

Collection/ecological information. This specimen was collected at a light trap.

Morphological identification. This specimen agrees with the description the synonym *E. cinnamomea* (Hebard 1926).

Juvenile

Voucher number: DECBA1702

GenBank accession number: KF155068

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W.

Date: 27 – December – 2011.

Collectors. Dominic A. Evangelista, Ian Biazzo, Joseph A. Evangelista, Paul Frandsen, William R. Kuhn and Jessica L. Ware.

Juvenile

Voucher number: DECBA1701

GenBank accession number: KF155069

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W.

Date: 10 – January – 2012.

Collectors. Dominic A. Evangelista, Ian Biazzo, Joseph A. Evangelista, Paul Frandsen, William R. Kuhn and Jessica L. Ware.

Collection/ecological information. Both of these juvenile specimens were collected at the edge of a small pond.

Genetic information and evolutionary placement. These three specimens (previous reported as “Blaberidae sp. 04”) were placed in the same clade with 90% bootstrap support.

Known geographic distribution. Venezuela, Guyana (new record), Suriname, French Guiana and Brazil

Zetoborinae (Princis, 1960)

Thanatophyllum Grandcolas, 1991

Thanatophyllum akinetum Grandcolas, 1991 Figure 1 - 9

Materials. *Adult* ♂

Voucher number: DECBA0611

GenBank accession number: KF155066

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W.

Date: 28 – December – 2011.

Collectors. Dominic A. Evangelista, Ian Biazzo, Joseph A. Evangelista, Paul Frandsen, William R. Kuhn and Jessica L. Ware.

Collection/ecological information. This specimen was collected by hand on vegetation in an uplands secondary forest.

Morphological identification. This specimen agrees with the description of the head and male genitalia of Grandcolas (1990).

Known geographic distribution. Guyana (new record) and French Guiana.

Ectobiidae Brunner von Wattenwyl, 1865

Anaplectinae Walker, 1868

Anaplecta parviceps (Walker, 1868) Figure 1 - 10

Materials. *Adult* ♂

Voucher number: DECBA1843

GenBank accession number: KF155137

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W.

Date: 16 – August – 2012.

Collectors. Dominic A. Evangelista and William R. Kuhn.

Collection/ecological information. This specimen and another adult male (Voucher number: DECBA1841) were collected at a light trap near the camp of CEIBA Biological Station on the date noted above. A juvenile of this species was also collected at the same locale, found crawling through a benab between 21 and 24 of August 2012 (Voucher number: DECBA1842).

Morphological identification. The specimen agrees with the description of the synonym *A. insignis* of Hebard (1926). Other specimens were identified by comparison with specimen DECBA1843.

Genetic information and evolutionary placement. The COI barcodes of this specimen (previously reported as "Blattodea sp. 18") falls sister to another specimen identified as *Anaplecta* sp. (previously reported as "Ectobiidae sp. 04"; Voucher number: DEDSM0111; GenBank accession number: KF155041) but with 25% bootstrap support. This other species is not reported in this paper due to an uncertainty in specific identification.

Known geographic distribution. Guyana, Suriname, French Guiana, Brazil (Rio de Janeiro), Brazil (Pará), and Brazil (Amapá).

Blattellinae Karny, 1908

Anisopygia Saussure, 1893

Anisopygia decora Hebard, 1926 Figure 1 - 11

Materials. *Adult* ♀

Voucher number: DEKBO0504

Collection locale. Capuchin Trail, Karanambo Ranch, Rupununi, Guyana.

GPS: 3° 44' 43.70" N 59° 18' 51.88" W

Date: 10 – June – 2013

Collectors. Dominic A. Evangelista, Oswin Ambrose, Susan George, and Megan M. Wilson.

Collection/ecological information. This specimen was collected by hand in an undisturbed forested area. This is the first record of this specimen from Guyana.

Morphological identification. This specimen was identified by comparison with Hebard's description (1926).

Known geographic distribution. Guyana (new record) and French Guiana.

Dasyblatta Hebard, 1921

History

The genus *Dasyblatta* was first erected by Hebard in 1921 and included two species: *Dasyblatta thaumasia* Hebard, 1921, and *Dasyblatta chopardi* Hebard, 1921. Hebard differentiated *Dasyblatta* from the group "Blattellae" in the fact that they were covered in hairs, and had a curled intercalated triangle when wings were at rest. In addition, Hebard noted similarities between individuals of *Dasyblatta* and *Ischnoptera* Burmeister, 1838 with regards to the general shape of the body, specifically the head and pronotum. He also believed *Dasyblatta* to be most closely related to those the genera *Platylestes* Hebard, 1919 and *Chromatonotus* Hebard, 1920.

Since 1921 the genus has expanded to include eight species, with the most recently added species being *D. charpentierae* Bonfils, 1975, *D. stylata* Bonfils, 1975 and *D. warei* sp. nov., which we describe here.

Dasyblatta thaumasia Hebard, 1921 (Figure 1-12)

2 adult males, 1 adult female, 1 adult unknown

Voucher number: DECBA1777, DEKBO0706, DEKBO1308, DEKBO0514

Collection locality: CEIBA Biological Station, Madewini, Guyana (CBA) and Karanambu EcoLodge, North Rupununi, Guyana, (KBO)

GPS: 6º 29’ N, 58º 13’ W (CBA), 3º 46’ N, 59º 20’ W (KBO)

Collection date: 15 August 2012 (DECBA1777), 7 June 2013 (DEKBO0706) 9 - 10 January 2015 (DEKBO1308), and 15 June 2013 (DEKBO0514).

Collectors: D. Evangelista, W. Kuhn (CBA voucher), S. George, O. Ambrose, M. Wilson (KBO vouchers)

Collection/ecological information: These specimens were collected both by hand and in pitfall traps baited with beer. Specimens from the Rupununi were found entirely at sites near flood zones or bordering bodies of water. CEIBA biological station has an overall wetter climate compared to Karanambu which might be why we did not collect the CBA specimen near a body of water.

Morphological identification: This species was identified by the shape of the subgenital plate, asymmetry of the penultimate tergite and coloration of the pronotum.

Genetic information and evolutionary placement: The individual from CEIBA Biological Station (DECBA1777 - KF155133) was a part of the tree in Evangelista *et al.* (2014) however they did not find a relationship to any other taxa.

Known geographic distribution: Guyana (new record), Suriname and Brazil (Para).

Dasyblatta warei sp. nov. Mendoza & Evangelista (Figure 1 – 13 & 1 – 14; Table 1 – 3)

Holotype information

Voucher number: DECBA0907

Locality: CEIBA Biological Station, Madewini, Guyana

GPS: 6º 29’ N, 58º 13’ W

Collection date: 11 August 2011

Collectors: I. Biazzo, D. Evangelista, M. Kohli, M. Sanchez, N. Sroczinski and J. L. Ware

Deposition: The holotype is stored in 70% ethanol and will be deposited in the Center for Biodiversity at the University of Guyana.

Collection/Ecological information: This individual was collected within a bromeliad at the crown of a tree (22 m above ground).

Morphological identification: Assigning this species to a genus was very difficult given its derived form. We placed this species in the Blattellinae based on the location of the hooked slcerite (left; L3). The shape of the right genital phallomere (R3 of Klass 1997) suggests a greater similarity to *Xestoblatta* Hebard, 1916, or *Ischnoptera* Burmeister, 1838. However, our specimens were lacking the dorsal tergal gland common in both groups. Given the overall hairy nature, lack of tergal gland, foreleg femur spination, and slight curling of male hindwings at rest we have placed this species in *Dasyblatta* Hebard, 1921.

Description of holotype: Male**.** Head pale, chestnut brown; covered in medium-sized hairs, almost uniformly. Interocular space approximately equal to interantennal space. Ocelli absent. Antennae same color as head, becoming increasingly light distally.

Antero-ventral margin of the forelegs armed with one large basal spine followed by a row of small spines (14-left and 9-right), one large preapical spine, and one large apical spine. Pulvilli present on all tarsomeres except the most distal (V). Arolia present; medium to large size (not quite meeting tip of the pretarsal claws). The antero-ventral margin of the middle leg with two large spines and one slightly smaller spine just before large apical spine. Genicular spine present. Leg coloration: foreleg coxa is almost entirely brown and lightening to buffy apical section; femur, tibia, and tarsus are a light reddish amber. The middle leg same as foreleg, except buffy region on coxa is more prominent and femur buffy as well.

Pronotum does not entirely cover head; uniformly dark, chestnut-brown; large hairs covering anterior and lateral sides of pronotum, most prominently; lateral margin slightly less chitinized and more translucent.

Tegmina long and thin, covered in long hairs uniformly; translucent, brown amber.

Abdomen dorsally covered in large hairs, most dense laterally. Dorsal abdominal gland absent. Supra-anal plate trapezoidal and truncated. Abdominal tergum anterior to supra-anal plate only subtly, if at all, asymmetrical. Coloration as rest of body. Tergites slightly lighter laterally. Abdomen ventrally covered in medium-sized hairs throughout, and most obvious on posterior margins of the segments. Supra-anal plate rounded and curved modestly dorsally at the lateral sides. Coloration is deep, chestnut-brown overall.

Right stylus of subgenital plate curved medially, terminating in a crown of spines. Left stylus projecting posteriorly; shorter than right stylus, and similarly crowned. Left ventral-medial phallomere (Lvm; L2 of Klass 1997) stout, branched into three prongs. Right phallomere (R2; R3 of Klass 1997) with a membrane of stout hairs or spines proximal to it. Paraprocts slightly asymmetrical, but not highly specialized.

Measurements can be found in Table 1 – 3.

Allotype: Voucher number**:** DECBA1803

Locality: CEIBA Biological Station, Madewini, Guyana

GPS: 6º 29’ N, 58º 13’ W

Collection date: 21 - August - 2012

Collectors: D. Evangelista, W. Kuhn

Deposition: The holotype is stored in 70% ethanol and will be deposited in the Center for Biodiversity at the University of Guyana.

Collection/Ecological information: This individual was collected on the trunk of a tree while it was ovipositing.

Morphological description of allotype: Female. Head is the same as described in male, except: interocular space is just slightly narrower than the inter-antennal space; antenna same color as head, but light amber both distally and basally.

Antero-ventral margin of foreleg lacking large basal spine (14 small spines present on both forelimb femurs). Middle leg antero-ventral margin of femur same as male, except

that small spine is much more minute. Hind leg antero-ventral margin is same as middle leg. Legs coloration same as in male. Hind leg femur and tibia are orange amber color, similar to that of forelegs.

Pronotum is equally or more hairy than male; small central region lacking large hairs. Tegmina and wings shortened, almost reaching first segment of abdomen (brachyptery). Tegmina covered in large hairs throughout; orange-amber coloration, darker at base of subcostal vein. Light color of the lateral margins of terga is more pronounced in female than in male.

Abdomen dorsally same as male except first two segments are lacking brown coloration. Ventral abdomen same as male except that subgenital plate is simple, rounded, and hairier than remainder of abdomen. Ootheca as in Figure 1-14 I-J, 4.2 mm long.

Measurements can be found in Table 1 – 3.

Juvenile paratypes: Voucher numbers**:** DECBA0911, DECBA0906
(All collection information same as the holotype).

Description of juvenile paratypes: Ventral morphology same as adults but may have a duller pale brown coloration. When present, styles are finger-like, simple, and symmetrical. Pronotum is same amber color as female thorax. Light amber color extends posteriorly to first abdominal segment. Pronotum is dusky brown posteriorly.

Molecular data and evolutionary placement of *D. warei* sp nov.: The tree of Evangelista et al. (2013) fails to associate the two individual sequences (DECBA0907 - KF155073,

DECBA0906 - KF155072) with the sequence for *Dasyblatta thaumasia* Hebard, 1921 (DECBA1777 - KF155133).

Differential diagnosis and diagnostic features: The major features in which our species differ from the known *Dasyblatta* (*D. charpentierae* Bonfils, 1975, *D. stylata* Bonfils, 1975, *D. chopardi* Hebard, 1921, *D. thaumasia* Hebard, 1921, *D. maldonadoi* Rocha E Silva Albuquerque, 1964, *D. vogli* Princis, 1955, *D. melanocephala* Princis, 1955) are: immaculate pronotum, styles only slightly curved, ocelli absent, subgenital plate not strongly asymmetrical, tergite anterior to supra-anal plate symmetrical, supra-anal plate trapezoidal. We suspect this species is not closely related to any of the known *Dasyblatta*.

Etymology: We name this species after Dr. Jessica Lee Ware. She has contributed significantly to knowledge of Blattodea, Odonata and other insects. Not only this, but we find that this *Dasyblatta* (particularly the female) fits her exceptional and admirable character. The etymology of the generic name (dasy = hairy) is unrelated.

Known geographic distribution: Guyana (Madewini).

Ischnoptera Burmeister, 1838

Ischnoptera atrata Hebard, 1916

Materials. *Adult* ♂ Figure 1 - 15

Voucher number: DECBA2153

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W.

Collection date: December – 2011.

Collectors. Dominic Evangelista, Ian Biazzo, Joseph A. Evangelista, Paul Frandsen, William R. Kuhn, and Jessica L. Ware.

Collection/ecological information. This specimen was collected in a pitfall trap baited with beer in an uplands secondary forest area.

Adult ♂ Figure 1 - 8

Voucher number: DEKBO0594

Collection locale. Karanamabu Ranch, Rupununi, Guyana.

GPS: 3º 45’ 0.1” N 59º 18’ 53.7” W.

Collection date: 10 – June – 2013.

Collectors. Dominic A. Evangelista, Oswin Ambrose, Susan George, and Megan M. Wilson.

Collection/ecological information. This specimen was collected in a pitfall trap baited with beer in a forest proximal to the Rupununi River.

Morphological identification. Both specimens mostly agree with the description and figures of Hebard (1916). However, there are slight differences in the supra-anal plate when compared to Hebard’s illustration. The white region on the SA plate of our specimen is

slightly larger than in Hebard's illustration. It is possible that this is a different species than that described by Hebard, but this cannot be fully determined without a full phylogenetic treatment of sexual morphology and genetic information of individuals from both Trinidad and Guyana.

Known geographic distribution. Trinidad and Tobago, and Guyana

Ischnoptera galibi Hebard, 1926 (Figure 1 – 16 & 1 – 17; Table 1 – 4)

7 adult males, 2 adult females, 2 juveniles

Voucher numbers: DECBA3301, DECBA1986, DEIWO0120, DEKBO0342, DEKBO0343, DEKBO0482, DEKBO1534, DEKBO0345, DEKBO0351, DEKBO0344, DEKBO0259

Collection Locality: CEIBA Biological Station, Madewini, Guyana (CBA), Saw Mill, Iwokrama Forest, Guyana (IWO), Karanambu EcoLodge, Rupununi, Guyana (KBO)

GPS: 6º 29' N, 58º 13' W (CBA), 4º 36' 33" N, 58º 43' 53 W (IWO), 3º 46' N, 59º 20' W (KBO)

Collection dates: June 2011 - June 2013 (CBA), 27 - December 2014 (IWO), June - 2013 and January - 2015 (KBO)

Collectors: I. Biazzo, D. Evangelista, M. Kohli, M. Sanchez, N. Sroczinski and J. L. Ware (CBA). M. Davis, M. Johnny, M. Carter (IWO). M. Wilson, O. Ambrose (KBO).

Morphological identification: We identified this as *Ischnoptera* because of the presence of the dorsal tergal gland of the form of *Ischnoptera* and foreleg femur spination. We

further identified this to species based on the appearance of the subgenital plate (styli that appear to be productions of the plate rather than distinct appendages) and the supra-anal plate shape (particularly the cone near the sinistral cercus and deflexed lateral sides). These characters are important for identification of this species as it otherwise appears very similar to *Ischnoptera paramacca* Hebard, 1926. Unfortunately, we are unaware of characters that separate the females of these two species. We have identified females and juveniles of *I. galibi* at Iwokrama and Karanambu only because *I. paramacca* was not collected at these two sites.

Collection/ecological information: We found this species to be numerous in the secondary coastal rainforests (Madewini) and even more numerous in the forests of the Rupununi savanna. We also found that this species was almost entirely absent from our collection localities in Iwokrama rainforest, except in the leaf litter at the edges of a deforested saw mill. Given this and data included with another publication (Evangelisa, Russell, Bourne & Ware, pers. comm), we might categorize this species as having an affinity for disturbed or secondary successional forests.

Known geographical distribution: Guyana (new record), Suriname, and French Guiana.

Xestoblatta Hebard, 1916

Xestoblatta berenbaumae Evangelista, Kaplan, & Ware, 2015

Authors of description. Evangelista, Kaplan, & Ware.

Holotype. *Adult* ♂ Figure 1 - 18 B-E, G

Voucher number: DECBA2109

Type locality. CEIBA Biological Station, Madewini, Guyana.

GPS: 6^{o} 29’ N 58^{o} 13’ W.

Collection date: 17 to 18 – August – 2012.

Collectors. Dominic A. Evangelista and William R. Kuhn.

Type information. The holotype specimen is stored in ethanol with genitalia in a separate ethanol vial and is deposited at the Center for Biodiversity at the University of Guyana.

Collection/ecological information. This specimen was collected in a pitfall trap baited with beer and fruit in an uplands secondary forest in CEIBA Biological Station.

Morphological identification. This specimen was identified as *Xestoblatta* Hebard, 1916 by the position of the hooked genital sclertie (left), the presence of the external modification of the tergum as part of the dorsal tergal gland (Figure 1 - 18 A), incomplete rami on the ulnar vein of the hind wing (Figure 1 - 18 I) and the spination (type A) on the ventro-anterior margin of the fore-femur.

Holotype morphological description. Head uniformly colored a deep mahogany. Clypeus pale buffy. Ocellar spots easily distinguishable, smaller than antennal pits and white. Ocellar spots slightly closer together than eyes. Facial grooves on lateral most edge. See Figure 1 – 18 H for a representative photo of the head.

Pronotum a uniformly reddish mahogany color (Figure 1 - 19 A). Medial expansion on posterior margin of pronotum is barely noticeable. Ventral margin of pronotum not lined with hairs. Anterior margin of pronotum significantly conformed around the head. Leg coloration deep orange amber. Coxae with some diffuse black regions. Ventro-anterior margin of fore-femur with 14 (left) or 13 (right) spines decreasing in size from basal to apical, one slightly larger pre-apical spine and one large apical spine (16 total left, 15 total right). Ventro-posterior margin of fore-femur with 4 large spines and 1 apical spine. Ventro-anterior margin of mid-femur has 7 large spines and 1 apical spine. Mid-femur also with 1 large genicular spine. Hind-femur ventro-anterior margin has 6 spines, 1 apical spine, and 1 genicular spine. Pulvilli present on tarsomeres except the most distal (V). Arolia present but not surpassing the tips of the pretarsal claws. Claws symmetrical and unspecialized.

Ulnar vein with three incomplete rami and three complete rami (Figure 1 – 18 I). Tegmina reddish mahogany with small patch of white under the base of the subcostal vein.

Supra-anal plate subtriangular with a blunt tip from dorsal view. Left paraproct modified into a tri-dentate spine (Figure 1 - 18 F; bi-dentate in some other specimens). Sub-genital plate has both styli highly modified (Figure 1 - 18 F&G). The right stylus is projecting dorso-medially from posterior margin, curving back posteriorly and terminating in a shape reminiscent of a bifurcated serpentine tongue. Left stylus projecting dorsally, shorter than right stylus and tipped with a small, translucent, irregularly shaped ball (Figure 1 - 18 F & G).

Left phallomere (L3; Figure 1 - 18 B & C) hooked in apical third (~1.5mm long). Left ventral-medial phallomere (Lvm or L2 of Klass 1997; Figure 1 - 18 D) approximately

three times the length of the L3, roughly uniform width, and a slight slender curve in the posterior end. R2c (Figure 1 - 18 E) divided into two sclerites that form dual concave cups that meet dorsally.

Dorsal modification of terga VII & VIII as part of the dorsal tergal gland. Modification represented by a small patch of hairs (terga VIII) with a concave semi-circular modification of the margin of the segment anterior to the gland (terga VII). See Figure 1 - 18 A for an illustration of a representative dorsum.

Medium sized hairs (~.2mm) covering entire body roughly uniformly, yet sparsely.

Other adult male paratypes. Voucher numbers: DECBA1967, DECBA0801, DECBA1958, DECBA2182, DECBA2092, DECBA2039

Measurements for all specimens can be found in Table 1 – 5.

Collection/ecological information. All additional male individuals reported here were collected in leaf litter pitfall traps baited with beer at various locations (dryer secondary uplands forest and wet primary lowlands forest) in CEIBA biological station.

Adult female paratype morphological description. Voucher number: DECBA2074

Head slightly darker in color than male with a more reflective surface. Other features of head similar to male.

Description of legs similar or identical to that of male with the following spination on the ventro-anterior margin of fore-femur: 13 (left) and 12 (right) spines decreasing in size from basal to apical, 2 larger preapical spines and 1 large apical spine (16 total left and

15 total right). Ventro-posterior margin of fore-femur 4 large spines and 1 apical spine. Ventro-anterior margin of mid-femur with 7 large spines, 1 apical spine, and 1 genicular spine. Ventro-anterior margin of hind-femur with 5 large spines, 1 apical spine, and 1 genicular spine.

Tegmina and wings reduced and not reaching end of abdomen. Three incomplete and three complete rami on ulnar vein. Ulnar vein very faint in the reduced wings of the female (Figure 1 - 19 B).

Pronotum matches description of the male.

Terminal sternum slightly more abbreviated than of the male. Symmetrical, simple and unspecialized. Paraprocts simple and unspecialized. Sub-genital plate simple and symmetrical.

Other adult female paratypes. Voucher numbers: DECBA1787, DECBA1791, DECBA1792, and DECBA1793

Collection/ecological information. All additional female individuals reported here were collected in leaf litter pitfall traps baited with beer in an uplands secondary forest at CEIBA biological station.

Summary of female morphology. All individuals match the description of the above female and have the following spination on the vento-anterior margin of the fore-limb: 13 spines decreasing in size from basal to apical, 1 or 2 slightly larger preapical spines and 1 large apical spine making a total of 15 or 16 spines. Measurements for all specimens can be found in Table 1 – 5.

Juvenile paratypes. Voucher numbers: DECBA1788, DECBA1789, DECBA1790, DECBA1796

Collection/ecological information. All additional juvenile individuals reported here were collected in leaf litter pitfall traps baited with beer in an uplands secondary forest at CEIBA biological station.

Summary of juvenile morphology. Juveniles are apterous and largely match the morphology of adults except for in the following. Simple styli present on the subgenital plate in some individuals but are short and abbreviated. Spines on ventro-anterior margin of fore-femur are as follows: 12 to 14 spines decreasing in size basally to apically, 1 or 2 slightly larger preapical spines and one large apical spine making a sum total of 15 or 16 total spines.

Molecular data and evolutionary placement. Vouchers number's and GenBank accession numbers: DECBA1791 - KF155114, DECBA1789 - KF155105, DECBA0801 - CBA0801, DECBA1827 - KF155103, DECBA1826 - KF155107, DECBA1814 - KF155115. The clade containing the above haplotypes (formerly reported as "Blattodea sp.1") is supported by 96% bootstrap support and the haplotypes are nearly identical.

Diagnostic features of *X. berenbaumae*. The morphology of modified styles on the subgenital plate is the most useful trait for discerning this species with other *Xestoblatta* Hebard, 1916. The simple dorsal tergal gland, shape of the paraprocts (left modified into a

tri-dentate or bi-dentate spine), and morphology of the internal genital sclerites of the male are also useful in identifying this species. Unfortunately the adult females and juveniles are largely lacking obvious identifying characteristics and there may be errors made in associating juveniles to the adults without the use of genetic information.

Etymology. We give this species the specific epithet "*berenbaumae*" in honor of the esteemed entomologist, Dr. May Berenbaum, who has made huge contributions to entomology through scientific products, service and public outreach.

Known geographic distribution. Guyana

Xestoblatta agautierae Grandcolas, 1992

Materials. *Adult* ♂ Figure 1 - 20

Voucher number: DEKBO0827

Collection locale. Wilson's pond trail (Honey pond trail), Karanambu Ranch, Rupununi, Guyana.

GPS: 3^{o} 44' 42.36" N 59^{o} 19' 15.21" W.

Collection date: 10 – June – 2013.

Collectors. Dominic A. Evangelista, Oswin Ambrose, Susan George, and Megan M. Wilson.

Adult ♀

Voucher number: DEKBO0826

Collection locale. Forest Island “Darwin”, Karanambu Ranch, Rupununi, Guyana.

GPS: 3º 47’ 47.62” N 59º 22’ 6.77” W.

Collection date: 14 – June – 2013.

Collectors. Dominic A. Evangelista, Oswin Ambrose, Susan George, and Megan M. Wilson.

Collection/ecological information. Both specimens above were collected in pitfall traps baited with beer in the forests of the Rupununi savannah.

Morphological identification. The left genital phallomere, right genital phallomere, absence of a dorsal tergal gland and body coloration match closely with the species description (Grandcolas 1992a). The styli differ slightly to the illustrations in the original description in that the left stylus of our specimen is shorter and originates more medially. The female was associated to the male by comparison of gross morphology and body coloration. See Figure 1 - 20 for photos of adult male and adult female.

Collection/ecological information for other specimens not reported here. We collected many individuals of this species from most forested areas surrounding Karanambu Ranch. We collected only one individual of this species in a similar trap at the edge of a forest, near open savanna. We found this species and *X. berenbaumae* sp. n. to be extremely abundant in their respective localities (>100 individuals of each collected). However, both are previously unreported for Guyana. We believe this can be attributed to the fact that we used beer and fermenting fruit to bait our pitfall traps. As Gurney (1939) reports,

Xestoblatta Hebard, 1916 were rare in collections until the contributions of an entomologist trapping fruit flies in Panama. We can speculate that these fruit flies were also collected with some sort of aromatic bait (as this is common for fruit fly trapping) that attracted the *Xestoblatta* Hebard, 1916 as by-catch.

Known geographic distribution. Guyana (new record) and French Guiana.

Xestoblatta surinamensis Bruijning, 1959 (Figure 10)

6 adult males, 16 adult females, 1 juvenile

Voucher numbers: DEIWO0197, DEIWO0415, DEIWO0441, DEIWO0480, DEIWO0457, DEIWO0354, DEIWO0497, DEIWO0503, DEIWO0382, DEIWO0420, DEIWO0184, DEIWO0373, DEIWO0442, DEIWO0504, DEIWO0305, DEIWO0229, DEIWO0292, DEIWO0306, DEIWO0419, DEIWO0445, DEIWO0449, DEIWO0450, DEIWO0458

Collection Locality: Turtle Mountain, Iwokrama River Lodge and Atta lodge in Iwokrama Forest, Guyana

GPS: 4º 39” N, 58º 41’ W; 4º 43' N, 58º 43' W; 4º 14' N, 58º 54' W

Collection dates: 20 29 December 2014

Collectors: D. Evangelista, M. Davis, M. Johnny, M. Carter, O. Ambrose

Morphological identification: We identified these specimens as *Xestoblatta* Hebard, 1916 through the foreleg anterior-ventral margin spination (spines all large), modified styles and

presence of abdominal tergal gland. We then further associated these species with *Xestoblatta surinamensis* Bruijning, 1959 by the shape of the right style being clubbed, and the modified shape of dorsal abdominal tergum 7.

Collection/ecological information: This species was mostly collected in pitfall traps baited with beer. It was fairly commonly caught by hand at night as well. This is the first record of this species in Guyana.

Known geographical distribution: Guyana (Iwokrama forest; new record), Suriname, French Guiana, and Brazil (Para)

Nyctiborinae Burmeister, 1838

Nyctibora dichropoda Hebard, 1926 Figure 1 - 22

Materials. *Adult* ♂

Voucher number: DECBA0302

GenBank accession number: KF155061

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W.

Collection date: 29 – July – 2011.

Collectors. Dominic A. Evangelista, Ian Biazzo, Manpreet K. Kohli, Melissa Sanchez-Herrera, Nicole Sroczinski and Jessica L. Ware.

Collection/ecological information. This specimen was collected in the leaf litter.

Morphological identification. This specimen matches the illustration and description by Hebard (1926) in the "striking pale" coloration on the surfaces of the tibiae, the definitive character for this species. However, the male we have is much larger than that which he described. It is matching in all other ways.

Molecular identification. The COI barcodes of this specimen are close to an adult female (Voucher number: DECBA0235; GenBank accession number: KF155062) and juvenile specimen (Voucher number: DECBA0104; GenBank accession number: KF155024) of *Nyctibora*. Based on both genetic distance and morphological dissimilarity, these individuals are likely members of a separate species. We do not report them further here.

Known geographic distribution. Guyana (new record), Suriname and French Guiana

Pseudophyllodromiinae Brunner von Wattenwyl, 1865

Chorisoneura inversa Hebard, 1926

Materials. *Adult* ♂ Figure 1 - 23

Voucher number: DECBA1782

GenBank accession number: KF155130

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29' N 58º 13' W.

Date: 7 to 11 – August – 2013.

Collectors. Dominic A. Evangelista, Ian Biazzo, Manpreet K. Kohli, Melissa Sanchez-Herrera, Nicole Sroczinski and, Jessica L. Ware.

Morphological identification. This individual was recognizable when comparing to the description of Hebard (1926) and the presence of the anteriorly pointing "V" shape on pronotum.

Genetic information and evolutionary placement. As discussed below, this specimen was placed near *Calhypnorna* Saussure & Zehntner, 1893 with 75% bootstrap support.

Known geographic distribution. Guyana, Suriname, French Guiana and Brazil.

Dendroblatta Rehn, 1916

History

Dendroblatta was originally described by Rehn (1916). Since its description, the genus has grown to include 19 species (including the one herein described) that have each slightly widened the morphological scope of the genus. The original description emphasized the following as the defining characters: intercalated triangle of wings small, elongate and narrow; dorsal tergal gland on 7th tergite (with; ventral surface hirsute (Rehn 1916). However, Rehn later revised this to say that the dorsal tergal gland was not common to all species of the genus and should therefore not be considered a diagnostic feature (Rehn

1932). Lopes *et al.* (2014) added *Dendroblatta iani* (Rocha e Silva-Albuquerque, 1964) to the genus (originally described as *Xestoblatta iani*). The inclusion of this species diversifies the forms of spination of the anterior-ventral margin of the foreleg femur found in *Dendroblatta*. *D. iani* is the only member of the genus with a series of moderately sized spines preceding the apical spines, rather than the typical spination (moderately size spines basally, a dense row of small spines, and 2 larger apical spines). *D. iani* should be considered atypical of the genus in this respect.

Thus far, all taxonomic work on this genus has failed to provide a set of strong characters delimiting it. In fact, further work may find that this genus is not monophyletic. From what work has been done thus far, we find that the following characteristics are typical of the genus, but may be different among atypical species: 3-5 protrusions of the subgenital plate, usually one medial protrusion being more densely sclerotized; pronotum typically with some black coloration in the central region; spination of the foreleg femur having 3-7 moderately large spines basally, followed by 19-31 minute spines, 1 large preapical and 1 large apical spine; dorsal tergal gland either absent, or represented by a simple patch of hairs on terga VII; supra-anal plate symmetrical, truncate, slightly bilobed in some species and simple in other species; body length between 8 and 20 mm.

Dendroblatta callizona Rehn, 1928 Figure 1 - 24

Materials. *Adult* ♀

Voucher number: DECBA0805

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ 57.75” N 58º 13’ 7.28” W.

Date: 14 – August – 2011.

Collectors. Dominic A. Evangelista, Ian Biazzo, Manpreet K. Kohli, Melissa Sanchez-Herrera, Nicole Sroczinski, and Jessica L. Ware.

Juvenile

Voucher number. DECBA0901

GenBank accession number: KF155067

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ 57.75” N 58º 13’ 7.28” W.

Date: 13 – August – 2011.

Collectors. Dominic A. Evangelista, Ian Biazzo, Manpreet K. Kohli, Melissa Sanchez-Herrera, Nicole Sroczinski, and Jessica L. Ware.

Collection/ecological information. Both of these specimens were collected in a cup baited with beer placed in the canopy. The cup was tied to the trunk of a tree 13.8 meters above the ground. The tree chosen was close to a swampy primary forest area and on the edge of grassy hillside (most likely a plot that had been burned in the past). There were traps placed in the same tree at other heights but both individuals of this species were caught in this particular trap.

Morphological identification. Our female specimen of *D. callizona* Rehn, 1928 is within the variation described by Rehn (1928). The juvenile specimen was identified by comparison with the adult and using genetic data as well.

Genetic information. In the tree of Evangelista et al. (2014) this species is placed near two individuals reported as "Ectobiidae sp. 10". The morphology of these specimens is consistent with *Dendroblatta cnephaia* Hebard, 1926, although we do not report them here because of a lack of adults to confirm identification.

Known geographic distribution. Trinidad and Tobago, Guyana, and Suriname.

Dendroblatta litura Sylvain & Evangelista, 2016 (Figure 1 – 25 & 1 – 26 ; Table 1 - 6)

Holotype information

Adult male

Voucher number: DEKBO1515

GenBank Accession number: KT906104

Locality: Karanambu EcoLodge, Rupununi, Guyana

GPS: 3º45'N, -59º18'W

Collection date: 31 December 2014

Collectors: Dominic A. Evangelista, Oswin Ambrose

Deposition: The holotype is stored in 70% ethanol and will be deposited in the Center for Biodiversity at the University of Guyana.

Collection/ecological information: Most specimens were collected by hand around camp and the surrounding trails. Some females were captured in beer traps.

Morphological identification: We assigned this specimen to *Dendroblatta* Rehn, 1916 based on its subgenital plate with multiple protrusions, small body size (8-20 mm), and general shape of the genital phallomeres. Furthermore, we find that the subgenital plate of our species is very similar to that of *D. matograssensis* Lopes & Oliviera, 2005 and *D. mineira* Lopes & Oliveira, 2005 with a general degree of similarity in the genital phallomeres as well.

Description of holotype: Male. Ocelli small, not obvious. Inter-ocular space very narrow (~0.25 mm). Inter-antennal space much wider (~0.75 mm). Maxillary palps long; second segment measures approximately 1mm with the third segment slightly shorter; terminal segment shorter than third. Overall head coloration is dark amber with brown regions. Inter-ocular space entirely brown. Frons mostly amber with brown patterning (as in Figure 1 – 25 C). Antennae sparsely covered with medium/long hairs throughout; beginning on the sixth or seventh segment of the flagellum, which is covered densely with minute hairs; coloration similar to the head.

Antero-ventral margin of the foreleg femur (right) has 4 large proximal spines followed by 31 minute spines, 1 large apical and 1 large pre-apical spine. Left foreleg is missing due to damage. Postero-ventral margin has 3 large spines and 1 apical spine. Ventral side of tarsus with two parallel rows of spines along entirety. Basal first, second, and third pulvilli very small or absent. Fourth pulvillus is large. Prearsal claws symmetrical

and unspecialized. Arolia medium to large, reaching halfway to tip of pretarsal claw. The antero-ventral margin of the medial legs have 6 large spines, 1 apical spine and 1 genicular spine. 5 spines on postero-ventral margin plus 1 apical spine. Tarsi are same as front leg. Spination of the hind legs the same as middle legs. Pulvilli are missing on the three proximal segments. Overall coloring of legs a light amber highlighted with dark brown.

The abdomen ventrally is an orange amber. Color is most prominent in posterior region. The lateral and anterior regions are a darker brown. Segments 2-6 are sparsely mottled with white, particularly on the posterior margins of the segments.

Four protrusions from the subgenital plate (Figure 1 - 26A). The most left lateral protrusion (LP1) begins laterally and is reflexed medially, dorsally and posteriorly, almost meeting the right protrusion at a point medially. LP1 has a clubbed and hairy distal end. The next protrusion (LP2) is shortened and curved dorsally and slightly medially. The right protrusion (RP) is very wide and sticks out laterally before curving back medially. Overall it is obliquely cupped. Medial protrusion (MP) is within the cup of the right protrusion and meets at the tip of the right protrusion. It is more heavily sclerotized and has numerous spines at the tip giving the appearance of a bear's paw.

Head is slightly visible from dorsal side and reaches past pronotum. Pronotum is more elliptical than trapezoidal with its widest point nearly halfway between anterior and posterior margins. Coloration of pronotum as in Figure 1 – 26A. Notably, the longitudinal stripes do not meet anterior margin. The ventral margin of the anterior edge of the pronotum is either lacking hairs entirely or with very small hairs sparsely distributed throughout.

Costal areas of tegmina are translucent; central regions dark brown; demarcated laterally by the cubital vein with the color reaching nearly the medial margin of the tegmina; radial veins bordered with small brown splotches.

Abdomen dorsally is lacking a tergal gland. Supra-anal plate simple, triangular with a broadly arched tip.

Dorsal coloration of abdomen same as ventral coloration but with brown being more prominent and white regions more pronounced at the lateral posterior margins. Dorsal side of cerci is a dark brown basally and predominantly white throughout the majority with a brown tip.

Measurements can be found in Table 1 – 6.

Paratypes: 2 males**.** Voucher numbers: DEKBO1083, DEKBO1084, DEKBO0975

Morphology:

Same as holotype except for the following. Antero-ventral margin of the foreleg femur (both) has 3-4 large proximal spines followed by 27-34 minute spines, 1 large apical and 1 large pre-apical spine. Postero-ventral margin of same with 2 spines on margin in addition 1 apical spine. Posterior margin of abdominal sterna lacking mottled white coloration. Middle leg not lacking pulvillus 1 and 2 entirely but they are greatly reduced as in the foreleg.

Allotype: 1 female.

Voucher number: DEKBO0695

Locality: Karanambu EcoLodge, Rupununi, Guyana

GPS: 3º45’N, -59º18’W

Collection date: 31 December 2014

Collectors: D. A. Evangelista, O. Ambrose

Deposition: The holotype is stored in 70% ethanol and will be deposited in the Center for Biodiversity at the University of Guyana.

Description: The interocular space is slightly wider than the male. Other features match male.

Hair on the antennae begins on the ninth segment of the flagellum instead of the sixth.

Antero-ventral margin of fore-femur has large basal spines (5-left, 4-right), a row of small spines (26-left, 27-right), 1 large pre-apical, and 1 large apical spine. All other leg morphology the same as in the male.

Subgenital plate is simple and the posterior portions are dark brown. Coloration of ventral abdomen same as male but lacking white.

Pronotum same as male except two dark spots present between the longitudinal bars on the posterior half.

Supra-anal plate similar to male but with more hairs posteriorly and a distinctly shaped notch cut out of the tip.

Tegminal coloration is same as in the male.

Abdomen dorsally has the same coloration as the male with no white spots and the lateral corners of the segments are lighter and translucent.

Measurements can be found in Table 1 – 6.

Paratypes: 7 females.

Voucher Numbers: DEKBO0689, DEKBO0974, DEKBO1280, DEKBO1402, DEKBO1468, DEKBO1506, DEKBO1507

Morphology:

The individuals closely match the description of the allotype. We found that two individuals had very pale (almost absent) patterning of the head and one had regions of white. One individual had a lighter ventral abdomen. Another individual had the same ventral markings as the male. One individual had a shallower supra-anal plate than that of the allotype.

Differential diagnosis and diagnostic features:

The subgenital plate of *D. litura* Evangelista and Sylvain, 2016 is distinct when compared to that of all other *Dendroblatta*. It is also separable by the facial and pronotal coloration.

D. litura brings this genus into conflict with *Macrophyllodromia* Saussure and Zehnter, 1893 because of the similar pronotal coloration. This superficial similarity alone may not cause confusion but the protrusions of the subgenital plate are also similarly arranged. Following (Vidlička 2013) the second left protrusion in *Macrophyllodromia* (LP2) typically crosses the medial gap and lays over the right protrusion (RP). This is not the case in our species and many other *Dendroblatta*. Furthermore, the spination of the

anterior-ventral margin of the fore-femur is distinct among these genera, with the exception of *D. iani*, who has spination similar to *Macrophyllodromia*.

Genetic information and evolutionary placement: The COI sequence we obtained for this species (KT906104) was found in a polytomy with *Dendroblatta callizona* Rehn, 1928 (GenBank accession number: KF155067), and an unidentified Pseudophyllodromiinae that Evangelista et al. (2015) speculated was *D. cnephaia* Hebard, 1926 (GenBank accession numbers: KF155070, KF155071).

Etymology: The specific epithet "litura" (=erasure or blot) refers to the blotted coloration of the frons that is unique to this species, which appears blotted with various degrees of intensity.

Known geographic distribution: Guyana (Rupununi savanna region)

Calhypnorna Saussure & Zehntner, 1893

History. The genus was originally established as a subgenus of *Hypnorna* Stål, 1860. It was then given generic status by Kirby (1904). The genera *Calhypnorna*, *Hypnorna*, *Hypnornoides* Rehn, 1917 and *Euhypnorna* Hebard, 1921 are thought to be closely related (Hebard 1921). These are known from a number of regions (Para and Rio de Janiero Brazil, Bolivia and Panama) but there are no records from the Guiana Shield. Therefore, a new record of this species from the coastal rainforests of Guyana is geographically disjointed

from all other records of these taxa. On this basis alone, we might distinguish this specimen as a new species. However, since our lone specimen is a juvenile, we have limited morphological basis for differentiating this from known taxa. We refrain from establishing this as new species until adult specimens can be found but we still give a synopsis of the biological traits of this specimen. This new record extends the potential range of *Calhypnorna* Saussure & Zehntner, 1893 and it has now been recorded from Para Brazil (south of Amazon), Bolivia, Panama, and Guyana (new record).

Calhypnorna sp. A

Authors of the description. Evangelista, Wilson, & Ware

Materials. *Juvenile* Figure 1 - 27

Voucher number: DECBA1802

GenBank accession number: KF155118

Collection locale. CEIBA Biological Station, Madewini, Guyana.

GPS: 6º 29’ N 58º 13’ W.

Collection date: 15 – August – 2012 .

Collectors. Dominic A. Evangelista and William R. Kuhn.

Specimen information. This specimen is stored in ethanol and is deposited in the Center for Biodiversity at the University of Guyana.

Identification and differential diagnosis. We identified this specimen as *Calhypnorna* based on the following comparisons. Our specimen is not lacking an interocular carina as in *Hypnornoides* (Rehn 1917). Our specimen also has a definitively truncate posterior margin of the pronotum (Figure 1 - 27 B), which differentiates it from *Euhypnorna* (Hebard 1921a). Our specimen is lacking the hairs covering most of the body as in *Hypnorna* (Saussure & Zehntner 1893) and most closely matches the illustration of *Calhypnorna* by Saussure and Zehntner (1893).

Description. The specimen is a juvenile that is likely in its penultimate instar. Overall, the body shape is elongated for a typical cockroach, and even for a typical Pseudophyllodromiinae. A large portion of the head is visible from a dorsal perspective, and reaches anteriorly past the pronotum significantly. The black coloration on the pronotum is the same width as the width of the head where it meets with the pronotal margin (Figure 1 - 27 B).

Antennae are hirsute to nearly plumose. The antennae are slightly clubbed basally with the widest point occurring at first segment of the flagellum. There are two major color regions of the antennae: a dark basal region and a light distal region. The dark basal region begins as slightly lighter than the remainder but becomes a dark black color by the end of the dark region. The 25^{th} segment of the antennae is the final dark segment. The 26^{th} antennal segment begins the light region of the antennae. The 26^{th} or 27^{th} and subsequent segments are nearly white, becoming more brownish orange after the 7^{th} white segment (33 total). The total number of antennal segments on the specimen is 38 (left) and 44 (right).

The head is very large in relation to the remainder of the body, triangular, and wider than typical for a Pseudophyllodromiinae (Figure 1 - 27 A). Inter-ocular space is sharply angled creating a carina that begins where the compound eye meets the antennae. The antennal pits are closer together than the eyes. Eyes are prominent and appear to bulge the head laterally. Facial grooves spanning from the posterior portion of the eye towards the mouthparts are prominent. Coloration on head is brown-orange overall with a slightly lighter, less brown, patch above and below the carina. Ocellar spots are either absent or not readily visible.

The pronotum is colored with a dark black region taking up the major two fifths of the medial area. The black area is opaque and reaches forward to the anterior margin but just stops short of completion in the posterior eighth of the segment. The black region is nearly rectangular, slightly rounded anteriorly and widened posteriorly (Figure 1 - 27 B). Bordering the black region laterally and posteriorly are translucent regions colored brown-orange similar to the remainder of the body.

Meta- and meso-thoracic segments bear lobes posterolaterally. Color is orange-brown overall with small amounts of black on the tips of the posterior pair of wing pads. Legs are light in color with a slight orange tinge overall. Dark regions are present on the medial side of the base of the fore-coxae.

The ventro-anterior margin of the fore-femur have 5 (right) or 8 (left) large piliform spines basally followed by 27 (right) and 20 (left) shorter piliform spines, which are then each followed by 1 larger piliform spine and finally 1 large distal spine that is not piliform. Arolia are large and extend beyond the tips of the pretarsal claws on all legs. Claws are symmetrical and unspecialized.

Both the venter and dorsum of the abdomen is the same orange-brown color as the remainder of the body, but with a slightly redder tinge. Soft black color borders the abdomen laterally and posteriorly.

The dorsal abdomen is mostly glabrous. Hairs that are present are most dense laterally and on segments five and six. Ventral abdomen is glabrous as well, with fewer hairs than on the dorsal side and no regions with any dense pubescence. Supra-anal plate is unspecialized and broadly subtrapezoidal or triangular. Subgenital plate is broadly subtrapezoidal with the posterior margin being broader than that of the subgenital plate. The posterior margin of the subgenital plate is not perfectly uniform and conforms around two large styli. Styli are equal in length to the entire subgenital plate. Their width is equal to half of the length of the visible portion of the styli.

Genetic information and evolutionary placement. Evangelista et al. (2014) recovers this sequence as being most closely related to a species reported as “Ectobiidae sp. 6” with 75% bootstrap support. This species is identified above as *Chorisonuera inversa* Hebard, 1926. Hebard hypothesized that these are closely related genera (Hebard 1921a) and we can now

say that genetic data supports this hypothesis. We cannot definitively say, however, that they are sister taxa because of incomplete phylogenetic sampling in this tree. Thus, we follow Hebard (1921b) and not Beccaloni (Beccaloni 2014) and consider this to be in the Psuedophylodromiinae.

Known geographic distribution. Guyana (new record), Para Brazil, Bolivia and Panama.

Collection/ecological information. This specimen was found crawling through a benab. The only individual of this species observed in the field was the one collected and described here. Given that our overall collecting effort was significant (>1000 individuals of Blattodea *s.s.*) and we only found a single individual of *Calhypnorna* sp. A, we consider this species to be quite rare.

Previous work (Shelford 1912) has cited species of this genus as being beetle mimics. However, we observed no beetle model in the field that this species may have been mimicking. We did notice a similarity in body coloration of a wasp and Hemipteran sympatric with this conspicuously colored Blattodea (Figure 1 - 28).

Euphyllodromia Shelford, 1908

History

Euphyllodromia, first described by Shelford in 1908 as a subgenus of *Pseudophyllodromia* Brunner von Wattenwyl, 1865, was established as a full genus by

Hebard (1920). Since then the genus has expanded to include 42 species. The most recent review of the genus was done by Anisyutkin (2011) who also described three species, and described a fossil *E. angustata* (Latrielle, 1811) from the Pleistocene-Holocene epoch.

Euphyllodromia are characterized by the following traits. Sizes ranging from 11-19 mm long, and possess unique pigmentation. The eyes protrude and the triangular head remains uncovered by the pronotum. The wings and tegmina are well-developed. A few spines are present on the basal half of ventral-anterior margin of the front femur, which precede smaller, chitinous spines and three slender apical spines (2 preapical and one 1 apical). Pulvilli are present only on the fourth (IV) tarsal segment (Rocha E Silva 1984). In addition, they also have a phallomere that is both hooked on the right side in the dorsal view and in possession of a pre-apical incision (Lopes & da Silva 2012).

Euphyllodromia amazonensis Rocha E Silva, 1984 (Figure 1 – 29)

1 adult male

Voucher number: DEIWO0173

Collection locality: Iwokrama River Lodge, Iwokrama Forest, Guyana

GPS: 4^{o} 43’ 58” N, 58^{o} 43’ 4” W

Collection date: December 2014

Collectors: D. Evangelista, M. Davis, M. Johnny, M. Carter, O. Ambrose

Collection/ecological information: This individual and other individuals that escaped collection were seen sitting on foliage in primary forest understory during the day.

Morphological identification: This specimen was easily identified by comparing the pronotal pattern and subgenital plate shape to the illustration of Rocha E Silva (1984).

Known geographic distribution: Guyana (new record), Brazil (Jutai and Manaus)

Cockroach fauna of the Guyana Shield: Summary

The checklist (Table 1 – 1) contains 5 families, 18 subfamilies, 79 genera, and 238 species. French Guiana and Suriname contribute the most to this richness, with 151 and 136 species respectively (Figure 1 – 30). The surprisingly low number of records from Guianan Venezuela, Roraima and Amapa Brazil (Figure 1 – 30) are most definitely due to an historical under sampling in these regions.

When pooling and examining the range data for all the taxa (Figure 1 – 31) small ranges are most common among species. This is also true when pooling taxa together into genera, although these range sizes are larger overall. 86 species (36%) and 19 genera (24%) are limited to a single region while 36 species (15%) and 24 genera (30%) are represented in four or more regions. Small ranges (<4 regions) are no longer the majority when lumping species into subfamilies or families.

The highest rates of endemism are seen in Guianan Venezuela, Amapa Brazil and French Guiana (Figure 1 – 32). However, we believe these values to be inaccurate due to lack of sampling. Compared on a pairwise basis, Guyana, Suriname and French Guiana had a high proportion of shared fauna (Figure 1 - 33). These are each proximal to each other and centrally located, thus their faunal similarity is expected. Roraima showed a high

number of its own species shared among each other region. However, most of the species recorded from Roraima are circumtropical taxa and the region is severely under sampled.

Most of the species in the checklist have neotropical distributions. There were few taxa listed with distributions that may be considered circumtropical or cosmopolitan: *Blatta orientalis* Linnaeus, *Neostylopygia rhombifolia* (Stoll) , *Periplaneta americana* (Linnaeus), *P. australasiae* (Fabricius), *P. brunnea* Burmeister, *Holocompsa nitidula* (Fabricius), *Phoetalia pallida* (Brunner von Wattenwyl), *P. circumvagans* (Burmeister),*Nauphoeta cinerea* (Olivier), *Rhyparobia maderae* (Fabricius), *Panchlora nivea* (Linnaeus), *Pycnoscelus surinamensis* (Linnaeus), *Blattella germanica* (Linnaeus), *Supella longipalpa* (Fabricius). Most of these may be considered non-native, or adventive.

Discussion

The majority of records used to compile the checklist were lacking in specific biological, geographic or ecological information. Most historical records we encountered only gave general collection locales within their respective country. GPS information was non-existent for nearly all records.

We present 18 new species records for Guyana. This includes one genus new to the entire shield (*Calhypnorna* Saussure & Zehntner, 1893) and three new species (*Xestoblatta berenbaumae, Dendroblatta litura* and *Dasyblatta warei*). Given the somewhat high local richness of cockroaches (Evangelista et al. 2014) in one small plot compared to the richness of the entire country (Figure 1 – 30) we believe that much of this country's diversity has yet to be discovered.

Among the regions considered here, Guyana and Amapa are moderately well sampled. Guianan Venezuela, and Roraima Brazil are sampled especially poorly and our

knowledge of the Blattodea of these regions is very much preliminary. In contrast, French Guiana and Suriname are some of the most well sampled cockroach faunas in all the neotropics, ranking as the 2nd and 7th most species dense regions respectively (Table 1 – 7). The most well sampled region in the neotropics, Rio de Janeiro, has a species density of 0.01 species per square mile (Table 4). If we consider this value as being typical of true species density, which is purely speculation, then no other neotropical region has been sampled thoroughly.

The levels of endemism we see (Figure 1 – 32) are surprisingly low compared with other known rates of endemism for the Guiana Shield (Funk *et al.* 2007; Hollowell & Reynolds 2005; Kelloff & Funk 2004; Naka 2011). One possible explanation would simply be that cockroaches have low rates of tropical endemism. However, this is contradicted by other cockroach faunas showing much higher rates of endemism (e.g. ~60% of all taxa in Hispaniola; Gutierrez & Perez-Gelabert 2000). The alternate explanation is that there is a collection bias for taxa with broad ranges. This could be true if geographic sampling is very sparse, which may be the case. The levels of endemism we report (Figure 1 – 32) are actually higher than what they are in reality, since we only considered strictly Guianan regions. There are likely a few species that appear endemic when only considering these regions but by expanding the geographic scope we would find that they are actually not Guianan endemics (e.g. also being present in Trinidad, Colombia or other parts of Brazil).

If we didn't already know that under-sampling for cockroaches (Pellens and Grandcolas 2008; Roth 2003) and other insects (Erwin 1982; Stork 1993) was generally problematic, we could infer this based on a number of clues in our data. First, as mentioned previously, an estimate of total species richness of cockroaches for one small plot in

northern Guyana nearly matches the recorded richness of the entire country (Evangelista et al. 2014). Furthermore, there are 21 cases of species with unusual distributions (Table 1 – 8), where it is absent from a region but recorded from neighboring regions. Without evidence to the contrary, the simplest explanation for these distribution "holes" is inadequate sampling. Finally, although specific locality information is severely lacking for most records, those that are recorded do not represent effective spatial sampling, and most records are from coastal areas of major rivers. Finally, the number of species per region is significantly lower than that of better sampled but less diverse taxa such as Odonata (Checklist of the Odonata of the Guiana Shield 2012; Garrison *et al.* 2006; 2010).

Although there is clearly a great under-sampling of cockroaches from this region, we cite 34 publications that contributed to this checklist, including the present (Figure 1 – 34). The earliest source was from 1868 (Walker 1868). Most of the publications contributing to the checklist were published between 1900 and 1940. Morgan Hebard, Isolda Rocha e Silva Albuquerque, Ashley Gurney and James Rehn contributed the most through primary taxonomic publications and species descriptions (in particular see: Hebard 1926; Rehn 1930; Rocha E Silva Albuquerque and Gurney 1962). Karlis Princis, J. Bonfils and Conrad F.A. Bruijning were also important in these capacities but more-so through their own published checklists. Jaime Perez and J. Bonfils were also great contributors to the fauna of Venezuela and French Guiana. Similarly, Roseli Pellens was an important contributor to the knowledge of the two Brazilian regions through her checklist. Philippe Grandcolas was also an instrumental author through this same checklist, as well as other primary taxonomic publications. The three most cited papers in the checklist are Princis' "Orthopterum Catalogus" (148 citations), Bruijning's "The Blattidae of Surinam" (138

citations), and Hebard's "The Blattidae of French Guiana" (105 citations) (Figure 1 – 34). It is worth restating that, although they are invaluable authors, Princis' and Bruijning's contributions were mainly through synthesizing work done by others. The significance of Hebard's contribution to the knowledge of the Guianan fauna through "The Blattidae of French Guiana", in which he alone described 53 new species, cannot be understated.

Conclusions

This checklist of Blattodea s.s. of the Guiana Shield, showing 238 species, is the most comprehensive to date. It is also functions as the first true checklist of cockroaches of Guyana, as all previous sources severely fall short of listing even the modest number of species we record here. Given the large number of species found in the small country of French Guiana, we see that the Guiana Shield may be one of world's hotspots of biodiversity for cockroaches. However, sampling is still severely lacking. What little sampling has been done in the Guianas was mostly completed before 1960. There are huge gaps to fill in, and until they are we will be unable to adequately address most questions about the nature and origins of cockroach biodiversity.

Works Cited

Alexander, E.E., Bassett, Y., Charles, E., De Dijn, B.P.E., Forget, P.-M., Hammond, D.S., Hounter, N.C., Pons, T.L., Rijkers, T., Rose, S.A. & Springate, N.D. (2005) Tropical Forests of the Guiana Shield: Ancient Forests in a Modern World. CABI Publishing, Cambridge, MA, 535 pp.

Anisyutkin, L.N. (2011) A review of the genus Euphyllodromia Shelford, 1908 (Dictyoptera: Ectobiidae), with description of three new species. Proceedings of the Zoological Institute RAS, 315, 369-398.

Beccaloni, G. (2014) Cockroach Species File Online. Version 5.0/5.0. World Wide Web electronic publication, World Wide Web electronic publication

Beccaloni, G. & Eggleton, P. (2011) Taxonomy of Blattodea. Zootaxa, 3148, 199-200.

Beccaloni, G. & Eggleton, P. (2013) Order: Blattodea. Zootaxa, 3703, 46.

Bonfils, J. (1975) Blattoptera [Orthopteroidea] récoltés en Guyane Française par la mission du muséum national d'histoire naturelle. Annales de la Société entomologique de France Medecine, 11, 29-62.

Bonfils, J. (1987) Les Blattes (Dictyoptera: Blattaria) du Venezuela. In: Fauna hipogea y hemieda´fica de Venezuela y de otros pais´es de Ame´rica del Sur 157-164.

Bruijning, C.F.A. (1959) The Blattidae of Surinam. Studies on the Fauna of Suriname and Other Guyanas, 2, 1-103.

Checklist of Odonata of the Guiana Shield (2012) Checklist of Odonata of the Guiana Shield. http://www.libellen.org/suriname/7checklist/Checklist_Guiana_Shield4.htm

Djernaes M, Klass K-D, Picker MD, Damgaard J (2012) Phylogeny of cockroaches (Insecta, Dictyoptera, Blattodea), with placement of aberrant taxa and exploration of out-group sampling. Systematic Entomology 37: 65–83. doi: 10.1111/j.1365-3113.2011.00598.x

Djernaes M, Klass K-D, Eggleton P (2015) Identifying possible sister groups of Cryptocercidae+Isoptera: A combined molecular and morphological phylogeny of Dictyoptera. Molecular Phylogenetics and Evolution. doi: 10.1016/j.ympev.2014.08.019

Erwin, T.L. (1982) Tropical Forests: Their Richness in Coleoptera and Other Arthropod Species. The Coleopterists Bulletin, 36, 74-75.

Evangelista, D.A., Bourne, G. & Ware, J.L. (2014) Species richness estimates of Blattodea s.s. (Insecta: Dictyoptera) from northern Guyana vary depending upon methods of species delimitation. Systematic Entomology, 39, 150-158.

Evangelista, D.A., Buss, L. & Ware, J.L. (2013) Using DNA Barcodes to Confirm the Presence of a New Invasive Cockroach Pest in New York City. Journal of Economic Entomology, 106, 2275-2279.

Funk, V.A., Berry, P., Kelloff, C. & Alexander, S.N. (2007) Checklist of the Plants of the Guiana Shield (VENEZUELA: Amazonas, Bolivar, Delta Amacuro; GUYANA, SURINAM, FRENCH GUIANA). Contributions from the United States National Herbarium, 55, 1-584.

Garrison, R., von Ellenrieder, N. & Louton, J.A. (2006) Dragonfly Genera of the New World. Johns Hopkins University Press, Blatimore, MD, 368 pp.

Garrison, R., von Ellenrieder, N. & Louton, J.A. (2010) Damselfly Genera of the New World. Johns Hopkins University Press, Blatimore, MD, 490 pp.

Grandcolas P (1990) Descriptions de nouvelles Zetoborinae guyanaises avec quelques remarques sur la sous-famille. Bulletin de la Société Entomologique de France 95: 241–246.

Grandcolas P (1992a) Evolution du mode de vie, repartition et nouveaux taxons dans le genre Xestoblatta Hebard, 1916 (Dictyoptera, Blattellidae, Blattellinae). Revue Francaise D'Entomologie 14: 155–168.

Grandcolas P (1992b) Paradicta n. gen. et Neorhicnoda n. gen., deux nouvaeux genres de Blaberinae (Dict., Blattaria, Blaberidae). Bulletin de la Société Entomologique de France 97: 7–15.

Grandcolas P (1993a) Le genre Paramuzoa Roth, 1973: sa repartition et un cas de xylophagiechez les Nyctiborinae (Dictyoptera, Blattaria). Bulletin de la Société Entomologique de France 98: 131–138.

Grandcolas P (1993b) Monophylie et structure phylogenetique des [Blaberinae+Zetoborinae+ Gyninae+Diplopterinae] (Dictyoptera:Blaberidae). Bulletin de la Société Entomologique de France 29: 195–222.

Gurney AB (1939) A revision of the neotropical genus Xestoblatta Hebard (Orthoptera; Blattidae; Pseudomopinae). Proceedings of the Entomological Society of Washington 41: 97–128.

Gutierrez, E. & Perez-Gelabert, D. (2000) Annotated Checklist of Hispaniolan Cockroaches. Transactions of the American Entomological Society, 126, 433-446.

Hebard M (1916) Studies in the group Ischnopterites (Orthoptera, Blattidae, Pseudomopinae). Transactions of the American Entomological Society 42: 337–383.

Hebard, M. (1920) The Blattidae of Panama. American Entomological Society Memoirs, 4, 1-148.

Hebard, M. (1921a) A note on Panamanian Blattidae with the description of a new genus and two new species. Entomological News, 32, 161-169.

Hebard, M. (1921b) South American Blattidae from the Museum National d'Histoire Naturelle, Paris, France. Proceedings of the Academy of Natural Sciences of Philadelphia, 73, 193-304.

Hebard, M. (1926) The Blattidae of French Guiana. Proceedings of the Academy of Natural Sciences of Philadelphia, 78, 135-244.

Hebard, M. (1929) Previously Unreported Tropical American Blattidae (Orthoptera) in the British Museum. Transactions of the American Entomological Society, 55, 345-388.

Hebard M (1931) Die Ausbeute der deutschen Chaco-Expedition 1925/26 – Orthoptera. Zeitschrift fur systematiische Insektenkunde 10: 257–285.

Hollowell, T. & Reynolds, R.P. (2005) Checklist of the terrestrial vertebrates of the Guiana Shield. Bulletin of the Biological Society of Washington, 13, 1-93.

Inward D, Beccaloni G, Eggleton P (2007) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. Biology Letters 3: 331–335. doi: 10.1098/rsbl.2007.0102

Kelloff, C.L. & Funk, V.A. (2004) Phytogeography of the Kaieteur Falls, Potaro Plateau, Guyana: Floral distributions and affinities. Journal of Biogeography, 31, 501-513.

Kirby, W.F. (1904) A synonymic catalogue of Orthoptera. Vol. 1. Zoology, B.M.N.H.D.o. (ed.). Order of the Trustees of the British Museum, London. doi: 10.5962/bhl.title.6745

Kukalova-Peck, J. and J. F. Lawrence (2004). "Relationships among coleopteran suborders and major endoneopteran lineages: Evidence from hind wing characters." Eur. J. Entomol. 101: 195-144.

Lopes SM, de Oliveira EH (2004) Two New Species of Helgaia (Blattaria: Blattellidae) from Brazil with Description of Male and Female Genitalia of Helgaia serrana and Keys to the Species. Studies on Neotropical Fauna and Environment 39: 57–61. doi: 10.1080/01650520412331270981

Lopez-Osorio F, Miranda-Esquivel DR (2010) A phylogenetic approach to conserving Amazonian biodiversity. Conservation Biology 24: 1359–1366. doi: 10.1111/j.1523-1739.2010.01482.x

Lopes, S.M. & da Silva, L.d.O.C. (2012) Four new species of *Euphyllodromia* (Ectobiidae, Pseudophyllodromiinae) from the Amazon. Biota Neotropica, 12, 1-9.

Naka, L.N. (2011) Avian distribution patterns in the Guiana Shield: implications for the delimitation of Amazonian areas of endemism. Journal of Biogeography, 38, 681-696.

Nickle, D. (1984) Epilampra maya Rehn, a Central American cockroach newly established in the United States (Blattodea; Blaberidae; Epilamprinae). The Florida Entomologist, 67, 487-489.

Pellens, R. & Grandcolas, P. (2008) Catalogue of Blattaria (Insecta) from Brazil. Zootaxa, 1709, 1-109.

Perez-Gelabert D (2008) Arthropods of Hispaniola (Dominican Republic and Haiti): A checklist and bibliography. Zootaxa 1831: 1–530.

Perez, J.R. (1988) Revision taxonomica de las cucarachas (Blattaria, Dictioptera) de Venezuela. Boletin de la Direccion de Malariologia Y Saneamiento Ambiental, 28, 128-149.

Peterson, W. & Cobb, K. (2009) First Record of the Turkestan Cockroach, *Blatta lateralis* (Walker), in Georgia (USA). Journal of Entomological Sciences, 44, 415-416.

Princis K, Kevan DKM (1955) Cockroaches (Blattariae) from Trinidad, B.W.I., with a few records from other parts of the Caribbean. Opuscula Entomologica 20: 149–169.

Princis K (1948) Uber einige neue bzw. wenig bekannte Blattarien aus dem Naturhistorischen Reichmuseum zu Stockholm. Arkiv for Zoologi 41: 1–23.

Princis, K. (1963) Orthopterum Catalogus. W. Junk, 's-Gravenhage, The Netherlands. 246 pp.

Rehn JA (1903) Studies in American Blattidae. Transactions of the American Entomological Society 29: 259–290.

Rehn, J.A. (1906) Records and descriptions of non-saltatorial Orthoptera from British Guiana. Proceedings of the Academy of Natural Sciences of Philadelphia, 58, 262-278.

Rehn, J.A. (1917) On Orthoptera from the Vicinity of Rio de Janeiro, Brazil. Transactions of the American Entomological Society, 43, 335-363.

Rehn JA, Hebard M (1927) The Orthoptera of the West Indies Number 1. Blattidae. Bulletin of the American Museum of Natural History 54: 1 – 320.

Rehn, J.A. (1928) New or little known neotropical Blattidae (Orthoptera): Number one. Transactions of the American Entomological Society, 54, 125-194.

Rehn, J.A.G. (1930) New or Little Known Neotropical Blattidae (Orthoptera). Number Two. Transactions of the American Entomological Society, 56, 19-71.

Rehn JA (1937a) New or little known neotropical Blattidae (Orthoptera): Number four. Transactions of the American Entomological Society 63: 207–258.

Rehn JA (1937b) A new species of Blattidae from British Guiana. The annals and magazine of natural history 20: 197–203. doi: 10.1080/00222933708655333

Rocha E Silva Albuquerque, I. & Gurney, A.B. (1962) Insecta Amapaensia. - Orthoptera: Blattoidea. Studia Entomologia, 5, 235-255.

Rocha E Silva, I. (1984) Revisao do genero *Euphyllodromia* Shelford, 1908 (Blattellidae: Blattodea: Dictyopera). Revista Brasileira de Entomologia, 28, 65-85.

Roth, L.M. (1969) The male genitalia of Blattaria. I. *Blaberus* spp. (Blaberidae: Blaberinae). Psyche, 76, 217-250.

Roth LM (1970a) The male genitalia of Blattaria. IV. Blaberidae: Blaberinae. Psyche 77: 308–342.

Roth, L.M. (1970b) The male genitalia of Blattaria. V. *Epilampra* spp. (Blaberidae: Epilamprinae). Psyche, 77, 436-486.

Roth, L.M. (2003) Systematics and Phylogeny Of Cockroaches (Dictyoptera: Blattaria). Oriental Insects, 37, 1-186.

Saussure, H.d. & Zehntner, L. (1893) Insecta. Orthoptera. Biologia Centrali-Americana. 1, 1-285

Shelford, R. (1910) Epilamprinae. Genera insectorum, 101, 1-21.

Shelford, R. (1912) Mimicry amongst the Blattidae; with a revision of the genus Prosoplecta Sauss. and the description of a new genus. Proceedings of the Zoological Society of London, 82, 358-378.

Stork, N.E. (1993) How many species are there? Biodiversity and Conservation, 2, 215-232.

Velez, A., Wolff, M. & Gutierrez, E. (2006) Blattaria of Colombia: List and distribution of genera. Zootaxa, 1210, 39-52.

Walker, F. (1868) Catalogue of Specimens of Blattariae in the Collection of the British Museum. London, 237 pp.

Ware JL, Litman J, Klass K-D, Spearman LA (2008) Relationships among the major lineages of Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. Systematic Entomology 33: 429–450. doi: 10.1111/j.1365-3113.2008.00424.x

Wolfram Research, I. (2012) Mathematica Edition: Version 9.1. Wolfram Research Inc., Chamaign, Illinois

CHAPTER 2

SPECIES RICHNESS ESTIMATES OF BLATTODEA SENSU STRICTO (INSECTA:DICTYOPTERA) FROM NORTHERN GUYANA VARY DEPENDING UPON METHODS OF SPECIES DELIMITATION

Reproduced from vol. 39 of Systematic Entomology

Full citation: Evangelista, D. A., et al. (2014). "Species richness estimates of Blattodea s.s. (Insecta: Dictyoptera) from northern Guyana vary depending upon methods of species delimitation." Systematic Entomology 39: 150-158.

Abstract

Cockroaches (order: Blattodea) comprise a taxon that, although very abundant in tropical forests, remains largely unstudied. Making sense of the diversity of species is a challenging task hindered by the large numbers of species and the abundance of cryptic or polymorphic forms. Here, we estimated species richness of cockroaches (*sensu sticto*) from northern Guyana while applying a method to deal with these confounding factors. We utilized two methods of species delimitation, the first using only morphological information, and the second using both morphological and genetic barcode information. The two methods greatly influenced the resulting estimates of species richness. When incorporating genetic barcodes our total species richness estimate decreased by 25%. Our results emphasize the importance of using independent datasets to delimit species boundaries and expert identification of specimens when possible.

Introduction

Describing diversity is fundamental to progress in taxonomy, conservation biology, ecological modeling and other fields. Unfortunately, measuring the total number of species of a particular taxon or the total number of species in an area is usually biased by species abundance patterns and sampling effort. There are numerous methods used to estimate the total number of species in an area (e.g. using distribution and abundance, species accumulation curves, species description curves, or ecological models). Ultimately, however, these all depend on how species boundaries are defined and how species concepts are applied to problems.

Biology is built on a scaffolding of the concept of a 'species' but the delimitation of species boundaries is difficult. This is compounded by the fact that there are many definitions of a species. These definitions may be crafted to reflect practicality of use (Mallett 1995; Mishler 1985), biological theory (Mayden 1997; Mayr 1942) or both in an attempt to balance these two ideals that are sometimes at odds (De Queiroz 2007; Sperling 2003). Three species concepts are relevant to our focus: (1) the genetic species concept; (2) the morphospecies concept; and (3) the phylogenetic species concept (Mayden, 1997; De Queiroz 2011).

The problems with definitions (1) and (2), and others, arise when they are applied under real world conditions. Many kinds of morphological crypsis, intraspecific polymorphism, and hybridization are culprits in confounding these species concepts (Cerutti-Pereyra *et al.*, 2012; Hebert *et al.*, 2004; Lumley & Sperling 2010; DeSalle *et al.*, 2005; Kuchta *et al.*, 2009). This can greatly influence our perceptions of diversity. Yet, one

can apply data consistent with definitions (1), (2) and (3) for a higher quality of species delimitation (Lumley & Sperling 2010).

Diversity and species delimitation in cockroaches

Cockroaches (order: Blattodea) currently comprise ~4500 species (*sensu stricto*) plus ~2700 termite species (Beccaloni & Eggleton, 2011). Known diversity of cockroaches is two orders of magnitude lower than that of the hyper-diverse insect orders such as butterflies (>157,000 species described; Van Nieukerken *et al.* 2011), or beetles (>350,000 species described; Maddison, 2000). Yet, even modestly speciose taxa like the Blattodea present a "taxonomic impediment", a problem where the amount of diversity and lack of taxonomists prevents us from describing species before their extinction (Giangrande, 2003). An additional complicating factor is the uneven taxonomic distribution of insect specialists. While Blattodea is a relatively small order there are fewer researchers studying them than other orders of similar size (e.g., dragonflies, which have national and international organizations devoted to their study, as well as an abundance of non-professional enthusiasts).

Cockroaches have not been commonly utilized in biodiversity studies, despite their ecological importance. They are large consumers of both plant and animal detritus (Bell *et al.*, 2007; Evangelista, Wilson & Ware, in prep.) and may represent the largest proportion of biomass among insects in tropical canopies (Basset, 2001). Some species are indicators of ecological variables (Fisk, 1983). Two major studies have been done which focus solely on the total regional diversity of cockroaches (Fisk, 1983; Wolda, 1983). Although other

studies have included cockroaches in diversity samples (Basset, 2001; Basset *et al.*, 2012; Paoletti *et al.*, 1991), little focus has been given to this cryptic group of insects.

From all systematic perspectives these insects are inherently difficult to assess. Comparable individuals of closely related species may have highly conserved external morphology and thus may be difficult to distinguish. Individuals may be highly polymorphic over the course of development and adults are often significantly different from juveniles (Hebard, 1920; Rehn & Hebard, 1927). This is very important when considering that juveniles may consist up to 90% of individuals in cockroach surveys (Fisk, 1983). Cockroaches also have high levels of developmental stochasticity, resulting in great variation in external spination, setation, and coloration (Bell *et al.*, 2007; Evangelista pers. obs.). Sexual dimorphism can also exaggerate male-female differences enough that the sexes may appear to be entirely different species (Bell *et al.*, 2007; Hebard, 1920; Roth, 2003). With the dearth of experts and keys in Blattodea many adults cannot be identified; certainly morphological identification of some immatures is nearly impossible.

Genetic barcoding as an alternative to traditional identification

Genetic barcodes (cytochrome oxidase I or COI) are useful pieces of information that can be used for both identifying (Hebert et al., 2003; 2004) and defining the boundaries of species (Blaxter, 2004). Recent studies have shown that other genes can be equally or more effective in these roles (Dupuis et al., 2012). Regardless, Steele and Pires (2011) give a good summative view of the potential role of barcoding in species identification.

There are many criticisms of the process of barcoding. COI sequences (i.e. barcodes) may not track species lines because of the presence of psuedogenes (Song et al.,

2008), hybridization, introgression, ancestral polymorphism, and recent evolutionary divergence (DeSalle et al., 2005; Schmidt & Sperling, 2008; Moritz & Cicero, 2004; Lumley & Sperling, 2010). Finally, substitution rate seems to not be an inherited trait (Kumar, 2005; Yi, 2007). This lends support to criticisms against using rules defining species based on percent differences in nucleotide substitutions, which have expectedly been shown to be violated for many taxa (Cognato, 2006). These are certainly not inconsequential problems, but one solution to these issues is the use of multiple independent data sets to delimit species (Zhou et al., 2007; Dupuis et al., 2012).

These issues highlight the need for a different approach to the identification of species. Given this, we explore how species richness is affected by two methods of species delimitation: (1) defining morphological types based on overall similarity and the presence of shared monomorphic traits, (2) defining phylogenetic types using mitochondrial cytochrome oxidase I (COI) haplotypes and morphological groupings as a guide for delimiting species in the case of ambiguities. Using method (2), COI haplotypes will reconstruct a tree topology but taxa will be divided into species only with support from our morphological evidence (figure 2-1).

Methods:

Specimen collection

We collected specimens from two sites in northern Guyana: CEIBA Biological Station in Madewini, Guyana (6° 29" N 58° 13" W) and Kamuni River near Santa Mission, Guyana (6° 33" N 58° 18" W). Along the Kamuni River, we sampled only from within bromeliads. At CEIBA we collected most specimens in cups baited with beer, light traps

and bromeliads. We used the baited cups both as pitfall traps and to sample the canopy by tying them to tree trunks at various heights (0, 2, 4.8, 9.2, 13.8, 17, and 21.3 meters). To supplement these methods, we did manual and visual searches of the local environment and collected cockroaches by hand. We stored all specimens in 139-proof vodka (locally sold as "High Wine") temporarily and then transferred to them to 70% ethanol in the lab. These specimens are temporarily stored in the Rutgers-Newark insect collection but are considered to be the ultimate property of the government of Guyana.

Morphological types

We defined our morphological types based on ~5-10 standard external morphological characters (spination on anterior-ventral margin of fore-femur, sub-genital plate shape, frons coloration, cerci shape, overall body shape, overall body color, supra-anal plate morphology, pronotal shape and coloration). We chose these characters because they are variable, easy to discern, and used in other literature (Choate; Helfer, 1953; Rehn & Hebard, 1927). We first categorized all the types into general body forms and then further delimited them into specific types.

Species richness estimates

We used three methods to estimate total species richness: bootstrapping (100,000 replicates), bias corrected Chao-1 and the abundance-based coverage estimator (ACE). These were implemented on the software Mathematica version 9.1 (Wolfram Research, 2012). Bootstrapping is a random sampling of data that estimates the level of inherent bias. Total species richness estimates are obtained in this case by assuming that the difference between the resampling richness and the sample richness is equal to the difference between

the sample richness and the total richness (Smith, 1984). Chao-1 is a non-parametric richness estimator that uses a modified ratio of singletons to doubletons as an estimate of the number of species unsampled (Chao, 1983). ACE is a similar non-parametric method that takes into account other abundance classes (Chao & Lee, 1992). We calculated cockroach richness using all metrics for the total dataset and for ecological subsamples (e.g. bromeliad fauna, leaf litter fauna, and other fauna). We defined our dataset solely by morphological grouping and redefined it using congruent morphological and barcoding data, as explained below.

Within each morphotype we chose a few individuals of good condition for barcoding (at least four when possible). We attempted to sample different variants of the same types in order to allow the genetic data to recognize separate species if possible. Due to the volume of samples we did not genetically sample each individual. In using the morpho-type variants as the base unit of variation, we are assuming that there is no variation within these groups. It is possible that this is not the case and that by genetically sampling all individuals we could uncover new diversity.

COI sequencing

For DNA extraction we used QIAGEN DNeasy extraction kits and their standard tissue extraction protocol. Once extracted, we amplified the COI fragment using a nested PCR with primers and to minimize the probability of COI pseudo-genes being amplified and prevent artificially increasing our total number of species (Song *et al.*, 2008). We chose a 600 nucleotide length fragment of the COI mitochondrial gene as our barcode sequence. Our nested PCR used universal primers LCO and HCO followed by a PCR cycle using

primers 1709 and 21921 (Simon *et al.*, 1994). Amplification of sequences was confirmed by gel electrophoresis. We only sequenced samples showing bands that were obviously more intense than the second band of shorter DNA to prevent amplifying the pseudo-gene region. We sent all amplified samples to MacroGen, NY for sequencing and used Sequencher (Gene Codes Corporation) for contig assembly and to resolve ambiguities.

We also used utilized other selected mantis, termite, and corydiid sequences as outgroup taxa, which were either sequenced using the above protocol or downloaded from Genbank.

Tree generation

We compiled all sequences, aligned them with the software CLUSTALX2, and then manually refined the alignment in Mesquite (Maddison & Maddison, 2011). Sequences that were difficult to align or that seemed to have improbable structure (insertions/deletions not in multiples of three, or multiple stop codons) compared to the majority of other sequences, were assumed to be pseudo-gene replicates and were excluded from the analysis. We recoded third codon position nucleotides as R-Y to decrease the probability of homoplasy affecting tree topology.

We then generated a maximum likelihood (ML) tree using GARLI 2.0 (Zwickl, 2006) that was the consensus of 500 bootstrap pseudo-replicates. The replicate trees were summarized to compose our final tree using DendroPy (Sukumaran & Holder, 2010). We deposited all sequences in GenBank.

Tree evaluation

We used the resulting barcode tree in concordance with morphological data to determine congruence for support of "true" species delimitations. An explanation of this process is given in supplementary documents.

Evaluating the two methods

We made an initial estimate of species richness using only morphological type information and then recalculated all richness metrics (as explained above) once we revised our list of relative species abundances with the barcoding data.

Results:

In total, 740 individuals were collected from the field. These were separated into 77 morphological types (table 2-1). Of these, we obtained and analyzed sequences from 64 out of the 77 types. An example of the process used to revise our species list is given in figure 2-3. Revisions to the original list of species based on our tree are summarized in table 2 - 1 and further explained in the supplemental material.

Sample richness was greatly affected by revising the type list with the data in our tree (figure 2-4). The entire data set exhibited a 25% reduction in total species count and leaf litter taxa showed the greatest discrepancy among the subsets with a 22% reduction. This may indicate that leaf litter taxa may show polymorphism more often than other taxa, however this should be explored further in future studies.

The estimates of total species richness showed similar trends. Total richness estimates using bootstrapping were 25% lower for the entire data set, 20% lower for the leaf litter subset and 22% lower for the "other" subset (figure 2-4). The differences in

bootstrap total richness estimates are significant (α=.05) for the full data set and for the "leaf litter" and "other" subsets.

Figure 2-5 illustrates how the two methods of species delimitation can differentially affect separate methods of total species richness estimates. In particular, unbiased Chao-1 estimates of total richness were affected differently by the addition of genetic data. This stems from the different sensitivity of the Chao-1 metric to sample richness and species of different abundance classes.

Discussion

Delimiting species with two independent datasets

The COI was largely polytomous but was highly informative in revealing morphotype associations. Using ecological collection information we can see that some previously unassociated groups found in similar habitats are likely closely related taxa, if not the same species. This is true for the Epilamprine morphotypes and their juvenile instars, which we were unable to associate to adults based solely on morphology. This was also true for unusual color morphs of the most common species, "Blattodea sp. 1".

Differing estimates of species richness

There was a significant difference in species richness estimates between the two methods. This was also true for two out of the three subdivisions of the data (figure 2 -4). This shows that, without expert identification of specimens, i.e. without morphological expertise, richness estimates may have been erroneous. Even with expert identification, however, many of the originally incorrectly categorized specimens still may not have been

associated with their proper morphotypes. This is particularly true with immatures as taxonomic literature is scarce with descriptions of juveniles, save for only the most common species (Hebard, 1920; Rehn, 1903).

By associating our morphotypes to one another or splitting morphotypes, we greatly affected the abundance profile of the data. Some abundant species became more abundant and the number of rare species was reduced. This is relevant because richness estimators (Chao-1 and ACE) are more sensitive to changes in the number of rare species than they are to the sample richness. Similarly, bootstrapping relies heavily on the abundance of the species that it samples.

Ecological relevance of cockroach diversity

A literature review of the cockroach fauna of Guyana shows that 105 species have been recorded from the country (Evangelista, *et al.*, 2015). This is roughly on par with our projected richness of 91 (figure 2 - 4) for the fauna of our two northern sites. Our sampling does not reach any significant representation of the geographical heterogeneity of the larger region, although we did not attempt to quantify this. Given this, we would most certainly assume that the total diversity of the countries' fauna is greater than what has been recorded thus far, a result that would have been predicted based on general knowledge of neotropical diversity and lack of prior sampling of cockroaches in Guyana.

Conclusions:

On the value of the morphotype

Other studies which primarily use morpho-types counts for richness estimates (e.g. Coddington *et al.*, 2009; Donoso *et al.*, 2010; Stork & Grimbacher, 2006; Stuntz *et al.*, 2002) may be adversely affected by problems associated with morpho-identification. Our results show that polymorphisms and variation in individuals create a potential of error in associating individuals to the correct types. If measuring β diversity, one can reduce these effects by keeping morphotype definitions and sampling conditions consistent across plots. However, if a certain morph of a given species is differentially prevalent across sites then improper association of this morph could result in erroneous conclusions. Another way to avoid these pitfalls, without using genetic information, would be to only sample certain morphs of all species, as is sometimes done with ants (Longino *et al.*, 2002). However, this will severely reduce sample size in many cases and may fundamentally change the distribution of species abundances due to sex ratio skews or age stage biases. This would thereby affect species richness estimates. We intentionally did not eliminate any types from our sample.

One of the major problems with the genetic barcode comes from the presence or absence of the so-called "barcode-gap". The barcode-gap is the point where one can distinguish intraspecific variation from interspecific variation (Wiemers & Fiedler, 2007). We found a similar problem in finding the "morphological-gap" when comparing among life stages and sexes. However this was due to the fact that we were unable to utilize genital morphology, which has been proven to be more effective in diagnosing taxa for the Blattodea (Klass & Meier, 2006; McKittrick, 1964; Roth & Gutierrez, 1998). Indeed, from a systematic perspective, genital characters can be very useful in delimiting and defining closely related taxa and when considering only these characters, the "morphological-gap"

should be easier to identify. Yet, this was not useful for us because genitalia are effectively irrelevant in the association of juveniles to adults. Similarly, it is extremely difficult to make reliable associations of males to females using genital morphology.

How to delimit species

The current body of information about how many species there are in the various families of cockroaches (Beccaloni & Eggleton, 2011) is highly dependent on the subjectivity and limitations of taxonomists who described them. The literature is abundant with examples of authors expressing their loss at adequately describing groups (Rehn, 1903; Rehn & Hebard, 1927; Shelford, 1909, 1911). Homoplasy and pleisiomorphy can be greatly confounding. Species richness in an ecological context is different from species richness in a taxonomic context, but clearly there is a connection between the two. Although presented in an ecological context, we believe our study represents an attempt to independently verify where species reside in evolutionary space using novel data. Although the morphological forms in this study were relatively limited when compared to the greater diversity of Blattodea or all insects, we exemplify a procedure that may prove useful when applied more widely.

It is true that a single mitochondrial barcode region may be insufficient to delimit species boundaries but this may also be true for morphology. Clearly, having more independent data to verify species delimitation is better than having less, no matter if that data is genetic, morphological, ecological or behavioral (Moritz & Cicero, 2004). Morphological divergence in genitalia can be direct evidence of secondary reinforcement; yet, in the case of species clines this may be as arbitrary as a genetic distance between

lineages and, as mentioned previously, is only useful when looking at adults of a single sex.

We should not take species for granted as their definition is tenuous. If less stringent methods (e.g. single data set, few characters) are used to define species these are subject to the tendency of the taxonomist for lumping or splitting taxa. Even if stringent methods (e.g. multiple independent data sets, many characters) are used, new geographic sampling may yield unexpected variability that may make for ambiguous cases. In truth, we can never know with absolute certainty what a species is, considering the probability of missing data or ongoing evolutionary novelty.

Works Cited

Basset, Y. (2001) Invertebrates in the Canopy of Tropical Rain Forests How Much Do We Really Know? Plant Ecology, 153, 87-107.

Basset, Y., Cizek, L., Cuenoud, P., Didham, R.K., Guilhaumon, F., Missa, O., Novotny, V., Odegaard, F., Roslin, T., Schmidl, J., Tishechkin, A.K., Winchester, N.N., Roubik, D.W., Aberlenc, H.P., Bail, J., Barrios, H., Bridle, J.R., Castano-Meneses, G., Corbara, B., Curletti, G., Duarte da Rocha, W., De Bakker, D., Delabie, J.H., Dejean, A., Fagan, L.L., Floren, A., Kitching, R.L., Medianero, E., Miller, S.E., Gama de Oliveira, E., Orivel, J., Pollet, M., Rapp, M., Ribeiro, S.P., Roisin, Y., Schmidt, J.B., Sorensen, L. & Leponce, M. (2012) Arthropod diversity in a tropical forest. Science, 338, 1481-4.

Beccaloni, G. & Eggleton, P. (2011) Taxonomy of Blattodea. Zootaxa, 3148, 199-200.

Bell, W.J., Roth, L.M. & Nalepa, C. (2007) Cockroaches: Ecology, Behavior and Natural History. Johns Hopkins University Press, Baltimore, MD pp.

Blaxter, M.L. (2004) The promise of a DNA taxonomy. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 359, 669-79.

Cerutti-Pereyra, F., Meekan, M.G., Wei, N.W., O'Shea, O., Bradshaw, C.J. & Austin, C.M. (2012) Identification of rays through DNA barcoding: an application for ecologists. PloS One, 7, 1-10.

Chao, A. (1983) Approximate mean squared errors of estimators of reliability in the two-parameter exponential case. Communications on Statistics, A12, 633-644.

Chao, A. & Lee, S.-M. (1992) Estimating the Number of Classes via Sample Coverage. Journal of American Statistical Association, 87, 210-217.

Choate, P.M. A Literature-based Dichotomous Key for the Identification of the Cockroach fauna (Insecta: Blattaria) of Florida. University of Florida - Department of Entomology and Nematology

Coddington, J., Agnarsson, I., Miller, J., Kuntner, M. & Hormiga, G. (2009) Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. Journal of Animal Ecology, 78, 573-584.

Cognato, A.I. (2006) Standard Percent DNA Sequence Difference for Insects Does Not Predict Species Boundaries. Journal of Economic Entomology, 99, 1037-1045.

Corporation, G.C. Sequencher: sequence analysis software. Gene Codes Corporation, Ann Arbor, MI USA

DeSalle, R., Egan, M.G. & Siddall, M. (2005) The unholy trinity: taxonomy, species delimitation and DNA barcoding. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 360, 1905-16.

Djernaes, M., Klass, K.-D., Picker, M.D. & Damgaard, J. (2012) Phylogeny of cockroaches (Insecta, Dictyoptera, Blattodea), with placement of aberrant taxa and exploration of out-group sampling. Systematic Entomology, 37, 65-83.

De Queiroz, K. (2007) Species concepts and species delimitation. Systematic Biology, 56, 879–886.

De Queiroz, K. (2011) Branches in the lines of descent: Charles Darwin and the evolution of the species concept. Biological Journal of the Linnean Society, 103, 19–35.

Donoso, D.A., Johnston, M.K. & Kaspari, M. (2010) Trees as templates for tropical litter arthropod diversity. Oecologia, 164, 201-11.

Dupuis, J.R., Roe, A.D. & Sperling, F.A. (2012) Multi-locus species delimitation in closely related animals and fungi: one marker is not enough. Molecular Ecology, 21, 4422–4436.

Fisk, F. (1983) Abundance and diversity of arboreal Blattaria in moist tropical forests of the Panama Canal area and Costa Rica. Transactions of the American Entomological Society, 108, 479-489.

Funk, V.A. & Richardson, K.S. (2002) Systematic Data in Biodiversity Studies: Use It or Lose It. Systematic Biology, 51, 303-316.

Giangrande, A. (2003) Biodiversity, conservation, and the Taxonomic impediment. Aquatic Conservation: Marine and Freshwater Ecosystems, 13, 451-459.

Grandcolas, P. (1996) The phylogeny of cockroach families: a cladistic appraisal of morpho-anatomical data. Canadian Journal of Zoology, 74, 508-527.

Hajibabaei, M., Singer, G.A., Hebert, P.D. & Hickey, D.A. (2007) DNA barcoding: how it complements taxonomy, molecular phylogenetics and population genetics. Trends Genetics, 23, 167-72.

Hebard, M. (1920) The Blattidae of Panama. American Entomological Society Memoirs, 4, 1-148.

Hebert, P.D., Cynwinska, A., Ball, S.L. & deWaard, J.R. (2003a) Biological Identification through DNA barcodes. Proceedings of the Royal Society of Biology, 270, 313-321.

Hebert, P.D., Cywinska, A., Ball, S.L. & deWaard, J.R. (2003b) Biological identifications through DNA barcodes. Proceedings: Biological Sciences, 270, 313-21.

Hebert, P.D., Stoeckle, M.Y., Zemlak, T.S. & Francis, C.M. (2004) Identification of Birds through DNA Barcodes. PLoS Biology, 2, 1657-1663.

Helfer, J., R. (1953) How to Know the Grasshoppers, Cockroaches and their allies. WM.C.Brown Company Publishers, Dubuque, Iowa,pp.

Klass, K.-D. & Meier, R. (2006) A phylogenetic Analysis of Dictyoptera (Insecta) based on morphological characters. Entomologische Abhandlungen, 63, 3-50.

Kuchta, S.R., Parks, D.S., Mueller, R.L. & Wake, D.B. (2009) Closing the ring: historical biogeography of the salamander ring speciesEnsatina eschscholtzii. Journal of Biogeography, 36, 982-995.

Kumar, S. (2005) Molecular clocks: four decades of evolution. Nature, 6, 654-662.

Longino, J.T., Coddington, J. & Colwell, R.K. (2002) The Ant Fauna Of A Tropical Rain Forest: Estimating Species Richness Three Different Ways. Ecology, 83, 689-702.

Lopez-Osorio, F. & Miranda-Esquivel, D.R. (2010) A phylogenetic approach to conserving Amazonian biodiversity. Conservation Biology, 24, 1359-66.

Lumley, L.M. & Sperling, F.A.H. (2010) Integrating morphology and mitochondrial DNA for species delimitation within the spruce budworm (Choristoneura fumiferana) cryptic species complex (Lepidoptera: Tortricidae). Systematic Entomology, 35, 416–428.

Maddison, D.R. (2000) Coleoptera: Beetles. In: Tree of Life Web Project. Vol. 2013. http://tolweb.org/

Maddison, W.P. & Maddison, D.R. (2011) Mesquite a Modular System for Evolutionary Analysis. Version 2.75 [WWW document]. URL http://mesquiteproject.org [accessed on 1 September 2012].

Mallett, J. (1995) A species definition for the modern synthesis. Trends in Ecology and Evolution, 10, 294–299.

Mayden, R.L. (1997) A hierarchy of species concepts: the denouement in the saga of the species problem. In: Claridge, M.F., Dawah, H.A. & Wilson, M.R. (Eds.) Species: The Units of Biodiversity. Chapman & Hall, London, pp.

Mayr, E. (1942) Systematics and the Origin of Species. Columbia University Press, New York, NY.

McKittrick, F.A. (1964) Evolutionary studies of cockroaches. Cornell University Agricultural Experiment Station Memoir, 389, 1–197.

Mishler, B.D. (1985) The morphological, developmental, and phylogenetic basis of species concepts in bryophytes. The Bryologist, 88, 207–214.

Meyer, C.P. & Paulay, G. (2005) DNA Barcoding: Error Rates Based on Comprehensive Sampling. PLoS Biology, 3, 2229-2238.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for Inference of Large Phylogenetic Trees.

Moritz, C. & Cicero, C. (2004) DNA barcoding: promise and pitfalls. PLoS Biology, 2, 1529-1531.

Paoletti, M.G., Taylor, R.A.J., Stinner, B.R., Stinner, D.H. & Benzing, D.H. (1991) Diversity of Soil Fauna in the Canopy and Forest Floor of a Venezuelan Cloud Forest. Journal of Tropical Ecology, 7, 373-383.

Rehn, J.A. (1903) Studies in American Blattidae. Transactions of the American Entomological Society, 29, 259-290.

Rehn, J.A. & Hebard, M. (1927) The Orthoptera of the West Indies Number 1. Blattidae. Bulletin of the American Museum of Natural History, 54, 1 - 320.

Roth, L.M. (2003) Systematics And Phylogeny Of Cockroaches (Dictyoptera: Blattaria). Oriental Insects, 37, 1-186.

Roth, L.M. & Gutierrez, E. (1998) The cockroach genus Colapteroblatta, its synonyms Poroblatta, Acroporoblatta, and Nauclidas, and a new species of Litopeltis (Blattaria: Blaberidae, Epilamprinae). Transactions of the American Entomological Society, 124, 167-202.

Schmidt, C.B. & Sperling, F.A.H. (2008) Widespread decoupling of mtDNA variation and species integrity in Grammia tiger moths (Lepidoptera: Noctuidae). Systematic Ecology, 33, 613–634.

Shelford, R. (1909) Descriptions of some new genera and species of Blattidae. Deutsche Entomologische Zeitschrift, 611-624.

Shelford, R. (1911) Preliminary Diagnosis of some new Blattidae. 47, 154-156.

Simon, C., Frati, F., Beckenbach, A., Crespi, B., Liu, H. & Flook, P. (1994) Evolution, Weighting and Phylogenetic Utility of Mitochondrial Gene Sequences and a Compilation of Conserved Polymerase Chain Reaction Primers. Annals of the Entomological Society of America, 87, 651-701.

Smith, E.P. (1984) Nonparametric Estimation of Species Richness. Biometrics, 40, 119-129.

Song, H., Buhay, J.E., Whiting, M.F. & Crandall, K.A. (2008) Many species in one: DNA barcoding overestimates the number of species when nuclear mitochondrial pseudogenes are coamplified. Proceedings of the National Academy of Sciences of the United States of America, 105, 13486-91.

Sperling, F.A. (2003) Butterfly molecular systematics: from species definitions to higher-level phylogenies. Butterflies: Evolution and Ecology Taking Flight (ed. by C. Boggs, W. Watt and P. Ehrlich), pp. 431–458. Chicago Press University of Chicago, Chicago, Illinois.

Steele, P.R. & Pires, J.C. (2011) Biodiversity assessment: state-of-the-art techniques in phylogenomics and species identification. American Journal of Botany, 98, 415-25.

Stork, N.E. & Grimbacher, P.S. (2006) Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. Proceedings: Biological Sciences, 273, 1969-75.

Stuntz, S., Ziegler, C., Simon, U. & Zotz, G. (2002) Diversity and structure of the arthropod fauna within three canopy epiphyte species in central Panama. Journal of Tropical Ecology, 18, 161-176.

Sukumaran, J. & Holder, M.T. (2010) DendroPy: A Python library for phylogenetic computing. Bioinformatics, 26, 1569-1571.

Ware, J.L., Litman, J., Klass, K.-D. & Spearman, L.A. (2008) Relationships among the major lineages of Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. Systematic Entomology, 33, 429-450.

Van Nieukerken, E., Kaila, L., Kitching, I. et al. (2011) Order: Lepidoptera Linnaeus, 1758. Zootaxa, 3148, 212–221.

Wiegmann, B.M. & Yeates, D.K. (2007) Diptera: True Flies. In: Tree of Life Web Project. Vol. 2013. http://tolweb.org/

Wiemers, M. & Fiedler, K. (2007) Does the DNA barcoding gap exist? - a case study in blue butterflies (Lepidoptera: Lycaenidae). Front Zool, 4, 8.

Wolda, H. (1983) Diversity, diversity indices and tropical cockroaches. Oecologia, 58, 290-298.

Wolfram Research, I. (2012) Mathematica Edition: Version 9.1. Wolfram Research Inc., Chamaign, Illinois

Yi, S.V. (2007) Understanding Neutral Genomic Molecular Clocks. Evolutionary Biology, 34, 144-151.

Zhou, X., Kjer, K.M. & Morse, J.C. (2007) Associating larvae and adults of Chinese Hydropsychidae caddisflies (Insecta: Trichoptera) using DNA sequences. Journal of the North American Benthological Society, 26, 719–742.

Zwickl, D.J. (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion, The University of Texas at Austin

CHAPTER 3

EVIDENCE THAT DISPERSAL BARRIERS INFLUENCE COCKROACH ASSEMBLAGES IN A NEOTROPICAL SAVANNA-FOREST MATRIX

Abstract

We examine the role of savanna, forests, and flood zones in affecting cockroach assemblage composition in a temporally and spatially heterogeneous landscape. We test whether flood zones and stretches of dry savanna are barriers to dispersal for leaf litter cockroaches. Leaf litter cockroaches are terrestrial but occupy a high-humidity microclimate; their distribution and dispersal may be limited by both flooding and hot, exposed savanna. The study location, the north Rupununi of Guyana, is an expansive savanna-forest matrix. During the wet season, large regions of both forest and savanna are submerged by up to 5 meters of water, further fragmenting this already complex landscape. Our main study area is the ~10,000 hectares of Karanambu Eco-Lodge. We collected >1300 individuals of 17 species from 28 sites. Using a landscape classification based on satellite imagery we generated models of the relative isolation of the 28 sites using a cost of travel algorithm. We also used non-metric multi-dimensional scaling and mantel tests to determine whether the similarity of cockroach assemblages could be explained by different landscape categories (savanna, forests, and flood zones) or by geographical distance. We identified a single model that best predicted observed variation in cockroach abundance and species richness. Differences in assemblage similarity were largely due to differences in the forest-savanna habitat axis. Geographic distance was also

found to effect assemblage similarity. Our data suggest that savannas and permanent waterways are barriers to dispersal but flood zones are not.

Introduction

The north Rupununi region of Guyana is a spatially and temporally variable landscape with high biodiversity. The Rupununi River, which defines the northern and southern bounds of this region, begins in the plains south of the Kanuku Mountains and flows northward until it meets the Rewa River and shortly thereafter into the large Essequibo River, which flows to the Atlantic Ocean. Although this region is largely forested, its huge savanna regions are unique in Guyana. The region also experiences extreme seasonal flooding, where the water table may rise 5 meters or more during the wet season (Eden 1970; Gerard Pereira pers. comm.). The Rupununi River and its riparian zone harbor a high diversity of birds, mammals (Funk *et al.* 1999), reptiles (Cole *et al.* 2013), fish (Souza *et al.* 2012) and other animals (Watkins 2010).

The savanna is strikingly different from the forest. There is relatively little vegetation cover and plant biomass compared to forests (Barbosa & Fearnside 2005) and thus reduced food availability and protection from abiotic stressors. Much of the savanna herbs there show xeric adapted morphology (Eden 1970), and indeed the savannas have become more prevalent during the driest periods of the Pleistocene (Eden 1970) or more recently (Rull 1992). The savannas are thought to be maintained as a community due to periodic fires (Myers 1936), which are both anthropogenic and naturally occurring.

The savannas of the Guianas are dispersal boundaries for some species (Naka 2011). Insects (such as cockroaches) may be especially limited because of low dispersal ability and limited capacity for water retention (Guthrie & Tindall 1968; Mullins 2015). Migrating or dispersing individuals of many species in the Rupununi region may use the narrow riparian corridor bordering the river. For example, the frequency of Jaguar sightings at the riverside tourist lodge and research center Karanambu, which is positioned at a bottle neck of forest between the Pakaraima and Kanuku mountains, is higher than expected given its size (Gerard Pereira & Salvador de Caires pers. comm), suggesting that the cats avoid dispersing through savanna.

However, the value of the riparian zone as a safe haven for fauna is challenged during the wet season. Water levels rise about 5 meters, a 5 fold increase from dry season depths. The flooding greatly fragments the terrestrial landscape for a large part of the year (May-August) (Eden 1970). Although the upper canopy is mostly free from seasonal floods, the florest floor can be submerged entirely. See figure 3 - 1 for the differences in exposed water from wet to dry season. For species living in the forest leaf litter, this means that for a portion of the year, their habitat is underwater, which may impose a selective pressure for habitat constancy and limited dispersal, a subject for future study.

Yet the savannas are heterogeneous no matter what the season. They are bounded by the riparian forests of the river and have small patches (hereafter referred to as forest islands) or galleries of forest punctuating them (figure 3 - 1). In some cases these forest islands are bordered on all sides by savanna, or they may be bordered by flooded grassland or flooded shrubland on one or more sides. The forest islands themselves may be within the flood zones. The distribution of the forest islands may be an related to

higher clay content and lower compaction of the loamy soils (Eden 1970). The forest islands, compared to the edges of mainland forests, have less deciduous species (Myers 1936). Although their origins are unknown, it is suspected that the forest islands may be isolated relics of a wider spread pre-Holocene forest (Eden 1964).

If savanna, forests or flood regions are limiting dispersal of a few species, we would see species distributions and abundances reflect these limitations. Our main goal is to determine if savanna, flood regions, or both are limiting species mixing and dispersal. We make two predictions about spatial patterns of diversity based on a few assumptions about diversity patterns across the landscape. We first test the validity of these assumptions, and then explicitly test our hypothesized predictions.

Preliminary assumptions

First, we expect that cockroach species present in forests will be effectively absent from savanna and flood-prone regions. Most non-desert adapted cockroaches are very vulnerable to water loss in dry environments (Bell*et al.* 2007; Guthrie & Tindall 1968; Mullins 2015). This would make savanna unsuitable habitat for these insects during the day. There is some vegetative cover on the savanna but it is largely bare ground with little to any discernable leaf litter. Large, subterranean, grass eating *Syntermes grandis* (among other termites) seem to clear most decaying plant matter before it can form a layer of leaf litter (pers. obs). For very different reasons, we predict that regularly flooded regions are also unsuitable habitat. Most cockroaches tend to be good swimmers, but few are truly aquatic or semi-aquatic (Bell *et al.* 2007). Regardless of ability to survive in water temporarily, a season long flood in a leaf litter habitat makes

all habitat space and resources effectively unavailable until the waters recede. Given this, we predict that these leaf litter taxa will be absent in flood regions during the dry season. This is also supported by our field observations

Second, we expect that large connected 'mainland' areas will have higher local species diversity than small forest islands isolated by savanna or water. This is in accordance with island biogeography theory, which predicts that larger areas will have a higher species diversity (Warren *et al.* 2015). If this wasn't the case, then savanna and water would not be limiting species movement. Our preliminary observations do suggest that forest islands have fewer species but high abundance of a select few species (*Ischnoptera galibi* and *Xestoblatta agautierae*).

Hypotheses

In order to determine if savanna, flood regions, or both are limiting species mixing and dispersal we test two major hypotheses. The first hypothesis assumes that there are forest islands and forest mainlands and predicts the cockroach distribution patters among this dichotomy. The effects of savanna and flood zones on assemblage composition are implicitly predicted by this hypothesis. The second hypothesis only distinguishes between the landscape categories forest, savanna and flood zone while only implicitly testing the island-mainland dichotomy.

Unique island assemblages hypothesis*:* Forest islands in the Rupununi will harbor unique assemblages that are differentiable from mainland forest assemblages. Cockroach assemblage similarity is best explained by shared patch type (island or mainland) rather than geographic distance.

Justification: Savannas may impede the dispersal of some thermal or dehydration intolerant species, which would explain why forest islands could be the primary habitat of other species. Given that forest islands are separated by savanna, forest islands may be more easily colonized by species that are have better flight ability and physiological tolerances. These "good dispersers" would need to travel across savanna in order to move among forest patches. As such, forest island assemblages may only contain those species that are good dispersers (i.e. presumably *Ischnoptera galibi* and *Xestoblatta agautierae*). Additionally, if our assumption that the mainland forests have a higher diversity is true, islands could be refuge habitats where species have escaped competitive pressures.

Landscape dispersal limitation hypothesis: Landscape models where savanna and flood regions act as barriers will best predict abundance patterns.

Justification: If our assumptions about species distributions across the landscape are true, savanna and flood regions are likely to be boundaries of dispersal.

In order to better understand how savanna, forests and flood zones affect the differences in composition among assemblages of leaf-litter cockroaches we surveyed blaberoid cockroaches (including *Anaplecta*) across 28 sites at Karanambu Eco-lodge. We include a special focus on the members of the Ischnopterini-a tribe that dominates leaf-litter cockroach communities across Guyana (Evangelista*et al.* 2014; Evangelista *et al.* 2015; Evangelista *et al.* in press, 2016).

Materials and methods

We conducted this study at Karanambu EcoLodge in the north Rupununi savanna region of Guyana, South America. Karanambu provided an area that was complex

enough to contain a sufficient diversity of habitats but not so complex as to make it an impractical study region. There are numerous trails that provide relatively easy access to forest islands in the savanna. We identified 28 sites (table 3 - 1) within Karanambu's ~10,000 hectares for specimen collection in this study. These were chosen to maximize the variety of habitat types (savanna, flood, forest island, forest mainland) and sample widely across the Karanambu region.

We collected cockroach specimens in two expeditions. The first (July 2013) was just prior to the peak of the rainy season and the second (December 2014 – January 2015) was in the peak of the dry season. We used pitfall traps baited with beer to collect leaf litter cockroaches. We used a solution of beer with small amounts of chlorine bleach (.25 ml per gallon) to reduce bacterial and yeast growth. At each collection site we setup 5-7 pitfall traps baited with beer in a linear arrangement spaced approximately 5 meters apart. We supplemented this with hand collection at some sites.

We brought specimens back to the lab for identification. All specimens are currently stored in the Rutgers University – Newark insect collection (Ware Lab collection) but will be donated to the AMNH and University of Guyana collections upon completion of taxonomic and systematic work. In some cases, specimens could not be identified to species and were assigned to a morphotype. Previous studies on cockroaches have shown that the usage of morphotypes adversely affects downstream calculations utilizing richness and abundance (Evangelista et al. 2014). To combat this, we omit morphotypes that we could not associate to an adult male type (males are more frequently used in cockroach taxonomy because of their distinct, highly variable genitalia) through the presence of synapomorphies. After identification of all types we input all specimens

into a database, which was then organized and analyzed in Mathematica 9 (Wolfram Research 2012) (table 3 - 2). We counted all species' abundances and the observed richness for each site. The data we used were corrected for unequal sampling and abundances were log transformed.

To test whether there were difference in species abundance with habitat type, we classified our sites into four categories: savanna, non-savanna, flooded, and non-flooded. Next, we compared individual species abundances among the four categories. It would not be surprising to collect a few individuals of some species in areas where they do not necessarily live, if for example they are using such areas as corridors. To account for this we looked for "effective absence" from a site, rather than complete absence. We used the abundance distribution of all species to calculate the top 95% abundance quantiles. Observed abundances in the bottom 5% of the distribution were counted as being "effectively absent" from a given site.

We compared species Shannon diversity among mainland and island sites to test our preliminary assumptions about them. We did not use total estimated richness because we have found these estimates to be highly chaotic when subject to uncertain morphotype associations (Evangelista et al 2014). To combat this we could have only used high quality sites (sites with equal sex ratios, equal age stage ratios and/or high sample size) but this would have resulted in a huge loss of statistical power. We compared Shannon diversity among sites to a binary independent variable with states "island" and "mainland". We did this using a linear model.

Testing the unique island assemblages hypothesis: Using the R package Vegan, we used non-metric multi-dimensional scaling (NMDS) of our species abundance data to test if the species assemblages are indeed different among the forest islands, forest mainlands, savannas or flood zones.

As a further step we tested if these differences were due to simply being spatially separated or due to specific habitat traits. We did this test by calculating Bray-Curtis community dissimilarities (function vegDist in Vegan) and comparing this pairwise matrix to a geographical distance matrix (calculated using a cost finding algorithm, as explained below) and four habitat dissimilarity matrices. The four habitat matrices considered pairwise difference in habitat types (seasonally flooding or not; forest island or mainland; forest or savanna; total differences in habitat). The pairwise habitat matrices were calculated as Euclidean distances in Vegan. We compared all matrices with a Mantel test (10,000 permutations) and calculated Pearson's product moment correlation coefficients and p-values. We also did separate Mantel tests to check for autocorrelation between habitat types and geographic distances. There was no evidence of correlation among these factors however we took a conservative approach and did a partial Mantel test as well. The partial Mantel test examines correlations between the predictor and response matrix while correcting for correlation with a third matrix, which on our case was the geographic distance matrix.

In addition to this test we also did a series of linear regressions testing the log-abundance of species per site by whether that site was a mainland or an island. Regardless of whether the entire assemblages were unique on forest islands or not, we wanted to be able to see if certain species had an affinity for forest islands or mainlands.

Testing the landscape dispersal limitation hypothesis: Through satellite imagery obtained from Google Earth (DigitalGlobe 2015) we separated landscape categories (savanna, forests and flood zones/water) using manually adjusted color and shape filtering in Mathematica 9 (Wolfram Research 2012) (see appendix S1 for full methodology and S2 for Mathematica code). We were able to differentiate forest, savanna, marsh, flooded forest and open water (figure 3 - 2). We verified our landscape image analysis using GPS associated field observations of the edges of flooded forests, and forest-savanna edges.

We used permutations of this landscape image to determine information about our collecting sites. Figure 3 - 3 shows the four images we chose to utilize in our analysis. The first image (figure 3 - 3A) is a null model where landscape categories don't matter, but distances between sites do. Figure 3 - 3B differentiates non-flooded forests from all all flooded and savanna areas. Figure 3 - 3C differentiates all regions that don't flood (forest and savanna) from all flooded regions and open water. The final image (figure 3 - 3D) ignores flooding and differentiates all forested areas from all savanna and open water areas.

We divided each image into circles of 60 pixel radius around each site. We implemented a fast-marching cost finding algorithm (Sethian 1999a;b) to determine the cost of travel among nine points arranged as in figure 3 - 3E. We calculated the average cost of travel among these points as a measure of isolation for each collection site. In order to determine the most realistic landscape category weighting for the cost finding analysis, we correlated isolation to various community metrics (diversity, abundances, richness etc.) while varying the weighting of the different landscape categories. We chose

the weights that gave the most overall improvement to model explanatory value and probability.

Using the best weighting for each landscape category we calculated isolation values for each site under the three alternative hypotheses (isolation under the null hypothesis is, by definition, equal among sites; Figure 3 – 3 B, C, D). We then included these isolation measures in a linear model as the independent variable testing against various community metrics, and the abundances of each individual species.

Finally, we used the cost-finding algorithm to determine the geographic distance between the sites. These were utilized in the Mantel tests mentioned earlier.

Results

We collected 1061 individuals (621 adult, 412 juvenile, 28 unknown age; 120 female, 98 male, 843 unknown sex) from beer traps (figure 3 - 4, table 3 - 2). We were able to identify these to 17 species level taxa (table 3 - 2). Many more individuals (50-200) were unable to be appropriately catalogued because of their poor physical condition (broken into irreconcilable pieces). Our collection yielded 527 identifiable individuals of *Ischnoptera galibi*. This was by far the most abundant Blattodea species collected from the field. Also, very abundant were *Xestoblatta agautierae* (n=232), *Ischnoptera atrata*/*hercules* (n=127) and *Epilampra opaca*/*substrigata* (n=69).

Islands were not found to have higher Shannon diversity overall ($p = .44$, $F = .62$, $R^2 = 0.03$). Islands did correlate positively with the abundance of *Ischnoptera galibi* ($p=.04$, $F=5.03$, $R^2=.19$) but only weakly. *Ischnoptera atrata/hercules* also showed a slight negative correlation ($p=.05$, $F=4.32$, $R^2=.164$). The abundances of all other species

did not correlate significantly with whether a site was categorized as an island or mainland (p values all > 0.05).

The R package Vegan gave results for environmental factors contributing to the species assemblage compostion. Figure 3 - 5 shows the results of the NMDS analysis. The trend we see that is least likely due to random error is the differences in assemblage composition as explained by whether the habitat was savanna or forest ($p = .009$, $R^2 = .21$). Whether an assemblage was on a forest island or mainland did not have a significant effect on difference in species assemblage composition ($p = .478$, $R^2 = 0.03$), nor did flooding or non-flooding of a site ($p = .729$).

In order to interpret these results we did a number of tests under various other conditions. First, we repeated this analysis with only those taxa that were not found on the savanna. Species that are limited in dispersing by savanna are least likely to be found on the savanna, so by omitting species found on savanna from this analysis we are increasing the possibility of seeing a trends due to savanna-limited dispersal. However, when we did this we saw no significant trends. We also repeated this analysis without the two most abundant species (*Ischnoptera galibi* and *Xestoblatta agautierae*). This would help us determine if our significant results were being driven by the presence of highly abundant species. We did see our significant trends disappear upon removal of these species. However, in both of the above tests we removed species which results in the necessity of removing sites as well, because certain sites become empty. This could result in a loss of power to see a significant trend. Finally, we repeated the analysis using the "Raup-Crick" dissimilarity index, which only utilizes presence-absence data. Under this method, once again, we do not see a significant effect of habitat type on differences in

assemblage composition. Therefore, the results from the NDMS analysis (figure 3 – 5) are mostly coming from species abundances and not only species presence/absence.

The Mantel test (table 3 - 3) shows that the savanna-forest landscape dimension explains assemblage variation (m=.224, p=.045) but not other landscape categories. This test also showed that geographic distance determined differences in species assemblage composition as well (m=.185, p=.024). Using the dissimilarities in all landscape categories gave the highest correlation and was also the most probable (m=0.269, p=0.005).

The mean geographic distance of one site to all others (calculated as cost of traveling among sites in figure 3 - 3A) did not offer any explanatory value to any of the community ecology metrics or species abundances (table S3.1 and table S3.2).

Tables 3 - 3 and 3 - 4 show the results from the linear modelling of isolation values under the three models (dry forests model, flood model, forests model) and their combinations. The forest model strongly explains differences in Shannon diversity and sample Ischnopterini richness among sites. The model, containing all factors, also explained a large proportion of the variation in these two community metrics (R^2=0.55 and 0.58 respectively). All cockroach sample richness was not significantly explained by any model (but see sources of error in discussion section below). On a per species basis we see that the forest model also strongly explains relative abundances among *Epilampra opaca/substrigata* (p=0.002), *Ischnoptera atrata/hercules (*p<0.00001) and *Ischnoptera* sp. cf. *rehni* (p<0.001). *Ischnoptera* sp. cf. *rehni* abundances also significantly correlated

with a combination of the dry forest and flood model ($p<0.00001$). Among all species where significant p-values were found, the model fit from 28-80% of the total variation.

Discussion

In large, our analyses did not verify our preliminary assumptions to be true. Out of the 17 species collected in beer traps, 10 species were found to be absent from the savanna and the remaining 7 were indeed present. Only 4 species were absent from flooded sites and 13 species were present. The lower 5% quantile for all species abundances equaled 0 (i.e. effective absence = observed absence). Although the data are somewhat conflicting, the assumption that forest dwelling cockroaches would not be present on the savanna is not entirely true. Cockroach absence from flood regions is rare, with a majority of species being found in both flooded and non-flooded sites; how living in a flooded region affects the behaviour and ecology of these species is unknown but presumably taxa recolonize areas when flooding has subsided.

Although we collected cockroaches on the savanna it is not clear that these species reside on the savanna; the savanna may be simply be a corridor between forested areas. However, we can only conclude this based on our abundance data, and assumptions about these species' tolerances. Future work on these species' ecology and physiological tolerances may further elucidate the true extent of their niches. However, savanna might be a significant part of for *Cariblatta* sp. 2's niche given that 24 out of 44 (45%) individuals collected were from savanna sites. We did collect *Ischnoptera galibi*, *Ischnoptera* sp. cf *rehni* and *Xestoblatta agautierae* on the savanna as well but their abundances were extremely low compared to within forest sites (<3% of all individuals

collected). Indeed, most individuals of all savanna species were collected near forest edges and not in savanna sites more isolated from forests. Certainly, sampling intensity can influence abundance. We intentionally sampled our savanna sites (SAV, SAT, SAT2 and SWT) for longer durations to confirm that the lower species yield initially observed there was not an artifact of poor sampling.

Finally, we have no evidence to suggest that forest mainlands harbor a higher diversity of cockroach species than forest islands. "Islandness" was not a significant explanatory factor for differences in diversity ($p=0.44$), hence a cockroach species' affinity for islands or mainlands may not be driven by competitive exclusion.

Testing our hypotheses

The "unique island assemblages hypothesis" suggested that an assemblages of leaf litter cockroaches found in forest islands would be more similar to each other than assemblages in mainland forests. This was not supported with our data. We found that assemblages in the landscape were most similar based on geographic distance or all combination of habitat types but specifically not whether a site was a forest or a mainland (Table 3). We did find a very weakly statistically significant effect of site "islandness" on *Ischnoptera galibi* and *Ischnoptera atrata/hercules* abundance (see results section) but these are likely not biologically meaningful because of the low amount of variation explained by these factors.

Our "landscape dispersal limitation hypothesis" suggests that certain landscape categories (savanna and flood zones) limit the dispersal of organisms, and thus create differences in assemblage composition. Consequently, there would be unique

assemblages on forest islands, because only strong dispersers would be able to reach them. We did not find this to be the case in the previously mentioned tests (e.g. figure 3 – 5 B, table 3 – 3). This could be explained by the fact that we see geographic distance as one possible explainer of differences in assemblage composition, more so than whether a site is an island or mainland (table 3). Yet, it is clear that savanna and forests are habitats with largely different assemblage compositions (figure 3 - 5 and table 3 - 3). It still seems possible that savanna is limiting in some way to the movement of species. Both the Mantel tests and the linear regressions by species greatly over-simplify differences among habitats. Thus, although these tests address patterns predicted by the "landscape dispersal limitation hypothesis" they may be the victim of a false dichotomy between "islands" and "mainlands".

The cost of travel analysis (which quantified isolation of each site by different savanna, or flood zones) was designed specifically to test the "landscape dispersal limitation hypothesis". These do not rely on assumptions over the "islandness" of a forest site but perhaps quantify "islandness" through the arrangement of savanna, forests and flood zones immediately surrounding each site. For example, under the "Dry Forest" or "Forest" (figure 3 - 3 B and D) models, sites such as "LFID" or "FICT" would appear highly isolated, since they are small forest islands surrounded by savanna. However, under the "Flood" model (which treats all unflooded savanna and forest as equally good habitat; figure 3 - 3 C) these sites would have a much lower isolation because there is relatively little water surrounding these islands. It is in this way that this analysis captures more detailed and complex information about the landscape.

Using the more informative isolation measures from the cost of travel analysis we saw a significant effect of savanna and forests on both the total species assemblies and the abundances of individual species (tables 3 - 3 and 3 - 5). It seems that the overall best model was the “Forest” model (figure 3 - 3 B and D), which treats any forested points as having a low cost of travel, and any water, savanna or flooded savanna points as being high cost of travel. Importantly, the “Forest” model does not differentiate between dry forests and flooded forests (as the “Dry Forest” model does).

Yet, pure geographic distance is also a measure of isolation, albeit one that does not take into account habitat heterogeneity. This is why we included the extra step of analyzing mean isolation by geographic distance, as can be seen in tables S3.1 and S3.2. These data are not compelling for explaining species abundance or assemblage differences among sites (no significant p values). This contradicts the results from the Mantel test. We believe this is because we lose information when we simply take the mean of all geographic differences instead of using each pairwise geographic distance. The Mantel test uses the full amount of geographic distance information, whereas the linear modeling of the isolation data uses more information content about habitat heterogeneity. Each test is informative in its own way.

Although the overall results are mixed with respect to the “landscape dispersal limitation” we do find strong evidence for it in the cost of travel analysis, which provided the results with the highest probability of being a true trend. The cost of travel analysis showed that a few of the landscape models are highly probable for some species and explain a large proportion of their distributional variation as well.

If the "landscape dispersal limitation" hypothesis is true then at least some species are being hindered by savanna and open water (the Rupununi River and various ponds). We have little evidence that flooding affected species distributions. It is important to highlight here that any potential limitations imposed by savanna (heat and water loss) are imposed and then relieved on a daily cycle from sunrise to sunset. Potential limitations of flooding (complete removal of terrestrial habitat) occur on an annual cycle, during the wet season.

Sources of error

The data we used to carry out this study have a number of limitations, which we attempted to correct, but nonetheless contribute to bias or random noise. Although our identifications are mostly robust, in a few cases we could not effectively differentiate cryptic species. For example, the *Ischnoptera atrata/hercules*, and *Epilampra opaca/substrigata* groups could not be effectively determined to the species level. In each case, the adult males are separated by only subtle differences. However, this was irrelevant because the juveniles and females of these species are entirely undifferentiable. We chose to lump these species into groups rather than throw out the juveniles, females and damaged males (which accounted for 96% and 75% of all individuals of *E. opaca/substrigata* and *I. atrata/hercules* respectively). There were similar, but much less extreme, problems with some other species collected that could contribute to error. The second issue was non-uniform sampling across all sites. We corrected for this by rescaling all abundances, however, this would not correct for the richness disparity created by uneven sampling.

The landscape models obtained from the satellite imagery analysis is not perfect. For one, very small forest islands and peninsulas are absent from the base image (figure 3 - 2) because of a reduction in precision after image filtering. In the fast-marching cost finding, this bias would slightly increase the estimated cost of travelling through the savanna, decreasing our type I error for accepting the "dry-forest model" or "Forest" model of dispersal (figure 3 - 3). We did indeed accept the "Forest" model in certain scenarios (see tables 3 – 3 and 3 - 5) and thus these results may be subject to this slight bias.

We interpret a number of our tests in light of dispersal. However, we only measured presence of individuals at our specific sites using baited pitfall traps (beer traps). We did set up light traps and malaise traps, which are more appropriate for catching actively dispersing individuals but we did not use these extensively enough to collect many cockroaches. In long term studies light traps have been found to collect cockroaches (Wolda 1983), but in our experience they are not useful in the short term.

Analytically we were at a loss for a single unifying test that could effectively discern differences in assemblage composition due to geographic distance or from isolation due to savanna or flood zones. As mentioned previously, each test that was most effective at utilizing one variable inherently oversimplified the other. As a result we found that both of these factors influenced different aspects of the spatial differences in species assemblage composition but in tests that emphasized different aspects of the landscapes. We did dispersal simulations using costs of travel among various landscape categories under the four landscape models (figure 3 - 3), however these simulations were

largely informed by geographic distances among sites and the outcomes were mostly similar.

Synthesis

Given the results of our various tests, our hypotheses about how the individual landscape categories affect assemblage organization were only correct for selective scenarios if at all. In the field we observed that *Ischnoptera galibi* were predominantly found on forest islands. This led us to predict that the differences between islands and mainlands would also correlate with differences among other species. Our underlying assumption in this hypothesis, that forest islands were intrinsically different habitats than forest mainlands, seems to be incorrect. There were no major differences in overall assemblage composition among forest islands or mainlands (figure 3 – 5, table 3 - 3) despite the fact that our initial observations of *Ischnoptera galibi* having an affinity for islands has some statistical support (see results).

We would expect differences in forest island assemblages from forest mainland assemblages if the habitat separating them (savanna, in most cases here) acted as an ecological filter, limiting movement of certain species. Although we did not see these differences between islands and mainlands, we do find strong evidence that isolation by by savanna ("forest" model) does predict differences in species composition among sites (table 5).

The nature of these relationships is up to interpretation. Assemblage diversity, abundance of *E. opaca/stubstrigata* and abundance of *Ischnoptera atrata/hercules* correlated positively with isolation under the "forests" model. Abundance of *Ischnoptera*

sp. cf. *rehni* correlated negatively with isolation under the "forests" model. A high isolation in the forest model indicates that a site was proximal to more savanna or open water. This means that more limiting habitat categories led to higher alpha-diversity and higher abundances of these species (except for *Ischnoptera* sp. cf. *rehni*). If these habitat categories are limiting dispersal then the high abundances could be due to an inability of individuals to leave their patch, and thus population numbers increase locally instead of being distributed more evenly across the landscape. However, in the opposite case of *Ischnoptera* sp. cf. *rehni* its high abundances in lower isolation patches could be due to sites acting as sinks and accumulating species from other patches. Species diversity being positively correlated with isolation under the "forest" model may be due to an effect of edge forests having a higher diversity than interior forests.

If indeed savanna is limiting movement of species this may have evolutionary implications. Savanna may be a barrier to gene flow and one would expect diversification rates due to genetic drift to be determined by distribution of savanna. This remains untested and may be an interesting future study.

We do have at least one promising model for how the landscape affects species assembly (the "forest" model). However, this model fails to explain the distributions of most of the species and community ecology metrics. If we wish to better explain species the differences in assemblage compositions we would need to look towards other ecological or historical factors.

The historical ranges of insects affecting contemporary ones is also a possibility. The biogeographical history of the Rupununi savanna is not well studied, but if the

current fragmented forests were recently part of a continuous forest landscape then relictual patterns of diversity could persist to the present day. In such a case we would see similar assemblages in all patches, regardless if they were forest mainlands or islands. This is indeed what we see (figure 3 - 5), however, as mentioned previously, this may be due to an overly simplified habitat categorization. The alternative possibility is that the current forest islands arose through ecological succession directly out of the savanna and species only came there by dispersal. Unless we can reconstruct the origins of the forest islands we must consider that either case is a possibility.

Another promising direction would be to look at habitat disturbance. In the 1980's Karanambu underwent a transition point for the forests around our TMB and ZMB sites. This large forest mainland is locally known as Pi-pi-chu forest (named in Mukushi for the Screaming Pia bird) or Three Mile Bush. Pi-pi-chu forest was subject to a series of fires during the El Nino southern oscillation events of the 1980's. It was then that the forest underwent a change from primary to secondary forests. The changes were limited to the north-western portions though. The parts bordering the river (e.g. our sites: LFMHT and LFMHDT) remained in a primary forest state (Gerard Periera pers. comm). Within this one large patch of forest, we do see differences in the abundance of *Ischnoptera galibi*, and *I. atrata/hercules* that correspond to the north west and riverine sections of the forest.

The potential effects of disturbance go further. Savannas are thought to be natural habitat in the region; however anthropogenic forces likely have increased their prevalence over the most recent 10,000 years (Godfrey Bourne, pers. comm). Slash and burn farming techniques common to the area quickly convert forest to savanna. Once

cleared, trees have difficulty reclaiming the land because of low organic matter and high clay content of soils (Barbosa & Fearnside 2005; Funk*et al.* 2007).

One might consider forest islands to be disturbed forest patches, given the high edge to interior ratio. The forest islands appear much more similar to the north-western portion of Pi-pi-chu forest than the riverine sections, although there is no floral data to support this. This may explain the very high abundance of *Ischnoptera galibi* on forest islands, moderate abundance at forest mainlands, and complete absence from the primary forests at sites LFMHT and LFMHDT. *I. galibi* may be a species characteristic of disturbed forests. Other areas in Guyana where *Ischnoptera galibi* has been collected have also been disturbed forests (Evangelista*et al.* 2014). Extensive sampling in the near-pristine rainforests at Iwokrama River Lodge did not yield any *I.galibi* individuals (although *I.atrata/hercules* were quite abundant) (Evangelista*et al.* in press, 2016). *I. galibi* has been reported from Iwokrama but only in the leaf litter at the edges of the Iwokrama saw mill (Evangelista*et al.* in press, 2016).

Conclusions

We find assemblages of leaf litter cockroach species to be influenced by three factors: (1) savanna-forest habitat type, (2) geographic distance among patches and (3) habitat specific dispersal limitation. However, we may not be able to make generalizations about such interactions between landscape and the resident fauna for all organisms in that community (even other leaf litter insects) as there was variation in the nature of the interactions, even among species of the same genus. We found strong results for only select species. Despite finding an impact of savanna on species assemblages

there was strong overlap in the composition of leaf-litter cockroach communities in small, isolated forest patches (i.e. forest islands) and those found in contiguous forests. We accept a more complex view of the landscape where individual forested site is best categorized through a quantification of isolation due to savanna and open water (i.e. rivers and ponds) and not simply as forest "islands" or "mainlands". Finally, flood-zones were not found to be an important predictor of differences among leaf-litter cockroach assemblage compositions.

Works Cited

Barbosa, R.I. & Fearnside, P.M. (2005) Above-ground biomass and the fate of carbon after burning in the savannas of Roraima, Brazilian Amazonia. *Forest Ecology and Management*, **216**, 295-316.

Bell, W.J., Roth, L.M. & Nalepa, C. (2007) *Cockroaches: Ecology, Behavior and Natural History*. Johns Hopkins University Press, Baltimore.

Cole, C.J., Townsend, C.R., Reynolds, R.P., MacCulloch, R.D. & Lathrop, A. (2013) Amphibians and reptiles of Guyana, South America: illustrated keys, annotated species accounts, and a biogeographic synopsis. *Proceedings of the Biological Society of Washington*, **125**, 317-578.

DigitalGlobe (2015) Map Data. In. Google

Eden, M.J. (1964) The savanna ecosystem - Northern Rupununi, British Guiana. *McGill University Savanna Research Series*, **1**

Eden, M.J. (1970) Savanna vegetation in the northern Rupununi, Guyana. *Journal Of Tropical Geography* **30**, 17-28.

Evangelista, D.A., Bourne, G. & Ware, J.L. (2014) Species richness estimates of Blattodea s.s. (Insecta: Dictyoptera) from northern Guyana vary depending upon methods of species delimitation. *Systematic Entomology*, **39**, 150-158.

Evangelista, D.A., Sylvain, E., Mendoza, C.M. & Guzman, K. (in press, 2016) New and enigmatic cockroaches (Insecta: Dictyoptera: Blattodea) of Guyana. *The Journal of Natural History*,

Evangelista, D.A., Chan, K., Kaplan, K.L., Wilson, M.M. & Ware, J.L. (2015) The Blattodea s.s. (Insecta, Dictyoptera) of the Guiana Shield. *ZooKeys*, **475**, 37-87.

Funk, V.A., Zermoglio, M.F. & Nasir, N. (1999) Testing the use of specimen collection data and GIS in biodiversity exploration and conservation decision making in Guyana. *Biodiversity and Conservation*, **8**, 727–751.

Funk, V.A., Berry, P., Kelloff, C. & Alexander, S.N. (2007) Checklist of the Plants of the Guiana Shield (VENEZUELA: Amazonas, Bolivar, Delta Amacuro; GUYANA, SURINAM, FRENCH GUIANA). *Contributions from the United States National Herbarium*, **55**, 1-584.

Guthrie, D.M. & Tindall, A.R. (1968) *The Biology of the Cockroach*. Edward Arnold Publishers Ltd., Great Britain.

Mullins, D.E. (2015) Physiology of environmental adaptations and resource acquisition in cockroaches. *Annu Rev Entomol*, **60**, 473-92.

Myers, J.G. (1936) Savannah and Forest Vegetation of the Interior Guiana Plateau. *Journal of Ecology*, **24**, 162-184.

Naka, L.N. (2011) Avian distribution patterns in the Guiana Shield: implications for the delimitation of Amazonian areas of endemism. *Journal of Biogeography*, **38**, 681-696.

Rull, V. (1992) Successional Patterns of the Gran Sabana (Southeastern Venezuela) Vegetation During the Last 5000 Years, and Its Responses to Climatic Fluctuations and Fire. *Journal of Biogeography*, **19**, 329-338.

Sethian, J.A. (1999a) Fast marching methods. *SIAM Review*, **41**, 199-235.

Sethian, J.A. (1999b) *Level set methods and fast marching methods*. Cambridge University Press, UK.

Souza, L.S.d., Armbruster, J.W. & Werneke, D.C. (2012) The influence of the Rupununi portal on distribution of freshwater fish in the Rupununi district, Guyana. *Cybium*, **36**, 31-43.

Warren, B.H., Simberloff, D., Ricklefs, R.E., Aguilee, R., Condamine, F.L., Gravel, D., Morlon, H., Mouquet, N., Rosindell, J., Casquet, J., Conti, E., Cornuault, J., Fernandez-Palacios, J.M., Hengl, T., Norder, S.J., Rijsdijk, K.F., Sanmartin, I., Strasberg, D., Triantis, K.A., Valente, L.M., Whittaker, R.J., Gillespie, R.G., Emerson, B.C. & Thebaud, C. (2015) Islands as model systems in ecology and evolution: prospects fifty years after MacArthur-Wilson. *Ecol Lett*, **18**, 200-17.

Watkins, G. (2010) *Rupununi Rediscovering a Lost World*. Earth in Focus Editions.

Wolda, H. (1983) Diversity, diversity indices and tropical cockroaches. *Oecologia*, **58**, 290-298.

Wolfram Research, I. (2012) *Mathematica Edition: Version 9.1*. Wolfram Research Inc.

CHAPTER 4

HOW DOES DISPERSAL ABILITY AFFECT THE SPATIAL ORGANIZATION OF GEOGRAPHIC RANGES?

Abstract

Dispersal ability is important to individual organisms, but its effect on some ecological patterns is contentious. If dispersal ability is a determining factor in how ranges evolve this should be evident in the spread of ranges among closely related taxa. In the event that there is such a relationship, the nature of this relationship could give insight into the processes governing range evolution. Three hypotheses about the effect of dispersal on colonization, gene flow, and habitat selection give two predictions about if strongly or weakly dispersing taxa will be more clustered together in space. We examine this here with two insect taxa (Blaberoidea and Anisoptera) in the Guiana Shield, a region where large waterways have been shown to be important boundaries for biogeographic zones. We analyze occurrence data within genera to discern the degree of spatial clustering of ranges of closely related species. We examine the relationship between the degree of range clustering with morphological features indicative of dispersal ability. In all cases we find direct relationships between dispersal ability and spatial clustering of taxon ranges. However, only subsets of these are found to be statistically significant. Despite mixed significance, we argue that the data are compelling to support the hypothesis that stronger dispersing taxa will be more clustered together in space. This could possibly be explained by a better ability to select appropriate habitats or higher rates of allopatric speciation.

Introduction

An organism's geographic range is an important biological trait (Brown *et al.* 1996) and can be studied in contexts that span disciplines. There are three components to a geographic range: size, shape, and position. The size of a range is important in considering niche breadth (Calosi *et al.* 2010; Morin & Lechowicz 2013), macro-ecological patterns (Naka 2011), population biology (Schnell *et al.* 2013), and heritability of species level traits (Borregaard *et al.* 2012; Brown *et al.* 1996; Hunt *et al.* 2005; Webb & Gaston 2003). The shape of a range is determined by geographic features (Naka 2011) and niche specifications (Calosi*et al.* 2010), and is thus important to questions in ecology and biogeography. The position of a range is usually not studied explicitly, but is an implicit part of any discussion in community ecology, biodiversity or systematics. The aggregated effect of these three components of geographical range results in biodiversity patterns in space.

The relevance of dispersal ability to range features is somewhat contentious, with some studies showing relationships (Brown*et al.* 1996; Laube *et al.* 2013; Paul *et al.* 2009; Rundle *et al.* 2007a) and others not (Calosi *et al.* 2010; Lester *et al.* 2007). There is a strong conceptual impetus for predicting a relationship between range features and dispersal ability, yet the empirical evidence is not as one sided. Our major goal is to test if there is a relationship between dispersal ability and the extent to which taxon ranges are clustered together in space. This is a novel approach to the dispersal-range relationship, as most other studies have focused primarily on range size.

Factors affecting the spatial clustering of ranges

What biological processes and patterns will cause ranges of closely related taxa to be clumped as opposed to spread apart? We can narrow the culprits down to: speciation dynamics, time since evolutionary divergence, extent of niche conservatism, spatial heterogeneity, and rate at which ranges can move (i.e. dispersal ability). Many of these are interdependent and have their own important effect on ranges. First, mode of speciation is important for the speed and frequency at which ranges move apart directly after divergence. At least in the very early stages of speciation, sympatric speciation does not necessitate that ranges will move away from one another while, by definition, allopatric speciation does. Second, it is known that there is a strong phylogenetic correlation among range positions of closely related animals (Nabout *et al*. 2010). Thus, the time since the most recent common ancestor can determine how diverged the range positions have become. This is closely related to the effect of niche conservatism on ranges. If niches are fully conserved through a speciation event then the ability of the sister taxa to move away from each other simply depends on the rate at which their habitats drift in position if they are separated at all (Mouillot & Gaston 2009). If niches are less conserved they are able to move through space accordingly. Through this, the heterogeneity of the ecosystem also plays an important role as these different levels and types of heterogeneity have different permeability and suitability for certain taxa (MacArther & Wilson 1967).

Dispersal and geographic ranges

We define a species' range as all geographic locations where its populations currently exist (modified from Brown et al. 1996). However, range positions can move over time because some populations go extinct, and both individuals and populations move through space (e.g. through dispersal). The temporal heterogeneity of geographic ranges

ties in directly to dispersal. Despite this, evidence for the relationship is not straightforward.

Dispersal ability has been show to positively correlate to range size in some cases (Böhning-Gaese *et al.* 2006; Paul *et al.* 2009; Rundle *et al.* 2007a) but not in others (Calosi *et al.* 2010; Lester *et al.* 2007). A general consensus of these studies is that the relationship may be dependent on the organismal and environmental context.

Lester*et al.* (2007) proposes a number of hypotheses about the relationship of dispersal ability to geographic ranges. Two of these are relevant to our question and we will refer to these as the "spread by colonization" hypothesis (figure 4 – 1A) and the "spread by speciation" hypothesis (figure 4 – 1B). We propose a separate hypothesis, which makes the same prediction as the "spread by speciation" hypothesis but under a different mechanism. We call this the "cluster by habitat" hypothesis (figure 4 – 1C).

Under the "spread by colonization" hypothesis, strong dispersing taxa can more easily colonize new regions (Gillespie *et al.* 2012) and thus they will have more rarified distributions. Here, large geographic boundaries (e.g. rivers, mountains) are thought to be limiting to the movement of poorly dispersing species while only smaller geographic boundaries (e.g. creeks, flooded lowlands) will be surmountable to them. On the rare occasions when poorly dispersing animals are brought across large boundaries, their lineage will be limited to the new range delimited by the large boundary. In this way, we would find that weakly dispersing higher taxa will tend to have the ranges of their constituent species more clustered in space (figure 4 – 1 A).

Under the “spread by speciation hypothesis”, allopatric speciation rates are higher for taxa that are poor dispersers. Here, we are ignoring the effect of dispersal ability on colonization but specifically considering dispersal as an important factor in determining speciation rates (via maintaining gene flow) (Gillespie *et al.* 2012). If each allopatric speciation event has some probability of increasing the spread of ranges in the taxon then the clade with a higher rate of allopatric speciation will tend to be less clustered in space (figure 4 – 1 B).

Under the “cluster by habitat” hypothesis we once again consider large geographic boundaries to be limiting for weak dispersers. However, we now ignore the effect of dispersal on the initial colonization and speciation but specifically consider the probability of a species to select its habitat. When there is differential habitat suitability, stronger dispersers will be more able to find and colonize their most suitable habitat. This would result in them being more clustered in space (figure 4 – 1 C) if their niches are similar, which is most likely the case for closely related taxa (Wiens *et al.* 2010; Wiens & Graham 2005). One might suggest that if dispersal ability affects colonization in this context then it should also affect the initial colonization rates preceding and leading up to speciation (i.e. if the “cluster by habitat” hypothesis is true then so should be the “spread by colonization” hypothesis). However, the dynamics in the two cases are different. A species range will always be contact with some barrier (biotic or abiotic) and thus the initial colonization leading to speciation is highly likely to happen, even in species that do not disperse actively. In contrast, the second colonization event of a specific habitat after speciation is highly dependent on the specific spatial heterogeneity of the area, so will more often require strong active dispersal ability to make colonization probable. In this study the

"spread by speciation" hypothesis and the "cluster by habitat" hypothesis are not differentiable but provide alternative explanations for the same biological patterns.

Study system: Blaberoidea and Anisoptera in the Guiana Shield

The technical boundaries of the Guiana Shield are defined by ancient (ca. 2.5 billion years old) geological features (Hammond 2005) but they also reflect contemporary biogeographical patterns. Alfred Russell Wallace was the first to identify Guiana as a distinct biogeographical province (Wallace 1852) and, although his conclusions were based on very little information, recent studies have shown agreement with his predictions (Naka 2011). As a biogeographical province, the shield has many endemic fauna (Cole *et al.* 2013; Funk *et al.* 2007; Naka 2011) and is one of the most bio-diverse regions on earth (Ceballos & Ehrlich 2006; Orme *et al.* 2005). It is also a region that is a high priority for conservation (Lopez-Osorio & Miranda-Esquivel 2010).

According to multiple studies, large rivers define faunal zones in the Guianas (Da Silva & Oren 1996; Naka 2011); likely as a result of them being an impediment to dispersal. Given that the same barriers (e.g. the Amazon River, Rio Branco, Rio Negro) are known to be limiting to dispersal for animals with very different dispersal abilities (i.e. birds and primates), the specific relationship of how active dispersal ability interacts with barrier size in determining ranges has not been quantified. Although it seems that major geographic boundaries must limit many species distributions, the ranges of many species span these boundaries (Evangelista *et al.* 2015; Naka 2011). So, it is not unreasonable to suggest that dispersal ability is important in determining spatial distribution patterns.

Blaberoidea: Although dispersal ability is difficult to quantify directly, we can say generally that cockroaches are poor dispersers if we equate this to flight ability (Bell*et al.* 2007; Guthrie & Tindall 1968). The modification of forewings into so-called "tegmina" (a leathery membrane used for protection) represents an evolutionary trade-off, sacrificing flight ability for added protection of the abdomen and hind wings. The value of flight to many cockroaches may also be inferred by the fact that wings are repeatedly lost or severely reduced in many distantly related taxa (e.g. *Anisopygia*, *Hormetica, Colapteroblatta, Thanatophyllum).* Furthermore, many species of cockroach may have a reduced opportunity for dispersal in their life cycle, as adults of many species are rare while juveniles are very common (Evangelista *et al.* 2014; Fisk 1983).

Anisoptera: Dragonflies have very different active dispersal traits. Aquatic habitat distributions are likely to determine species ranges, as the vast majority of Anisopteran larva are aquatic. Furthermore, all dragonflies have some flight ability and all are aerial as adults. Other than this, their ability to disperse likely varies greatly. Flight strategy and wing morphology are quite variable among species. Some species have been observed doing mass intercontinental migrations while others have very limited ranges (Garrison*et al.* 2006).

Methods

Range data is partially taken from chapter 1 of this dissertation and the Checklist of Odonata of the Guiana Shield (2012). These were all analyzed in Mathematica 9.1. Obtaining data for some peripheral regions of the shield (i.e. Brazil and Venezuela) were difficult because the boundaries of the shield do not match with political boundaries.

These records were composed by combining presence records with inferences of expected presence based on presence in neighboring regions. Thus, the five regions analyzed are: Guayanan Venezuela (Amazonas, Bolivar and Delta Amacuro), Guyana, Suriname, French Guiana and Guianan Brazil (north eastern Amazonas, northern Para and Amapa).

Analyzing spatial clustering of distributions

The method we used to quantify clustering relied on a comparison of actual number of occurrences of species in the five Guianan regions, with the number of occurrences expected under a model of random dispersal. This was done using a Monte-Carlo (MC) simulation utilizing a null Poisson distribution generated from a model that takes into consideration region size, and relative sampling effort/baseline richness. The process for doing this is described below.

First we calculated D_r, the regional species density for each region, as:

$$\frac{N_r}{\ln A_r}$$

where N_r is the sample richness of all taxa in region *r*, and A_r is the area of region *r* in km^2. We used log-area as opposed to raw area to buffer the effects of the large disparity in region size among the five regions. We then transformed these values into a scaling coefficient, *d*, by dividing each D_r by the maximum D_r. We then calculated O_r, the expected abundance of species occurrences per regions, as:

$$d * \frac{n}{R}$$

where *n* is the total number of occurrences for the taxon, *R* is the total number of regions (i.e. five). Each value of O_r represents a null expectation of species occurrences for

a region. It is based on the total number of species in that region, the region's log-area, and the number of species occurrences per region. We therefore treat O_r as the mean of a Poisson distribution, from which we randomly draw from in a Monte-Carlo (MC) simulation (100,000 trials). In cases where O_r equals 0, we treat it as .00001 to satisfy the criteria that the mean of a Poisson distribution be greater than 0. We then compared the actual richness of a taxon (genus) in a region to this distribution to receive the probability of getting that richness under random conditions given the parameters of the model. In this case, probability is a proxy for spatial clustering of ranges within a taxon, where a high value (closer to one) indicates a very high probability that the actual distribution of species richness isn't significantly different from randomness and a low value (closer to 0) indicates a higher probability that species richness is clustered. We iterated this across all genera in each subject taxa (Anisoptera and Blaberoidea) for each of the five regions.

The resulting matrix has a length equal to the number of genera and a width equal to the number of regions (i.e. $R = 5$) with a probability in each position. No single value in each row would suffice as a metric for spatial clustering as it is only a measure of probability for that taxon in that individual region. Therefore, we used the first principal component (PC) of this matrix to represent the extent of spatial clustering. We found that the first PC represented 63% and 56% of the total variation in the Anisoptera and Blaberoidea data respectively and was highly, negatively correlated (A: m = -.42, R^2 = .98; B: m = -.42, R^2 = .99) with the mean SCV for each genus (see figure 4-2).

Quantifying dispersal

Although these animals disperse in a variety of ways, for sake of simplicity and practicality, we will focus on active dispersal by flight as inferred from a morphological proxy. There is empirical evidence (De Bie *et al.* 2012) and precedent (Rundle *et al.* 2007a) for using body size and wing size as an indirect quantification of dispersal ability. Body length and wing length are frequently recorded in species descriptions and identification tools and are thus easily available for most of the taxa analyzed.

We used mean body length and wing length of females. If information on females was not present we used the male measurements. We Log transformed body lengths but not wing size because many cockroach species lack wings in both or one of the sexes. We also recorded wing type of the cockroaches based on their presumed flight ability: non-flight (apterous or brachypterous), full flight (macropterous), and flight adapted (macropterous with apical expansion of hindwing).

Comparing among taxa

We made correlations between taxon PC and morphometric values associated with dispersal ability (e.g. Log-body length, wing length, and categorical wing state). We used a linear regression to test the relationships between the continuous dispersal metrics and range spread PC. We used a general linear model to test the relationship between categorical dispersal metrics and range spread PC.

Results

We analyzed the ranges of 226 species in 66 genera of Blaberoidea and 327 species in 71 genera of Anisoptera. There were 465 and 614 total occurrences for the respective

taxa in the five regions of the Guiana shield. The distribution of the richnesses of respective genera is shown in figure 4-3.

The analysis of range spread indicated a high degree of spatial bias in the richness of certain genera. These are difficult to interpret biologically in an organismal specific context and such a discussion would be beyond the scope of this paper. A summary of all the probabilities is shown in figure 4-4.

Body length and wing length data were collected for 66 genera of Blaberoidea and 71 genera of Anisoptera. Due to the highly diverged nature of cockroach wings, we separated taxa based on large morphological features in the wing that we could connect to flight ability. Upon comparing the three wing states (apterous/brachypterous, simple macropterous, macropterous + apical expansion of hind wing) we found a significant relationship to the range spread principal component (PC; Figure 4-5) that indicated that the ranges of taxa who were functionally deficient in flight were significantly less clustered in space ($p=.01$, $F = 4.6$). No categorical analysis was done using the Anisoptera data because we could not categorize their wing morphology in a way that would have benefited the analysis. However, both Anisoptera and Blaberoidea were included in the analysis examining the relationship between the continuous metrics of dispersal and range spread (Figure 4-6). Here we see that the trends trends are in agreement but with generally low statistical support for the relationships and a low effect size (see figure 4-6).

Discussion

When examining the relationship between fine scale active dispersal ability (e.g. continuous body length and wing length) and range clustering, there was little to no support for any dispersal-range relationship on a case by case basis. This would indicate that minor differences in dispersal ability do not have any effect on range patterns or that our recorded data have low power in predicting actual dispersal ability or range clustering. If there truly was no causal relationship between active dispersal ability and range clustering we would not expect to see the similar trend among results that we do, although this should be considered lightly as we are really only looking patterns within two taxa (Anisoptera and Blaberoidea). If we consistently saw the same relationship across multiple taxa then the pattern may be more meaningful.

However, we did have strong evidence for the dispersal-range relationship when comparing among cockroach taxa with vastly different dispersal schemes. Given that the loss of wings has occurred many times in the evolution of cockroaches (Bell *et al.* 2007) this allowed us to do such a comparison across a phylogenetically disparate array of taxa within Blaberoidea. Thus, when distilling our analysis down to the comparison of range spread with three simple categories of flight morphology (non-flight, flight "capable", and flight "adapted") the results clearly show that taxa not capable of flight have less spatially clustered distributions than flight capable (macropterous) or flight adapted (macropterous + apical expansion of hind wing) clades. This suggests that dispersal ability may indeed affect relative range positions among closely related taxa. These results are also interesting in that they refute the enticing logic of the "spread by colonization" hypothesis. We have no data to support whether the mechanism of the "spread by speciation" or "cluster by

habitat" hypothesis are actually predominating but these both currently appear to be valid hypotheses for further examination.

Considering all the available information, one may come to the conclusion that the relationship between dispersal and ranges is highly contextual. However, another possibility is that active dispersal ability and ranges may be overly generalized concepts and our inability to see relevant dispersal-range relationships is due to our inability to effectively define and quantify these biological processes and patterns. For one, passive dispersal could account for a large proportion of dispersal events even among active dispersers and thus quantifying one without the other would be ineffective. Also, the opportunity for dispersal in an organisms lifetime (Lester *et al.* 2007) or in an evolutionary context (Paul *et al.* 2009) combined with other dispersal ability may prove to be more determinant of species ranges. Finally, our analysis only captures certain aspects of range spread (co-occurrence and scale-specific proximity) but not others (smaller or larger scale proximity).

Another explanation of disagreement among studies and taxa or the inability to see signal through noise could be due to the antagonistic nature of the many complex factors involved in range evolution. Allopatric speciation does not necessarily cause ranges of the derived taxa to drift apart. If successive vicariance events split ancestral taxa (and thus ranges) into smaller pieces, increases in richness are occurring without a change in the relative range positions. It has also been suggested that dispersal ability is inconsequential to colonization rates over large evolutionary timescales, in particular when population size is very high (Lester *et al.* 2007). Furthermore, range overlap is likely to be high among closely related species with large ranges. This creates spatially biased distributions because

the position of their range is largely conserved over time. Yet, large range sizes are often the product of more evolutionary time (Böhning-Gaese *et al.* 2006; Webb & Gaston 2000) and older species have more opportunity for dispersal. Under the "spread by colonization" hypothesis, this decreases the clustering of ranges in space. Additionally, larger ranges are also more likely to include geographic boundaries, which means increasing rates of speciation (Lester *et al.* 2007).

Of course it is certainly possible that the results are the source of inherent biases or weaknesses of our data. The occurrence data suffer from poor spatial resolution, particularly for Blaberoidea (Evangelista et al 2014). If it is the case that true range sizes are smaller among a certain group, then poor spatial sampling could lead to erroneous conclusions being drawn. This is because large ranges overlap in more places in space and thus coarse spatial sampling does a better job of capturing true diversity. We could not find significant differences among the range sizes of our taxa.

Conclusion

We did find evidence for the relationship between clustering of range positions among closely related taxa and their dispersal ability. The specific relationship supports the hypothesis that decreased dispersal ability contributes to range spread through increased allopatric speciation rates and/or a decreased rate of habitat selection. Although we found no support for the idea that stronger dispersers are better colonizers of new regions it is not necessarily disproven, but our findings may simply mean that speciation rates and habitat selection are more important factors in determining patterns of range evolution in nature.

Works Cited

Alexander EE, Bassett Y, Charles E, De Dijn BPE, Forget P-M, Hammond DS, Hounter NC, Pons TL, Rijkers T, Rose SA, Springate ND (2005) Tropical Forests of the Guiana Shield: Ancient Forests in a Modern World. CABI Publishing, Cambridge, MA, 535 pp.

Bell WJ, Roth LM, Nalepa C (2007) Cockroaches: Ecology, Behavior and Natural History. Johns Hopkins University Press, Baltimore, pp.

Böhning-Gaese K, Caprano T, Ewijk Kv, Veith M (2006) Range Size: Disentangling Current Traits and Phylogenetic and Biogeographic Factors. Am Nat 167: 555-567

Borregaard MK, Gotelli NJ, Rahbek C (2012) Are range-size distributions consistent with species-level heritability? Evolution 66: 2216-2226. doi:10.1111/j.1558-5646.2012.01581.x

Brown JH, Stevens GC, Kaufman DM (1996) THE GEOGRAPHIC RANGE: Size, Shape, Boundaries, and Internal Structure. Annu Rev Ecol Syst 27: 597-623

Calosi P, Bilton DT, Spicer JI, Votier SC, Atfield A (2010) What determines a species' geographical range? Thermal biology and latitudinal range size relationships in European diving beetles (Coleoptera: Dytiscidae). J Anim Ecol 79: 194-204. doi:10.1111/j.1365-2656.2009.01611.x

Ceballos G, Ehrlich PR (2006) Global mammal distributions, biodiversity hotspots, and conservation. Proceedings of the National Academy of Sciences of the United States of America 103: 19374-19379. doi:10.1073/pnas.0609334103

Checklist of Odonata of the Guiana Shield. http://www.libellen.org/suriname/7checklist/Checklist_Guiana_Shield4.htm [accessed

Cole CJ, Townsend CR, Reynolds RP, MacCulloch RD, Lathrop A (2013) Amphibians and reptiles of Guyana, South America: illustrated keys, annotated species accounts, and a biogeographic synopsis. Proceedings of the Biological Society of Washington 125: 317-578. doi:10.2988/0006-324X-125.4.317

Da Silva JMC, Oren DC (1996) Application of parsimony analysis of endemicity in Amazonian biogeography: an example with primates. Biological Journal of the Linnean Society 59: 427-437

Evangelista DA, Bourne G, Ware JL (2014) Species richness estimates of Blattodea s.s. (Insecta: Dictyoptera) from northern Guyana vary depending upon methods of species delimitation. Systematic Entomology 39: 150-158. doi:10.1111/syen.12043

Evangelista DA, Chan K, Wilson MM, Ware JL (in prep 2014) A checklist of the Blattodea sensu stricto (Insecta:Dictyoptera) of the Guiana Shield and Trinidad. Zookeys:

Fisk F (1983) Abundance and diversity of arboreal Blattaria in moist tropical forests of the Panama Canal area and Costa Rica. Transactions of the American Entomological Society 108: 479-489

Funk VA, Berry P, Kelloff C, Alexander SN (2007) Checklist of the Plants of the Guiana Shield (VENEZUELA: Amazonas, Bolivar, Delta Amacuro; GUYANA, SURINAM, FRENCH GUIANA). Contributions from the United States National Herbarium 55: 1-584

Gillespie RG, Baldwin BG, Waters JM, Fraser CI, Nikula R, Roderick GK (2012) Long-distance dispersal: a framework for hypothesis testing. Trends Ecol Evol 27: 47-56. doi:10.1016/j.tree.2011.08.009

Guthrie DM, Tindall AR (1968) The Biology of the Cockroach. Edward Arnold Publishers Ltd., Great Britain, pp.

Hammond DS (2005) Tropical Forests of the Guiana Shield: Ancient forests in a modern world. In: Hammond DS (Ed), pp.

Hunt G, Roy K, Jablonski D (2005) Species-Level Heritability Reaffirmed: A Comment on "On the Heritability of Geographic Range Sizes". Am Nat 166: 129-135

Laube I, Graham CH, Böhning-Gaese K, McGill B (2013) Intra-generic species richness and dispersal ability interact to determine geographic ranges of birds. Global Ecology and Biogeography 22: 223-232. doi:10.1111/j.1466-8238.2012.00796.x

Lester SE, Ruttenberg BI, Gaines SD, Kinlan BP (2007) The relationship between dispersal ability and geographic range size. Ecol Lett 10: 745-758. doi:10.1111/j.1461-0248.2007.01070.x

Lopez-Osorio F, Miranda-Esquivel DR (2010) A phylogenetic approach to conserving Amazonian biodiversity. Conservation Biology 24: 1359-1366. doi:10.1111/j.1523-1739.2010.01482.x

MacArther RH, Wilson EO (1967) The theory of island biogeography. Princton University Press, pp.

Morin X, Lechowicz MJ (2013) Niche breadth and range area in North American trees. Ecography 36: 300-312. doi:10.1111/j.1600-0587.2012.07340.x

Mouillot D, Gaston K (2009) Spatial overlap enhances geographic range size conservatism. Ecography 32: 671-675. doi:10.1111/j.1600-0587.2009.05679.x

Nabout JC, Terribile LC, Bini LM, Diniz-Filho JAF (2010) Phylogenetic autocorrelation and heritability of geographic range size, shape and position of fiddler crabs, genusUca(Crustacea, Decapoda). Journal of Zoological Systematics and Evolutionary Research 48: 102-108. doi:10.1111/j.1439-0469.2009.00531.x

Naka LN (2011) Avian distribution patterns in the Guiana Shield: implications for the delimitation of Amazonian areas of endemism. Journal of Biogeography 38: 681-696. doi:10.1111/j.1365-2699.2010.02443.x

Orme CD, Davies RG, Burgess M, Eigenbrod F, Pickup N, Olson VA, Webster AJ, Ding TS, Rasmussen PC, Ridgely RS, Stattersfield AJ, Bennett PM, Blackburn TM, Gaston KJ, Owens IP (2005) Global hotspots of species richness are not congruent with endemism or threat. Nature 436: 1016-1019. doi:10.1038/nature03850

Paul JR, Morton C, Taylor CM, Tonsor SJ (2009) Evolutionary time for dispersal limits the extent but not the occupancy of species' potential ranges in the tropical plant genus Psychotria (Rubiaceae). Am Nat 173: 188-199. doi:10.1086/595762

Reed RN (2003) Interspecific patterns of species richness, geographic range size, and body size among New World venomous snakes. Ecography 26: 107-117

Rundle SD, Bilton DT, Abbott JC, Foggo A (2007) Range size in North American Enallagma damselflies correlates with wing size. Freshwater Biology 52: 471-477. doi:10.1111/j.1365-2427.2006.01712.x

Schnell JK, Harris GM, Pimm SL, Russell GJ (2013) Estimating extinction risk with metapopulation models of large-scale fragmentation. Conservation Biology 27: 520-530. doi:10.1111/cobi.12047

Terribile LC, Diniz-Filho JAF, Rodríguez MÁ, Rangel TFLVB (2009) Richness patterns, species distributions and the principle of extreme deconstruction. Global Ecology and Biogeography 18: 123-136. doi:10.1111/j.1466-8238.2008.00440.x

Wallace AR (1852) On the Monkeys of the Amazon. Alfred Russel Wallace Classic Writings 3:

Webb TJ, Gaston KJ (2000) Geographic range size and evolutionary age in birds. Proceedings: Biological Sciences 267: 1843-1850. doi:10.1098/rspb.2000.1219

Webb TJ, Gaston KJ (2003) On the Heritability of Geographic Range Sizes. Am Nat 161: 553-566

CONCLUSIONS

There are many process based questions one can ask about faunal/community assembly and these can be generalizable, to a degree, in other organisms and locations. Yet, gaining specific organismal knowledge is in itself desirable. With more knowledge about organisms we can ask new questions or test new phenomena that assists with our understanding of both those organisms and the processes that create and maintain life. That is the purpose of this dissertation. Below we continue with that aim, integrating information from all the above projects and applying a general perspective.

Cockroach data at a glance

In the country of Guyana, which this thesis pays special attention to, cockroaches are most diverse in the rainforests. The coastal rainforests of the north and the interior rainforests both have a high number of species when compared to the drier forests surrounding the savannas in the south. In chapter 2 we get a best estimate of the total number of species from CEIBA at 68 species. From a bootstrap estimate of total species richness on the data from the savanna-forest region of Karanambu (n= 1386, 10000 replicates) we see a total species richness of only 36 species (95% confidence between 33.2 and 38.3 species). When taken in context of each region's size (CEIBA: approx. 280 ha; Karanambu: approx.. 10,0000 ha) we see that there is a huge diversity among these habitats. Species distributions in many of the other forest types or on tepuis is unknown, and certainly a subject for future investigation.

The faunas of the Madewini region, Iwokrama forest, and Rupununi savannas all differ widely in their species composition. However, the dominant taxa were usually the

Ischnopterini genera *Xestoblatta* and *Ischnoptera*. These were very common in all three regions we investigated.

In Madewini (CEIBA biological station) *Xestoblatta berenbaumae* was the dominant species. The dominant *Ischnoptera* were *I. galibi* and *I. paramacca*. Neoblattellini cockroaches (*Amazonina, Cariblatta, Neoblattella* and others) were also very common here, more-so than at the other sites. The Neoblattellini of the Madewini include a leaf litter dwelling species (possibly, *Cariblatta*) and a species of *Neoblattella* (most likely undescribed) extremely common in bromeliads (see below). The Blattid species native to the area, *Eurycotis* sp., was also more common here than at other sites (observed but not caught at Karanambu). *Epilampra guianae* was the dominant *Epilampra* species, which was very rare or absent from the other two localities.

In Iwokrama the dominant species was *Ischnoptera atrata* or *Ischnoptera hercules* (it is difficult to differentiate these two because many specimens are broken). *I. galibi* was apparently isolated to the edges of disturbed forests in Iwokrama and not widely common. *Epilampra colorata* was abundant here but not in other areas. The most surprising resident of Iwokrama is *Lamproblatta ancistroides*, a member of the rare tri-generic family Lamproblattidae. *L. ancistroides* was quite common here. The dominant *Xestoblatta* was *Xestoblatta surinamensis*, which was not collected at the other two sites. Other noteworthy species from Iwokrama are two unidentified species, one a member of the Corydiidae, and the other a possible beetle mimic of unknown taxonomic affiliation.

The Rupununi savanna (Karanambu) is where we put in the greatest collection effort. *Ischnoptera galibi* was the most dominant species (*I. paramacca* was not found) and *I. atrata/I. hercules* were the second most abundant. The dominant *Xestoblatta* was *X.*

agautierae and the other two species of *Xestoblatta* mentioned above were absent from here. A savanna dwelling species of *Cariblatta* was common, as was *Dendroblatta litura, Anisopygia* and *Eublaberus*.

It is interesting to note that although *Xestoblatta* were among the most abundant species at each site, the three species of *Xestoblatta* did not coexist. This may suggest competitive exclusion among these species. In contrast, the most common *Ischnoptera* (*I. galibi, I. paramacca, I. hercules/atrata*) did co-occur.

Notes on ecology

We know little about our dominant genera beyond what we can infer from their morphology. By examining the gut contents of *Xestoblatta berenbaumae* and *Ischnoptera galibi* we can only discern that both species are omnivorous. Perhaps *I. galibi* prefers animal material, at least in the presence of *X. berenbaumae* as a competitor (Figure C – 1).

Water-holding bromeliads containing insect communities are very common in northern Guyana. From a sampling of 21 bromeliads we reconstructed the typical bromeliad insect community (Figure C – 2). In this community, cockroaches had very high abundance, with an undetermined *Neoblattella* species being the second most numerous occupant of the bromeliad tanks. The 3rd and 5th most abundant occupants were also cockroaches. Most of these are not identified to the species level because juveniles were the most abundant forms found.

Juvenile *Epilampra* (probably *Epilampra opaca*) were observed diving into the water in the bromeliad and clinging to submerged plant material. This was usually provoked by disturbance to the water. When the bromeliad water is left undisturbed the

juvenile *Epilampra* are seen to rise and wait closer to the top, only exposing their slightly elongated hind spiracles, before they emerge entirely.

Bromeliad ecosystems are usually studied for their aquatic component since these are confined to the bromeliad microhabitat, but the cockroaches reside in the terrestrial portion of the ecosystem. Although they are not as numerous as the larval Helodidae, they may be just as ecologically important, considering their much greater individual size. From dissections of the *Neoblattella* sp.'s gut material we think this species primarily grazes on plankton and algae of the bromeliad tank (Wilson & Evangelista, unpublished data). Very little solid plant or animal material was identified in their guts (Figure C – 1).

Notes on evolution

Our findings from Chapter 3 suggest that savannas may limit gene flow among populations of certain species. We preliminarily investigated this by looking at the spatial distribution of haplotype diversity (COII and COI) in *Ischnoptera galibi.* Haplotype networks (Figure C – 3 A & B) of both genes show that gene flow may be unhindered by savanna or flood zones within the Rupununi or even the huge geographic distances between the Rupununi and Madewini, Guyana. This could simply mean that *Ischnoptera galibi* is a strongly dispersing species. Different trends may be found in other taxa (e.g. *Ischnoptera* sp. cf. *rehni* and *Ischnoptera atrata/hercules* who showed the strongest correlations between isolation by savanna and abundance; Chapter 3). However, achieving necessary sample sizes with other taxa may be more difficult.

Summary

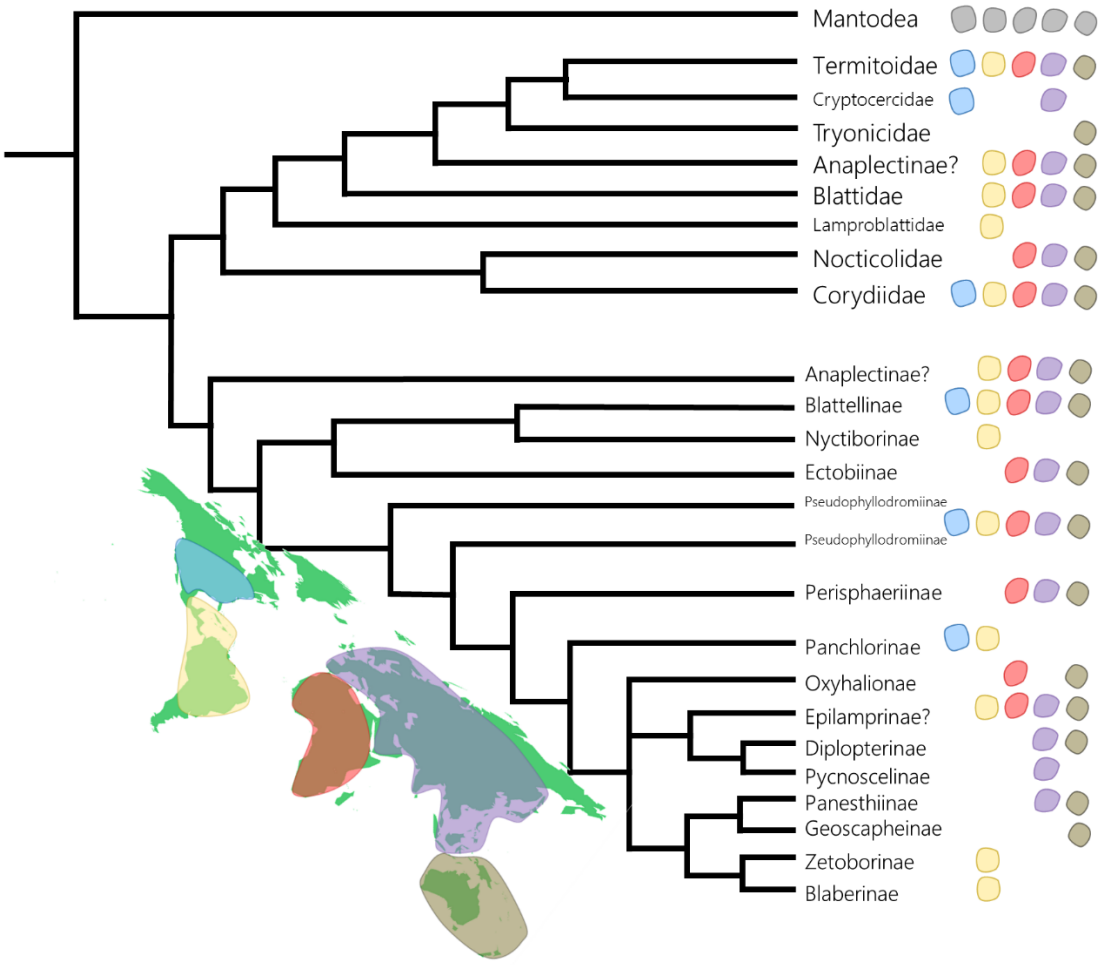
Chapter 1 of this dissertation lists 238 species of cockroaches (*sensu stricto*) known from the Guiana shield, 18 of which are new species records for Guyana, and 3 of

which are new species entirely. Chapter 2 showed how different approaches to species delimitation can have large (~25% discrepancy) effects on estimated species richness. In Chapter 3 we saw that savannas limit the distributions of cockroach taxa but patterns of flooding do not. Chapter 4 showed that flight ability may affect how geographic ranges evolve, with better flying taxa having ranges more clustered in space.

Although this dissertation contributes four chapters of new information on this fauna, a plethora of new studies can be done. Many specimens in our collection still await description. Additionally there are countless new species that have yet to be found at all. Roraima, Brazil and Venezuelan Guayana in particular are poorly studied regions. The phylogenetic relationships of nearly all of the taxa discussed in detail here (e.g. *Ischnoptera*, *Xestoblatta*, *Neoblattella*, *Epilampra*) are entirely unknown. Yet, investigating these require a broadening of the geographic scope to beyond the Guiana Shield. The ecology and ethology of these species has barely been approached, if at all. The role of cockroaches in bromeliad ecosystems is one potentially fruitful avenue of research but this is just one of many microhabitats inhabited by cockroaches. After nearly a century of research, the Guiana Shield persists as a land that is home to a largely mysterious fauna of cockroaches.

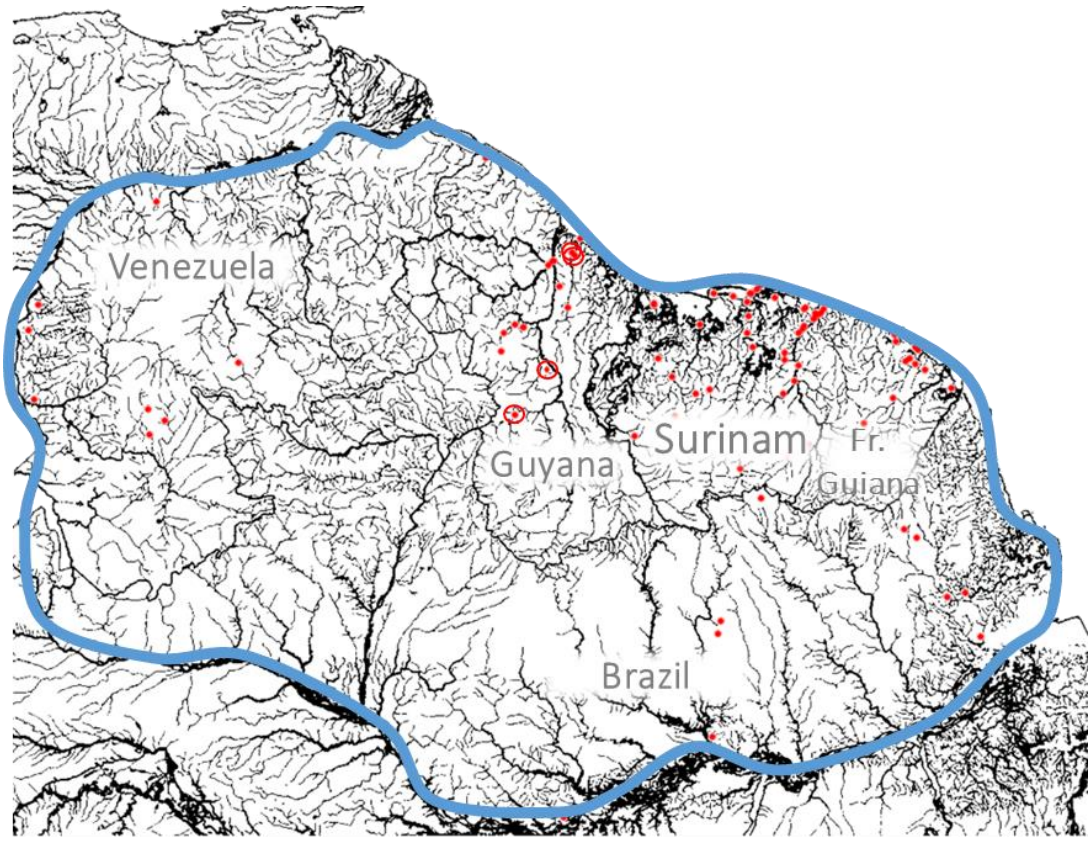
APPENDIX I
FIGURES

Figure I - 1 Phylogeography of Blattodea



Phylogeography of Blattodea. The phylogenetic topology Blattoidea (the top half of the tree) is taken from Djernaes et al. (2015). The phylogeny of Blaberoidea is a topology synthesized from Djernaes et al. (2015, 2012), Inward et al. (2007), Klass and Meier (2006), Maekawa et al. (2003) and McKittrick (1969). Question marks next to names indicate uncertain phylogenetic position from incongruence among studies. *Attaphilinae* and *Gyninae* are missing because of lack of phylogenetic treatment. Biogeographical data are taken from the Cockroach Species File database (Beccaloni, 2014).

Figure I - 2 The Guiana Shield

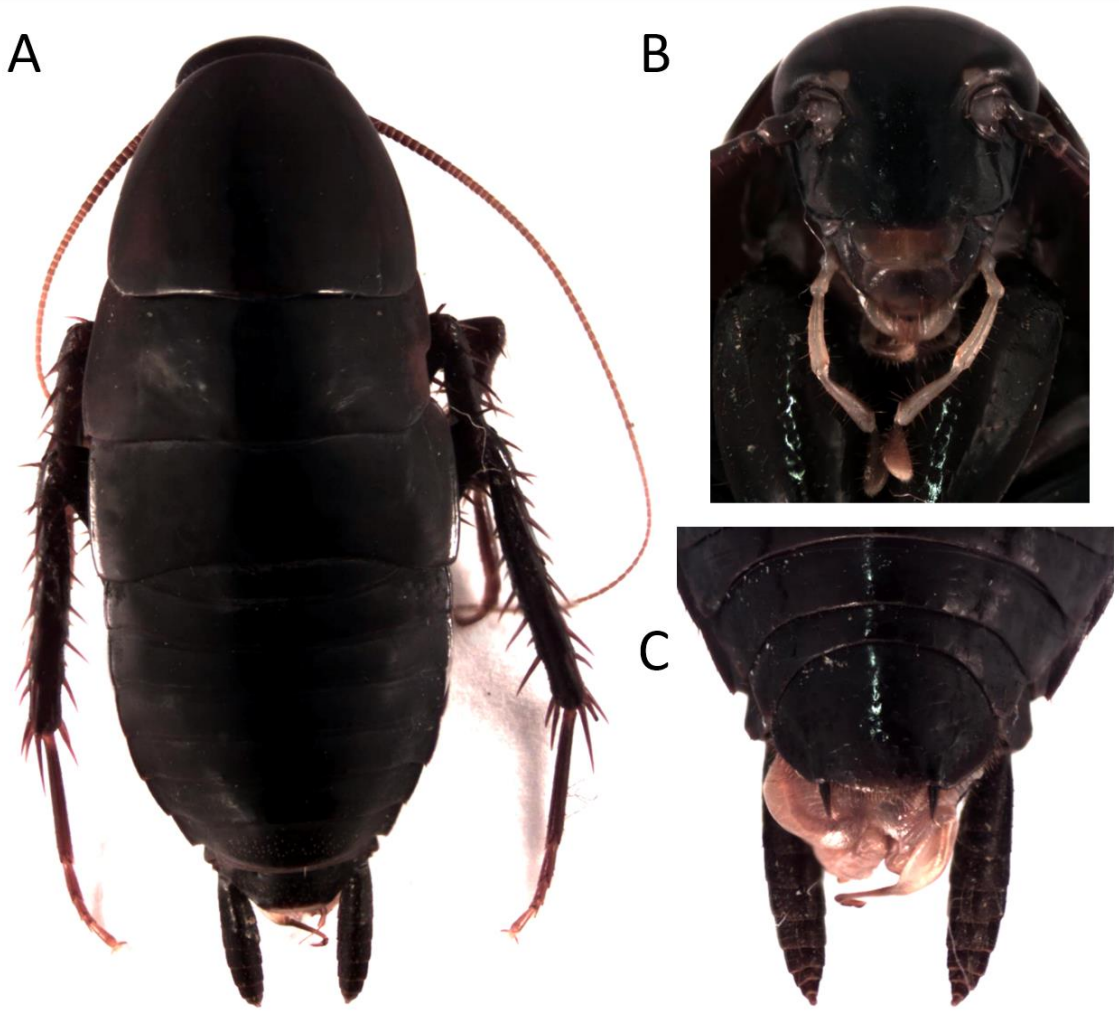


The Guiana Shield with cockroach collection localities. Waterways are emphasized. The blue perimeter represents the boundaries of the Guiana Shield following the Orinoco, Negro, and Amazon Rivers. Red dots are all the recorded areas from which non-termite cockroaches have been collected in the Guiana Shield. Four of the locations in Guyana (Madewini, Kamuni Creek, Iwokrama and Karanambu) are added from this thesis and highlighted with red circled (see chapter 1 for GPS localities).

Figure I - 3 Explanation of terms

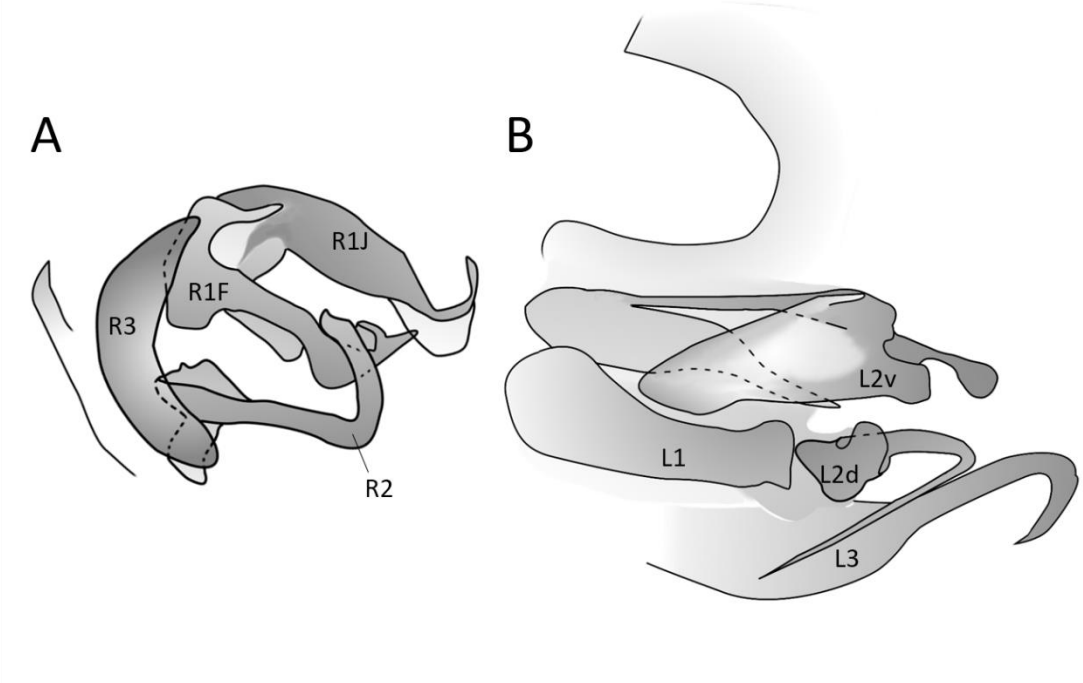
Checklist– a list of species occurring in a region. Synonymous with catalogue here. A checklist is the physical list naming all the species in a "fauna" (see below) but can also name the species in a community, or assemblage.
Cockroaches – all non-termite members of the order Blattodea sensu Inward et al. (2007). "Blattodea sensu stricto" or "Blattodea s.s." is used interchangeably with "cockroaches".
Fauna – all species occurring in a region. These are named in a "checklist"
Guyana – the country of the Guiana Shield once known as British Guiana or British Guyana. See FIGURE I-2.
Guiana – either the entire biogeographic region i.e. "Guiana Shield" or the country "French Guiana". See FIGURE I-2.
Guayana (as in Guayanan) – The portion of Venezuela falling within the boundary of the Guiana Shield (i.e. south of the Orinoco River).
Dominant taxon – the most abundant species in a species assemblage

Figure 1 - 1 *Lamproblatta ancistroides* Rehn



Lamproblatta ancistroides Rehn, 1930. Adult male. Voucher number: DEIWO0470. A Dorsal body. B Ventral head. C Ventral subgenital plate, terminal sternites and cerci.

Figure 1 - 2 *Lamproblatta ancistroides* Rehn



Lamproblatta ancistroides Rehn, 1930. Adult male genitalia. Voucher number: DEIWO0470. A Right genital phallomeres. We have differentiated two sections of R1 in accordance with Klass (1997). B Left genital phallomeres.

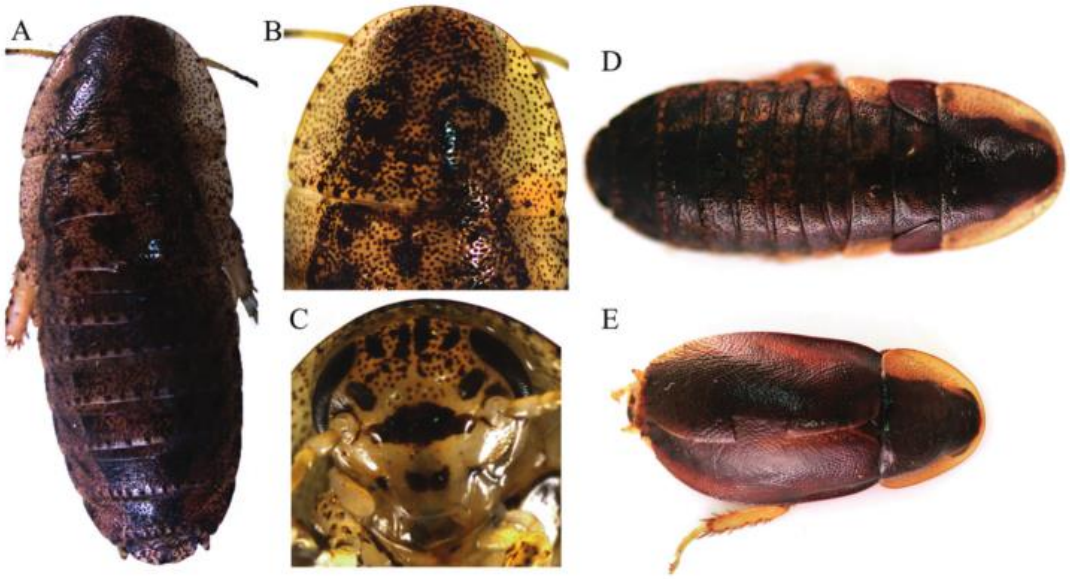
Figure 1 - 3 *Eublaberus marajaora* Rocha E Silva Albuquerque

Eublaberus marajaora Rocha E Silva Albuquerque 1972. Adult female. Voucher number: DEKBO1034. A Body, dorsal. The individual was collected with a damaged right tegmen.

Figure 1 - 4 *Neorhicnoda maronensis* (Hebard)

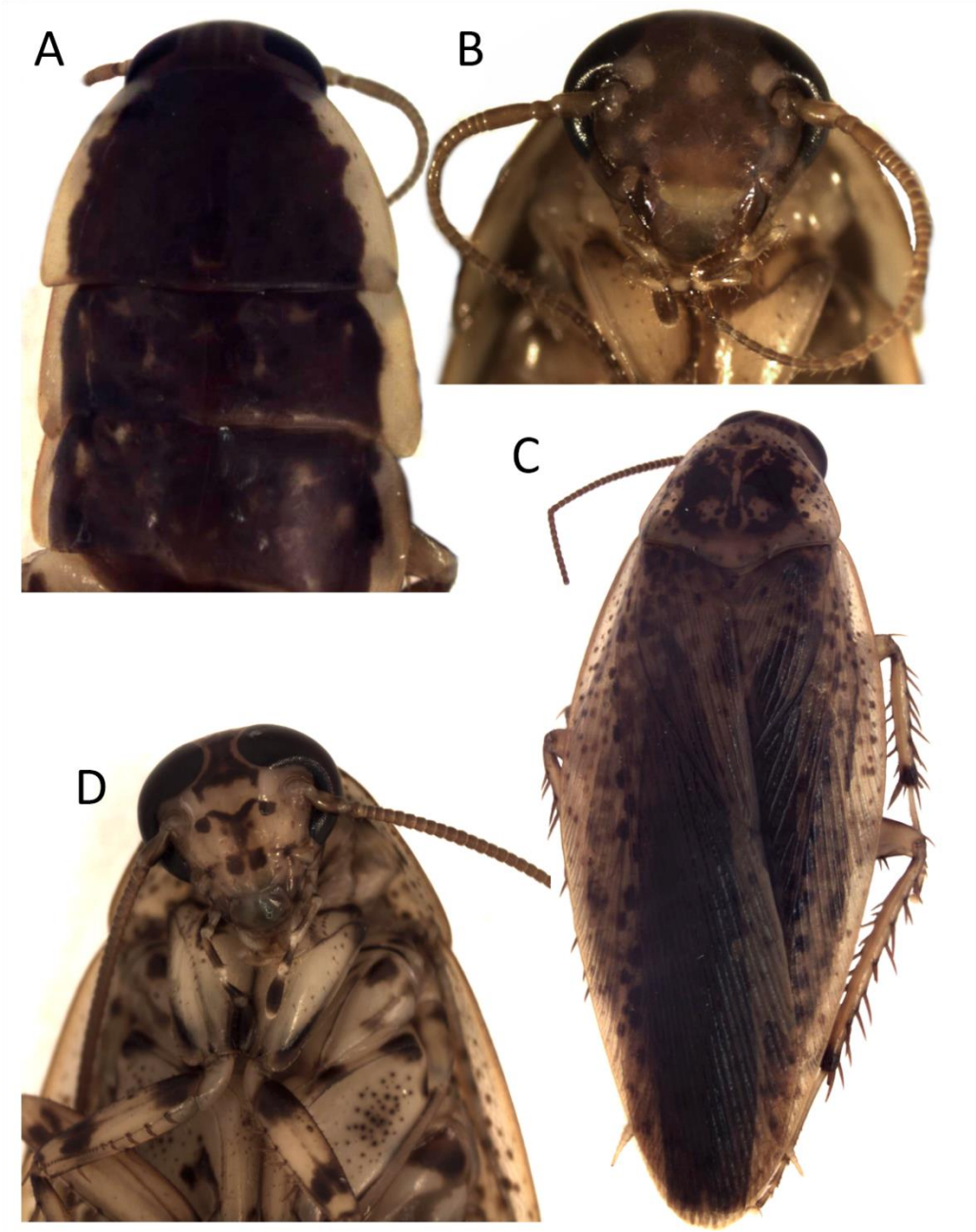
Neorhicnoda maronensis (Hebard, 1921) adult male (DECBA0615).

Figure 1 - 5 *Colapteroblatta surinama* (Saussure)



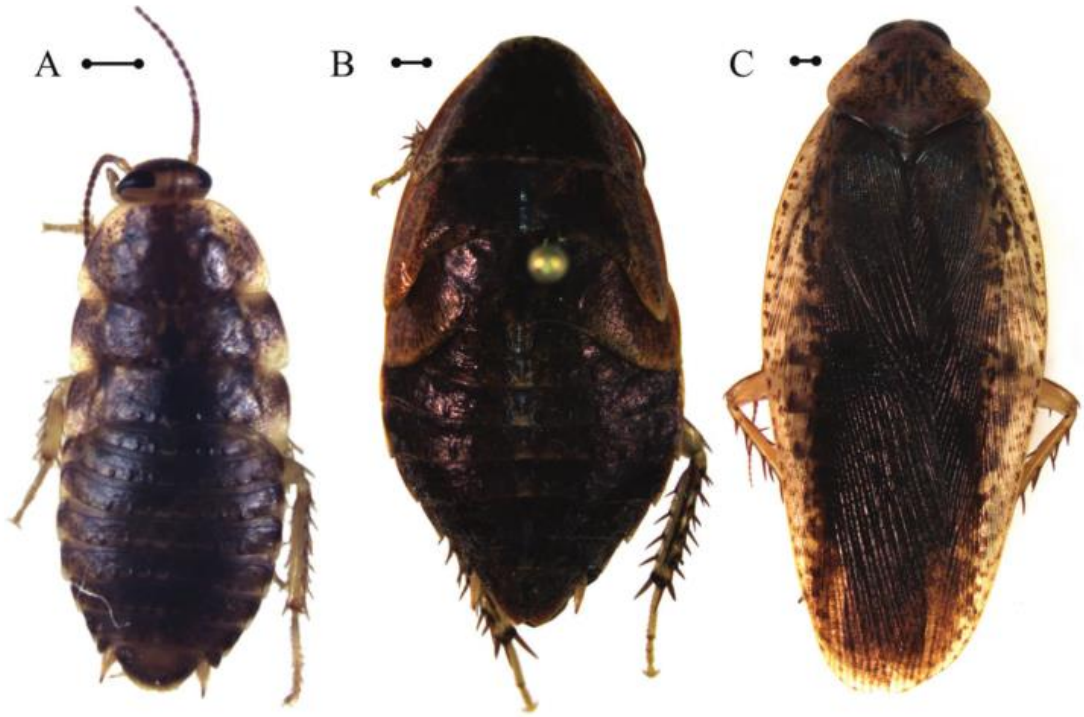
Colapteroblatta surinama (Saussure, 1868). A–C Juvenile (dorsal aspect, pronotum, ventral aspect of head). D Adult female, dorsal aspect. E Adult male, dorsal aspect. Photos not to scale.

Figure 1 - 6 *Epilampra colorata* Rocha E Silva Albuquerque and Gurney



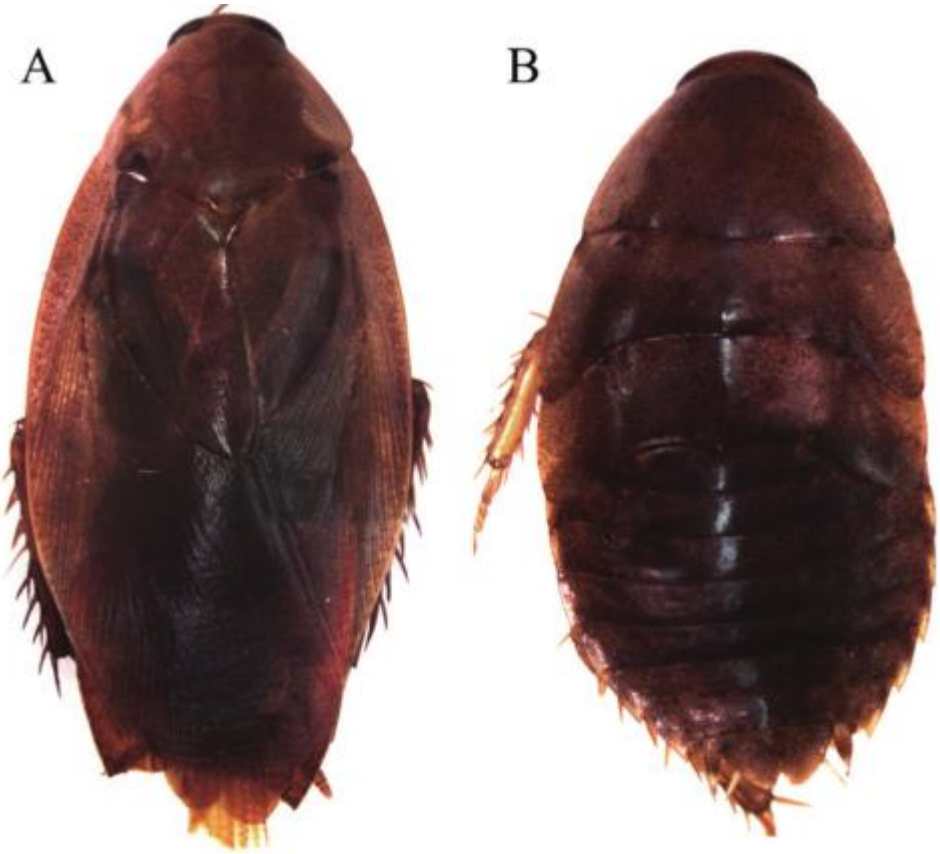
Epilampra colorata Rocha E Silva Albuquerque and Gurney 1962 A Juvenile thorax, dorsal. B Juvenile head, ventral. Voucher number: DECBA0501. C Adult male dorsal aspect of body. D Adult male head. Voucher number: DEIWO0190.

Figure 1 - 7 *Epilampra opaca* Walker.



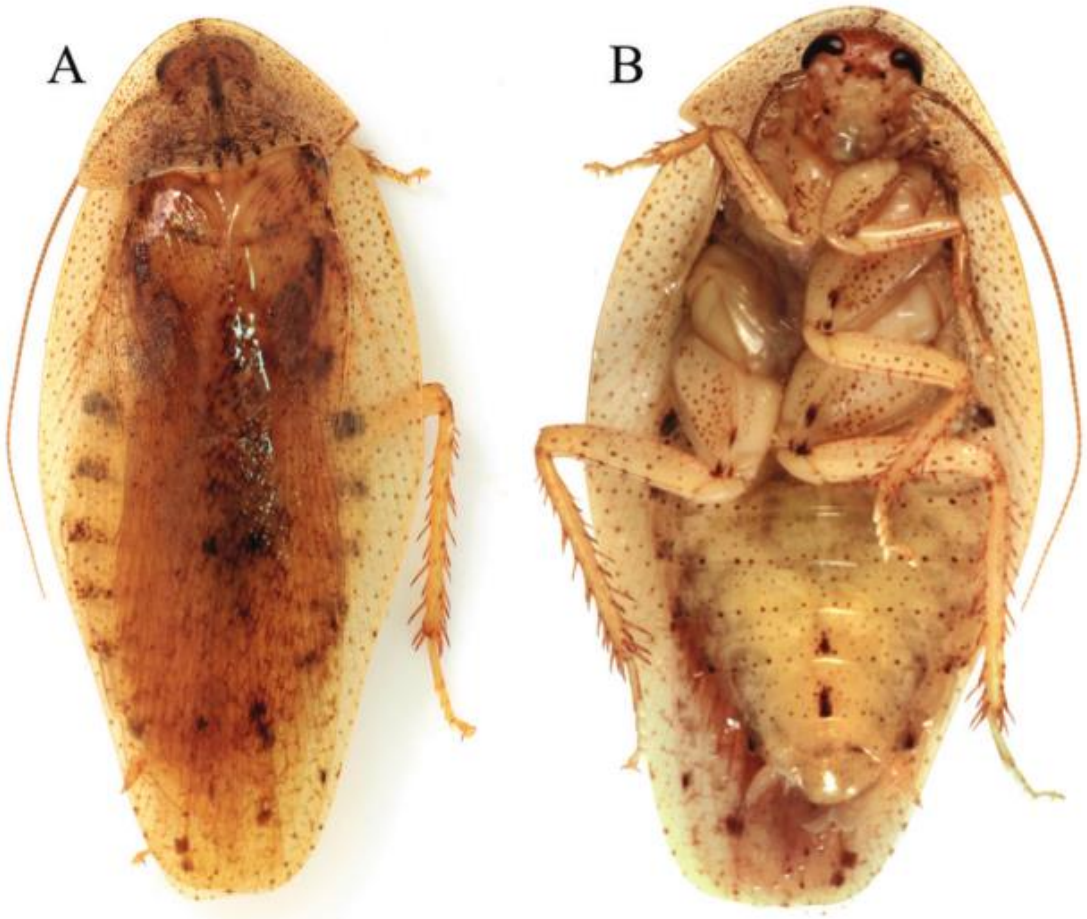
Epilampra opaca Walker, 1868. A Early juvenile instar (DEDSM0141). B Late juvenile instar (DECBA1706). C Adult (DECBA1845). Scale bars approximate 1 mm.

Figure 1 - 8 *Epilampra sodalis* Walker



Epilampra sodalis Walker, 1868. A Adult male dorsal view (DECBA0401) B Juvenile dorsal view (DECBA2163).

Figure 1 - 9 *Thanatophyllum akinetum* Grandcolas



Thanatophyllum akinetum Grandcolas, 1991 adult male (DECBA0611). A Dorsal view. B Ventral view.

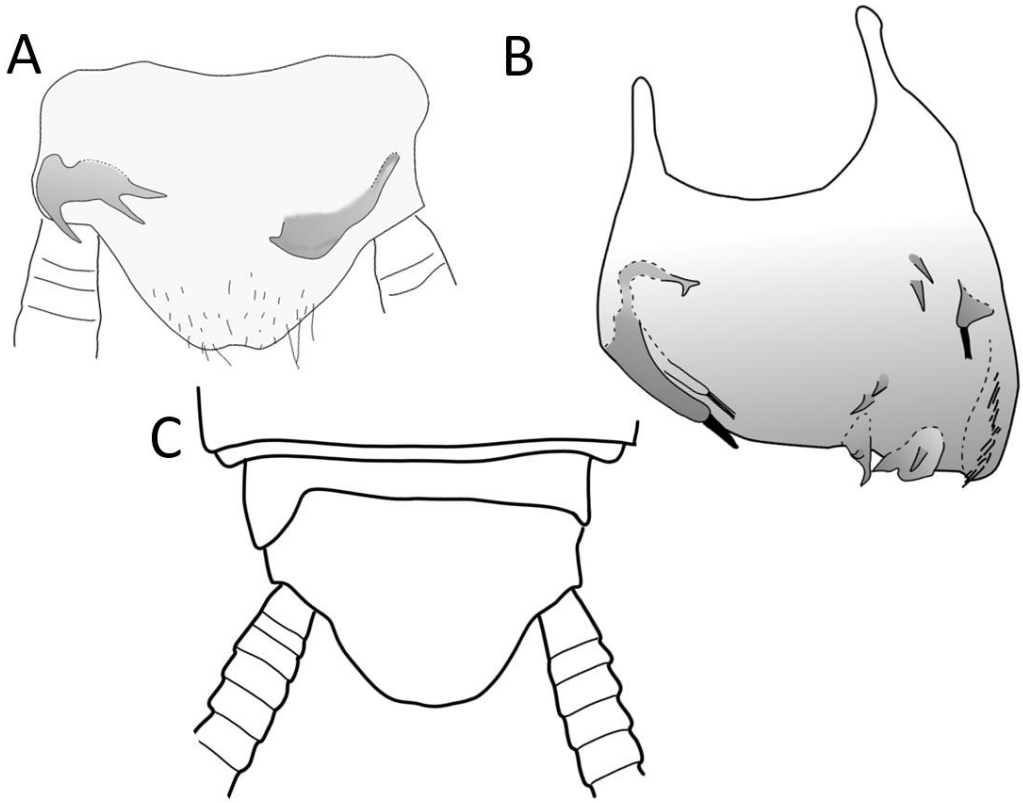
Figure 1 - 10 *Anaplecta parviceps* (Walker)

Anaplecta parviceps (Walker, 1868) adult male (DECBA1843).

Figure 1 - 11 *Anisopygia decora* Hebard

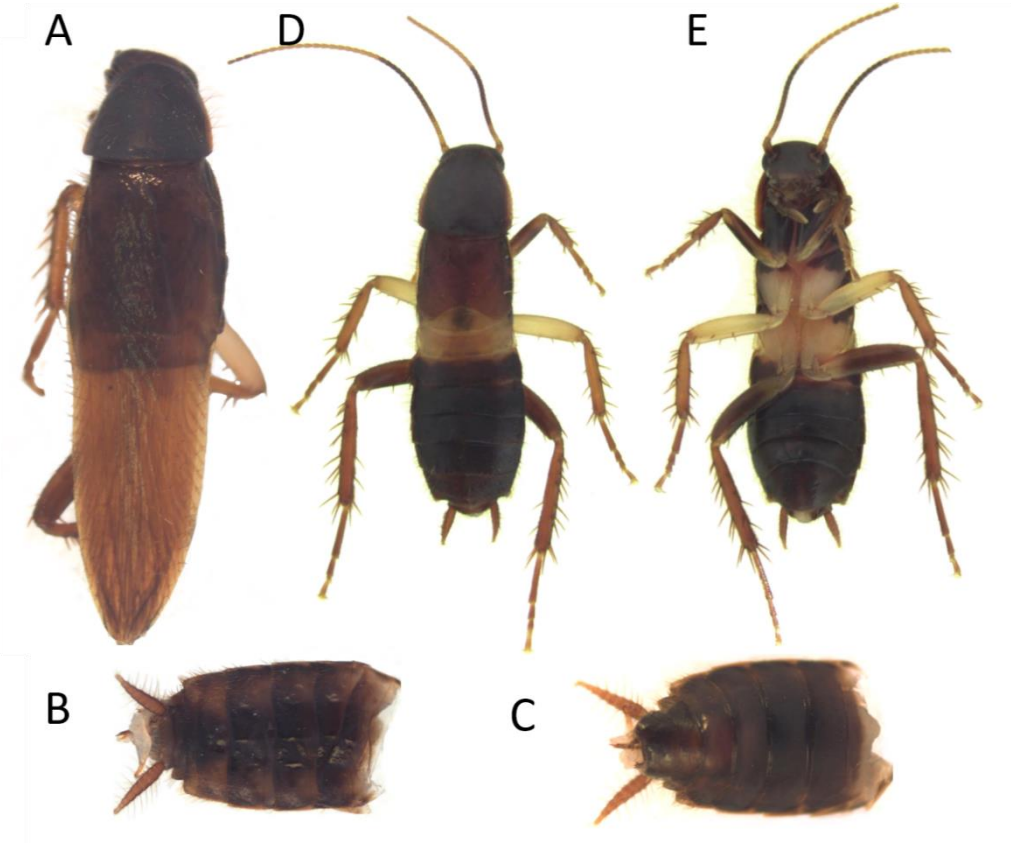
Anisopygia decora Hebard, 1926 adult female (DEKBO0504).

Figure 1 - 12 *Dasyblatta thaumasia* Hebard



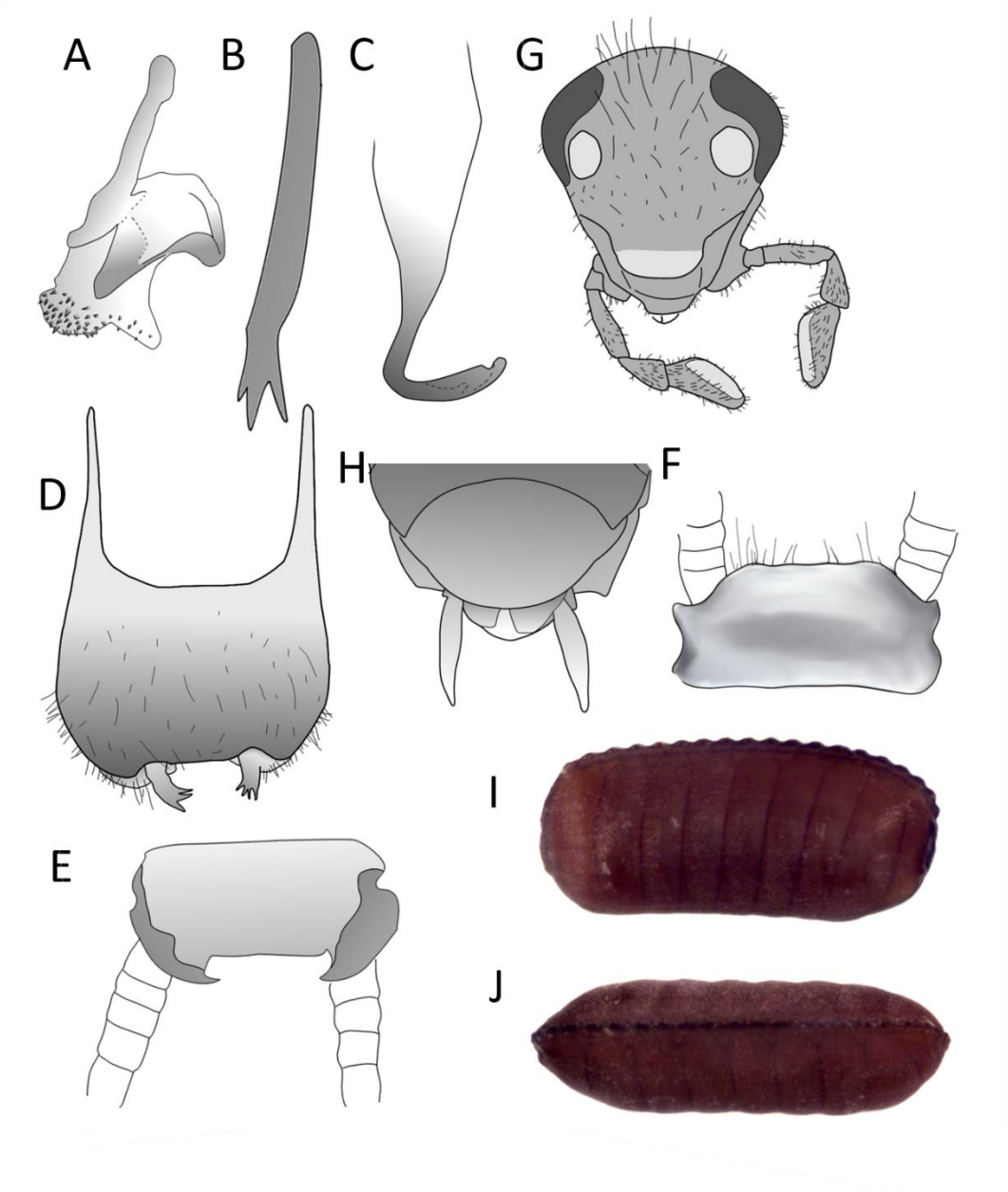
Dasyblatta thaumasia Hebard, 1921. Adult male. Voucher number: DEKBO0706. A Supra-anal plate, ventral aspect. B Terminal abdominal terga, dorsal aspect. C Terminal abdomen, dorsal aspect.

Figure 1 - 13 *Dasyblatta warei* Evangelista & Mendoza



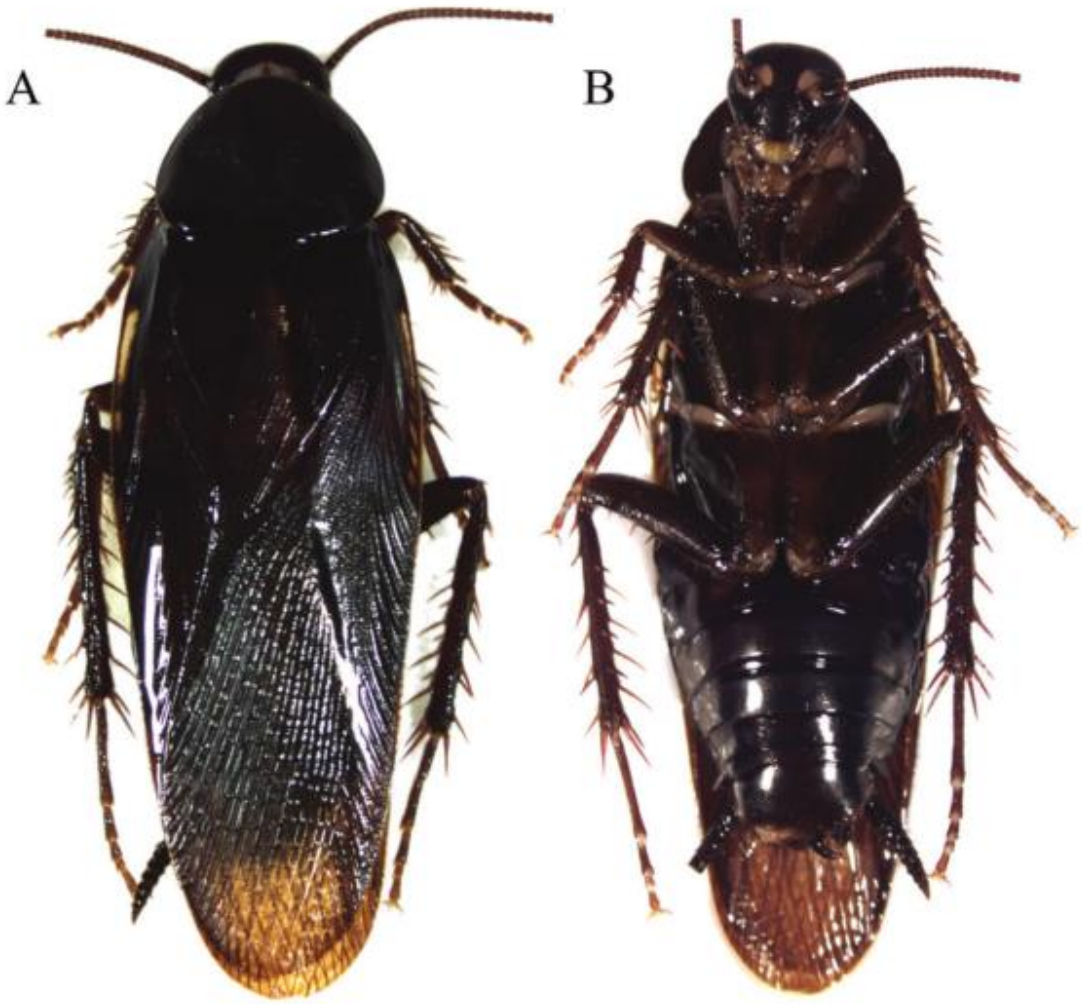
Dasyblatta warei Evangelista & Mendoza, 2016. A-C Adult male holotype. Voucher number: DECBA0907. A Dorsal body. B Dorsal abdomen. C Ventral abdomen. D-E Adult female allotype. Voucher number: DECBA1803. D Dorsal body E. Ventral body.

Figure 1 - 14 *Dasyblatta warei* Evangelista and Mendoza



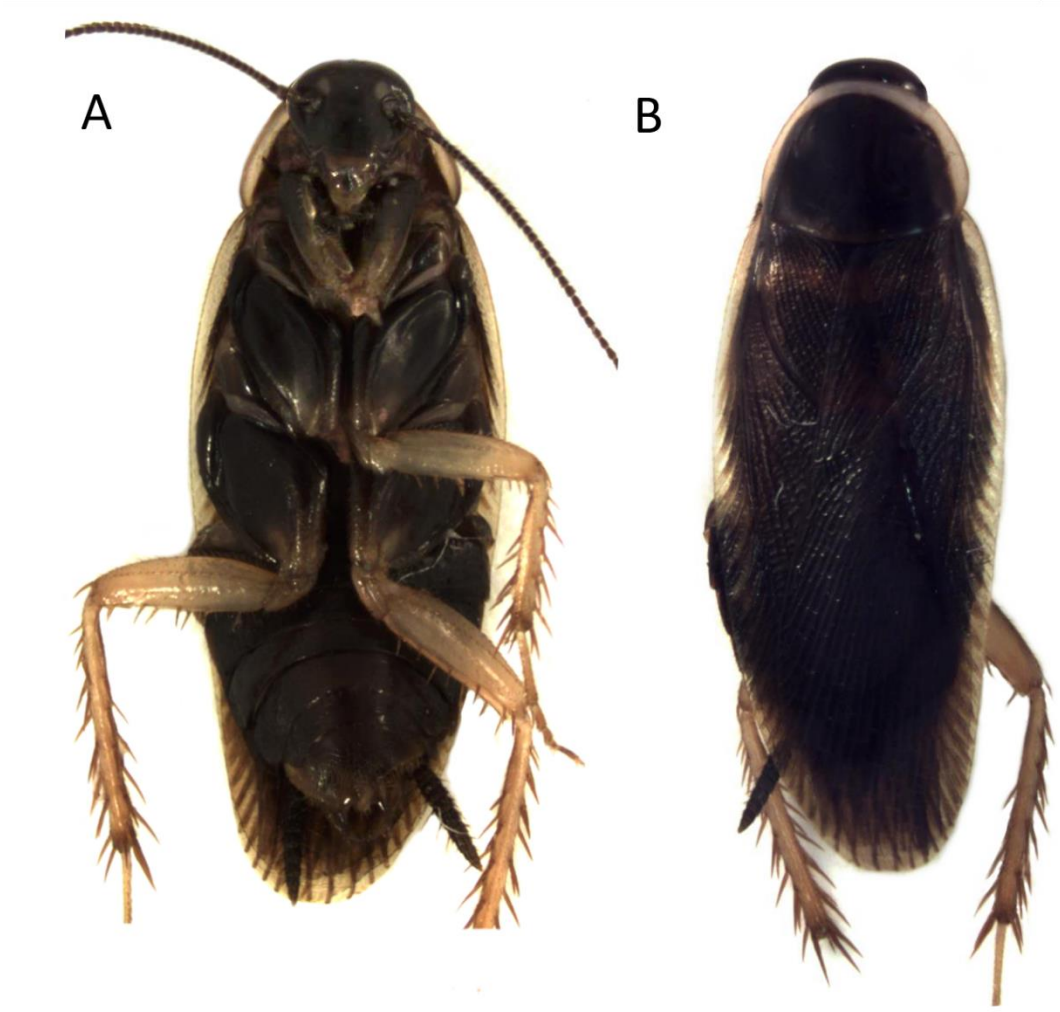
Dasyblatta warei Evangelista and Mendoza, 2016. A-F Adult male holotype. Voucher number: DECBA0907. A Right phallomere (R2; R3 of Klass 1997). B Medial phallomere (Lvm; L2 of Klass 1997). C Left phallomere (L3). D Ventral subgenital plate. E Ventral supra-anal plate. F Dorsal subgenital plate. G-H Female allotype. Voucher number: DECBA1803. G Head, ventral. H Ventral subgenital plate. I-J Ootheca taken from allotype during live collection.

Figure 1 - 15 *Ischnoptera atrata* Hebard



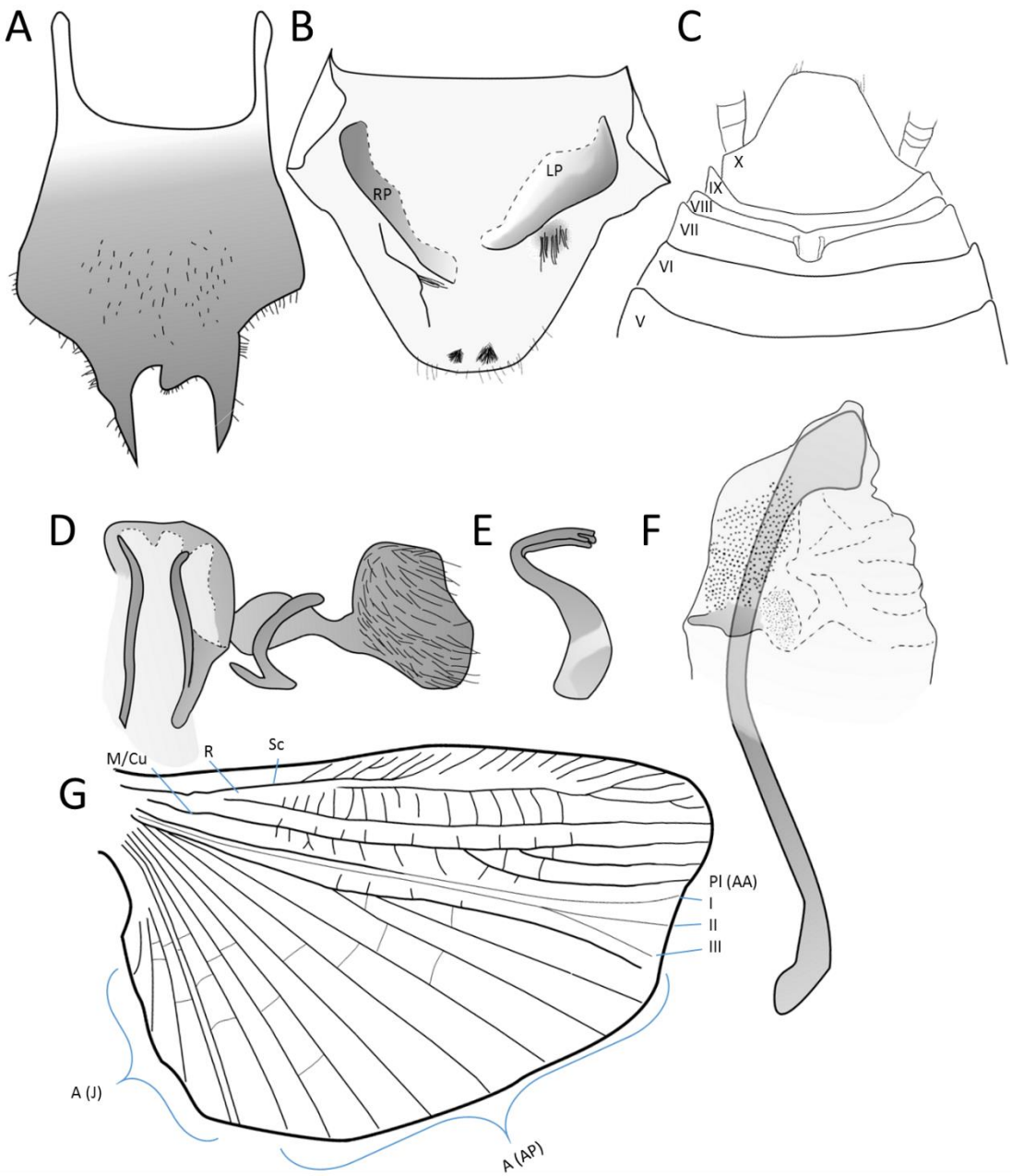
Ischnoptera atrata Hebard, 1916 adult male (DEKBO0594). A Dorsal view. B Ventral view.

Figure 1 - 16 *Ischnoptera galibi* Hebard



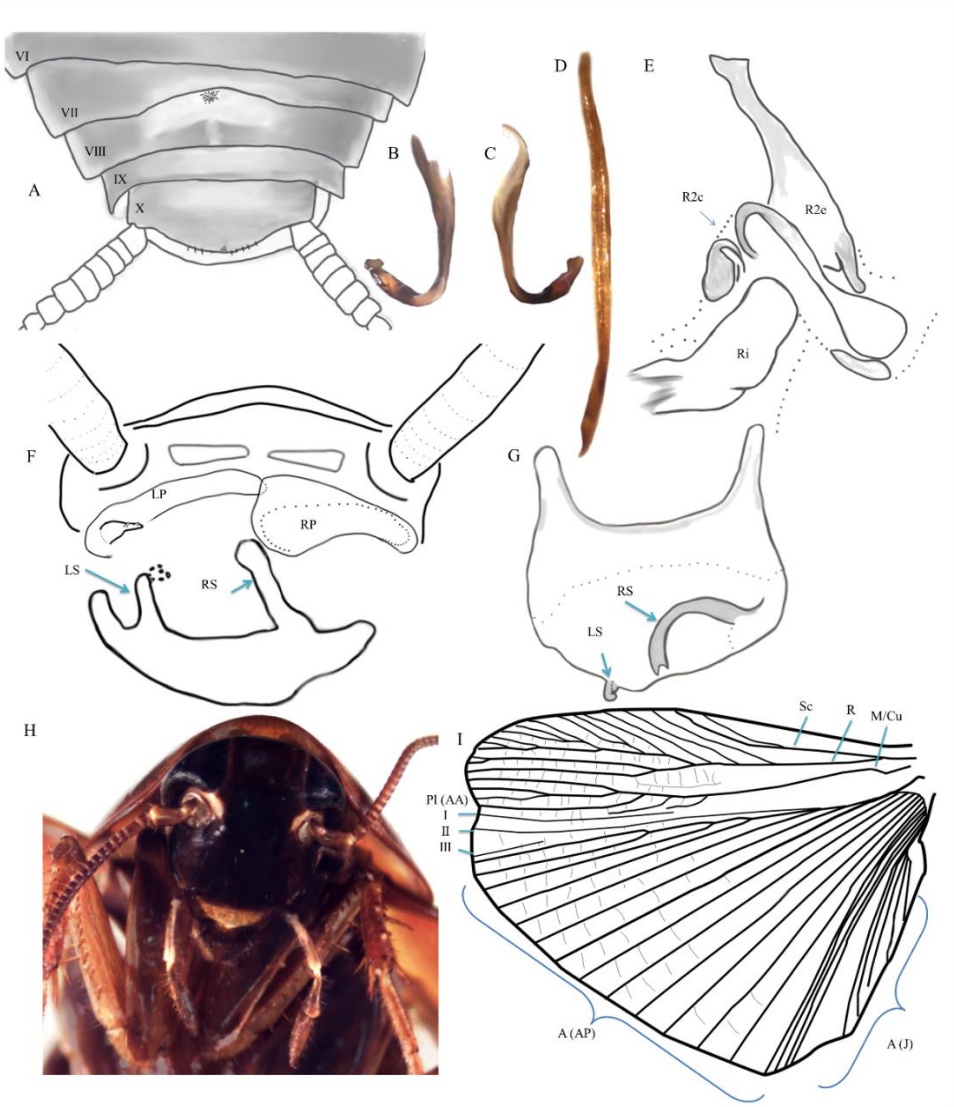
Ischnoptera galibi Hebard, 1926. Adult male. Voucher number: DEIWO0120. A Ventral aspect. B Dorsal aspect.

Figure 1 - 17 *Ischnoptera galibi* Hebard



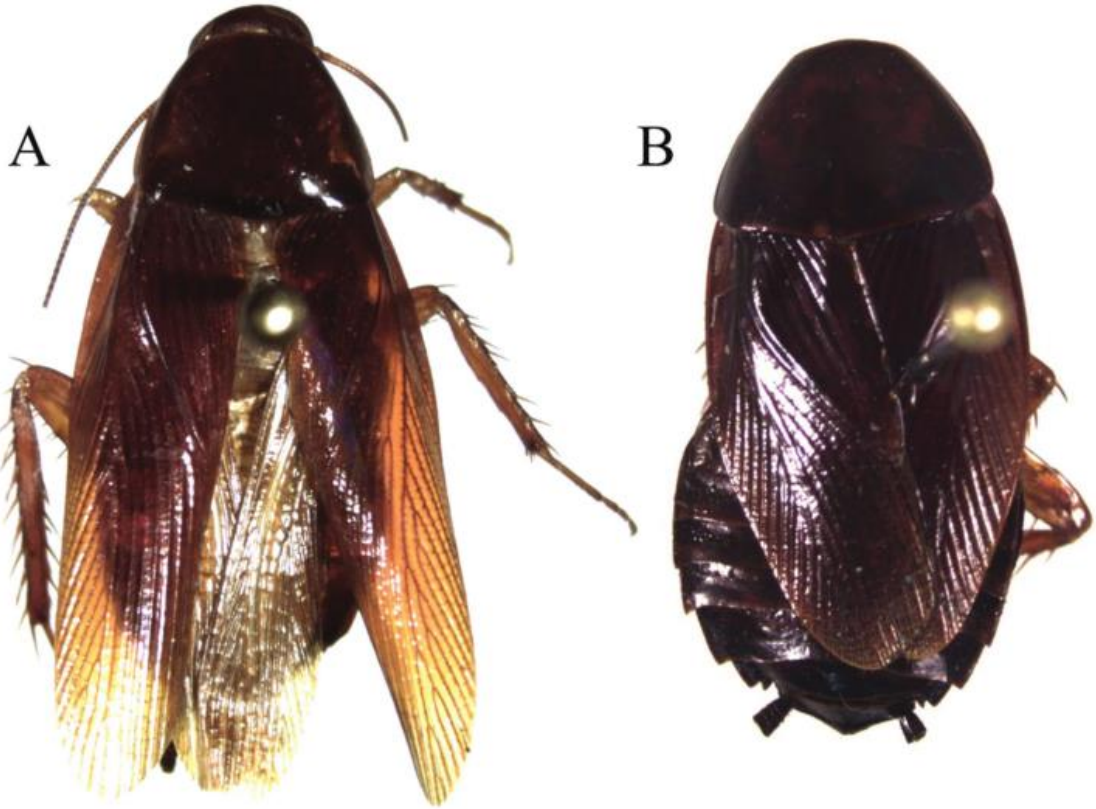
Ischnoptera galibi Hebard, 1926. Adult male. A Ventral subgenital plate. Voucher number: DEKBO0869. B Ventral supra-anal plate with left (LP) and right (RP) paraprocts labelled. Voucher number: DEKBO0348. C Dorsal view of abdomen showing supra-anal plate and tergal gland (segments VII and VIII) with terga V-X labelled. Voucher number: DEKBO0344. D Right phallomere (R2; R3 of Klass 1997). E Left phallomere (L3). F Left ventral-medial phallomere (Lvm; L2 of Klass 1997). Voucher number: DEKBO0869. G Wing with major veins labelled according to Rehn (1951) and Kukalova-Peck & Lawrence (2004) in parentheses. Voucher number: DEKBO0634.

Figure 1 - 18 *Xestoblatta berenbaumae* Evangelista, Kaplan & Ware



Xestoblatta berenbaumae Evangelista, Kaplan & Ware, 2015. A Dorsal view of abdomen showing the simple tergal gland on segments VII and VIII (DECBA2023) and other terga numbered as well. B, C Hooked left phallomere (L3). D Left ventral-medial phallomere (Lvm; L2 of Klass 1997) E Right phallomere (R2; R3 of Klass 1997). R2e – external sclerite, R2i – internal sclerite, R2c – cleft sclerite. F Posterior view of abdomen showing paraprocts and subgenital plate. RS-right stylus, LS-left stylus with small translucent ball at tip, LP-left paraproct reduced and specialized with polydentate spine, RP-unspecialized right paraproct. Illustration is a composite of multiple individuals. G Dorsal view of sub-genital plate (DECBA1967) H Head of adult male. I Hindwing (DECBA0801) with major veins labeled in accordance with Rehn (1951) and Kukalova-Peck & Lawrence (2004) in parentheses. Photos and illustrations contributed by Kayla Kaplan and Dominic Evangelista.

Figure 1 - 19 *Xestoblatta berenbaumae* Evangelista, Kaplan & Ware

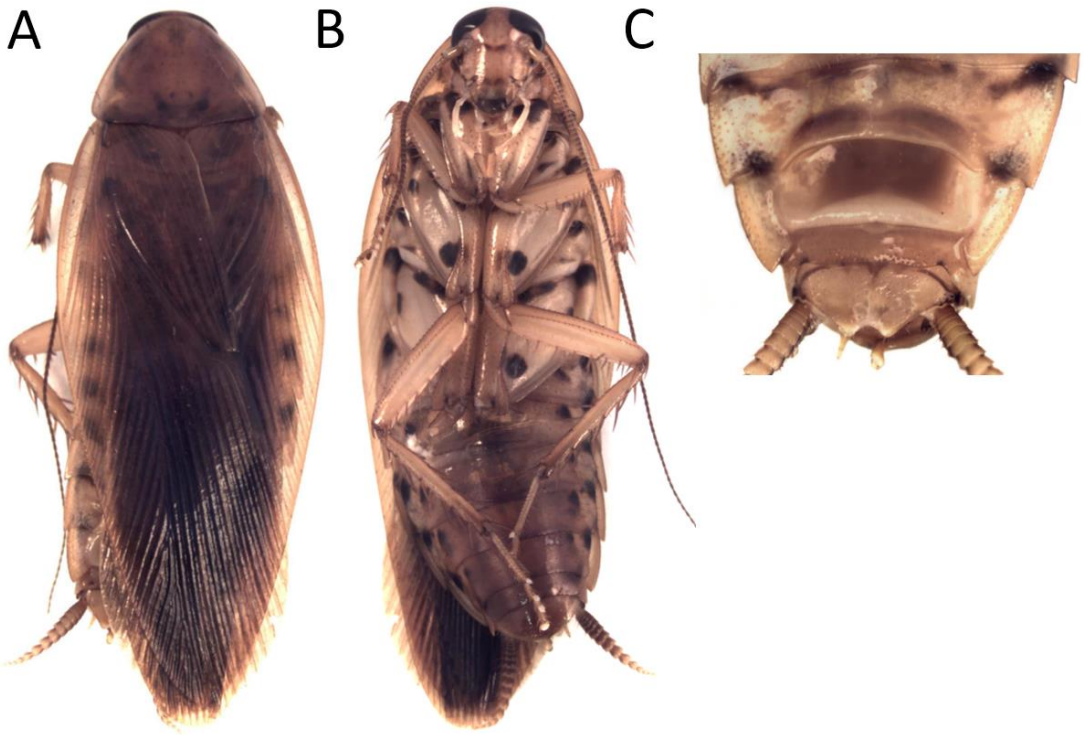


Xestoblatta berenbaumae Evangelista, Kaplan & Ware, 2015. A Adult male dorsal view (DECBA2182) B Adult female
dorsal view (DECBA2210).

Figure 1 - 20 *Xestoblatta agautierae* Grandcolas

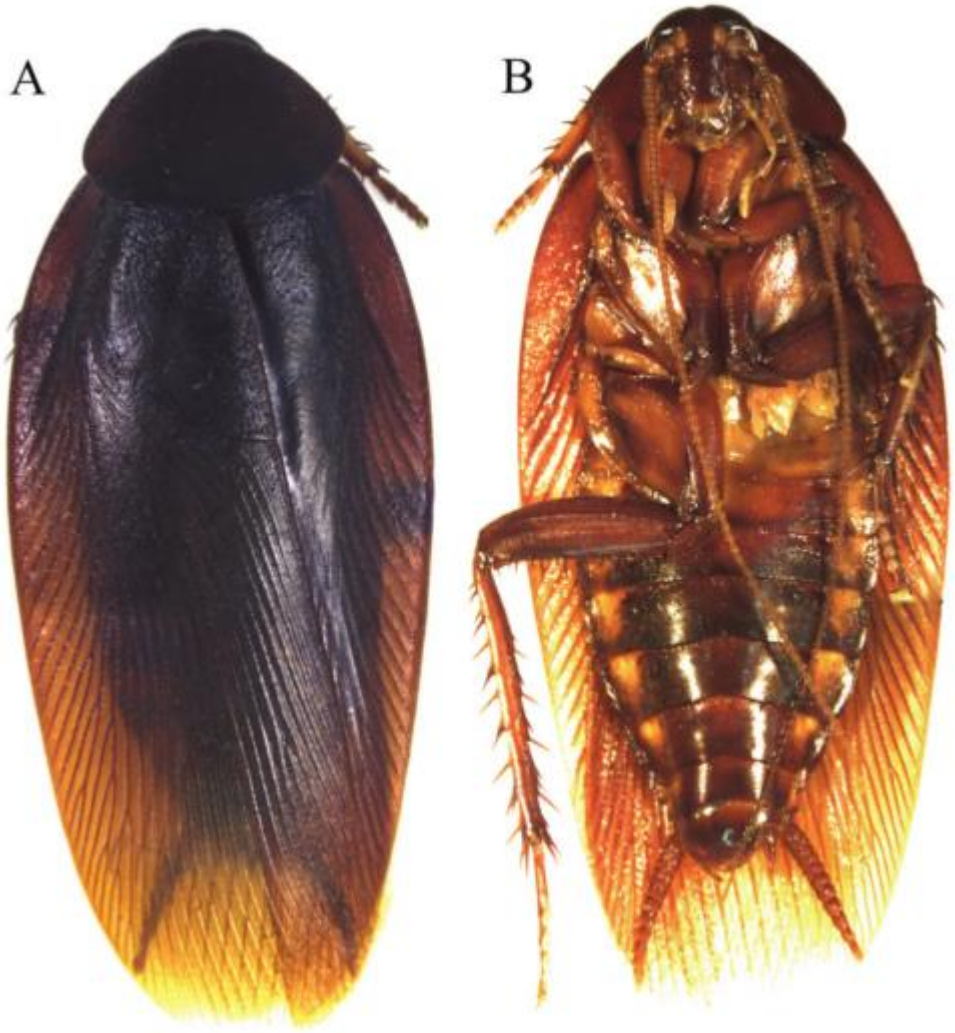
Xestoblatta agautierae Grandcolas, 1992. A Adult male dorsal view (DEKBO0442). B Adult female dorsal view (DEKBO0445).

Figure 1 - 21 *Xestoblatta surinamensis* Bruijning



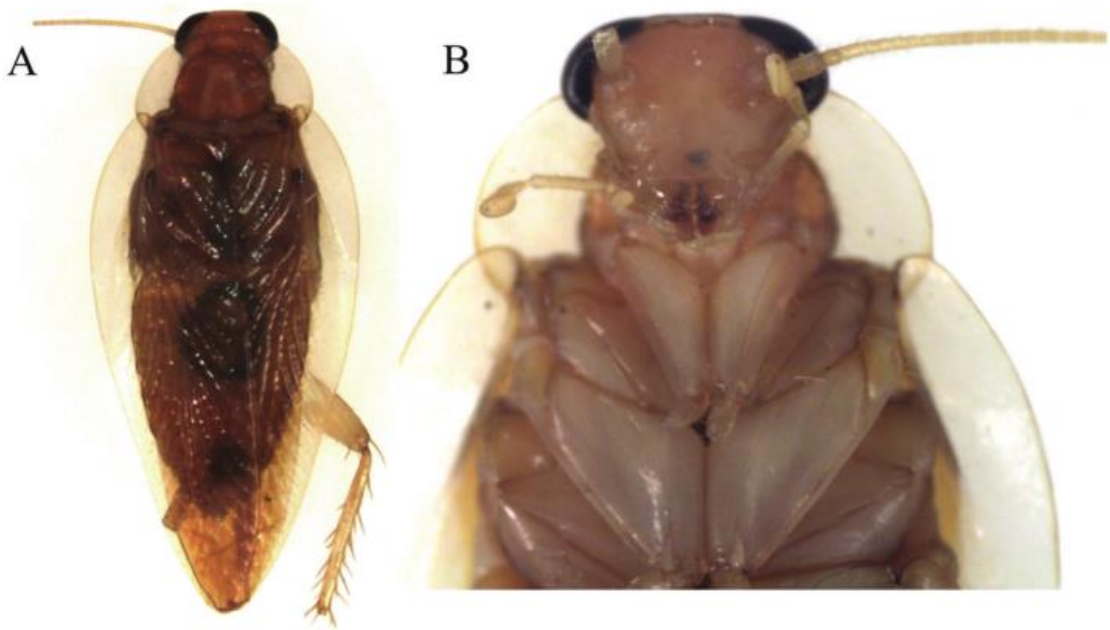
Xestoblatta surinamensis Bruijning, 1959. Adult male. A Dorsal body. B Ventral body. C Terminal terga, showing supra-anal plate and tergal gland (terga VII and VIII). Voucher number: DEIWO0354.

Figure 1 - 22 *Nyctibora dichropoda* Hebard



Nyctibora dichropoda Hebard, 1926 adult male (DECBA0302). A Dorsal view. B Ventral view.

Figure 1 - 23 *Chorisoneura inversa* Hebard

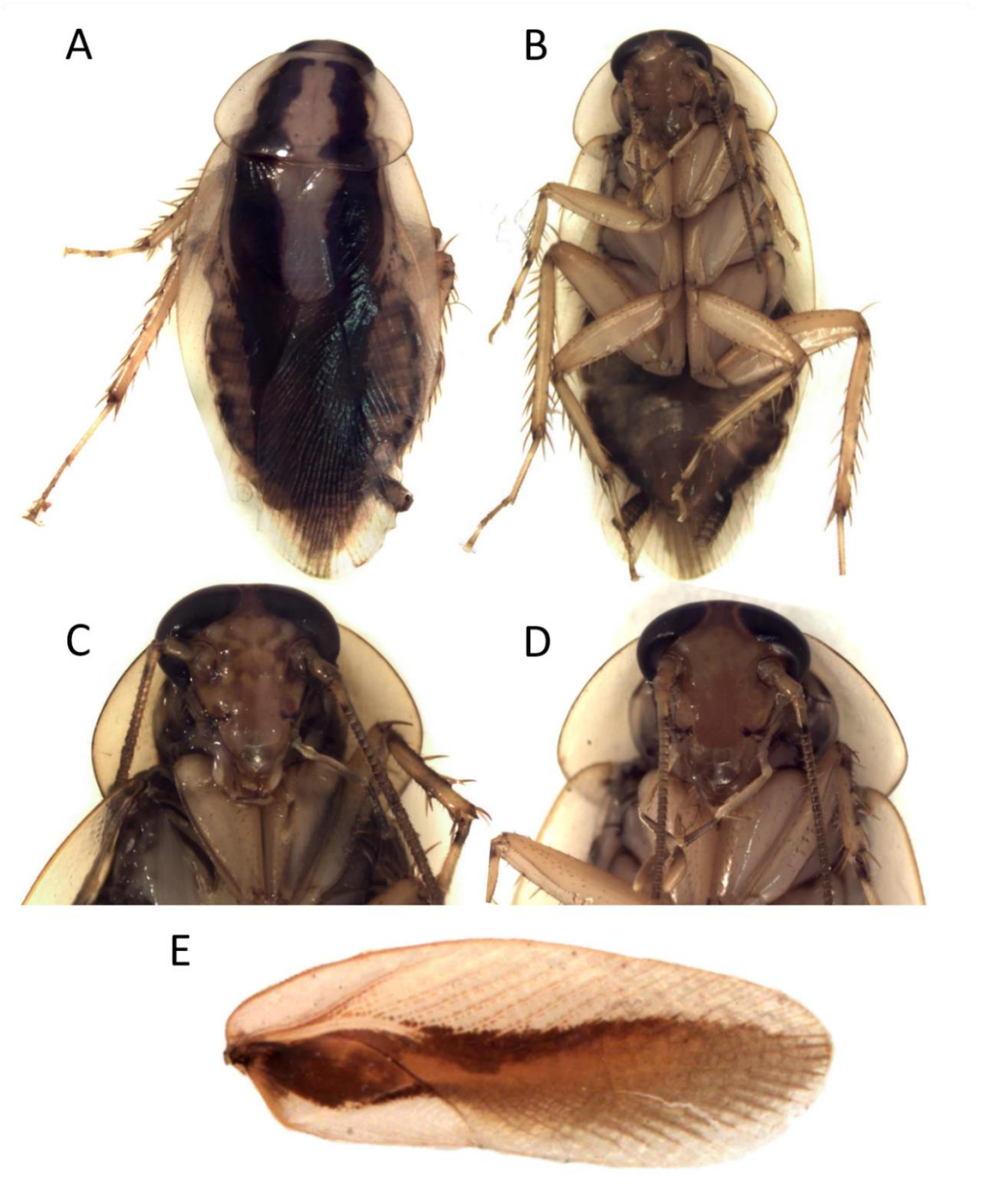


Chorisoneura inversa Hebard, 1926 adult male (DECBA1782). A Dorsal view. B Ventral view of head.

Figure 1 - 24 *Dendroblatta callizona* Rehn

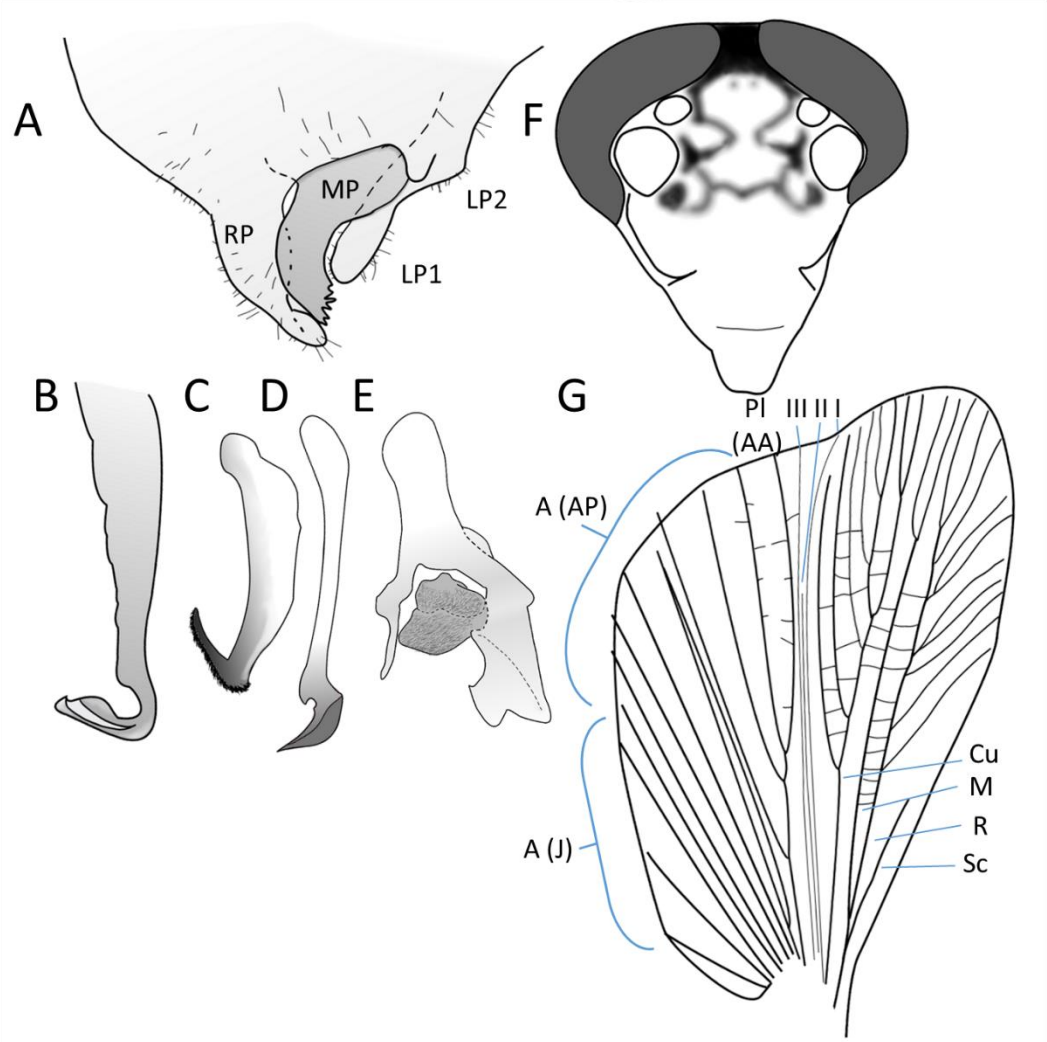
Dendroblatta callizona Rehn, 1928 adult female (DECBA0805). A Dorsal view. B Ventral view.

Figure 1 - 25 *Dendroblatta litura* Evangelista & Sylvain



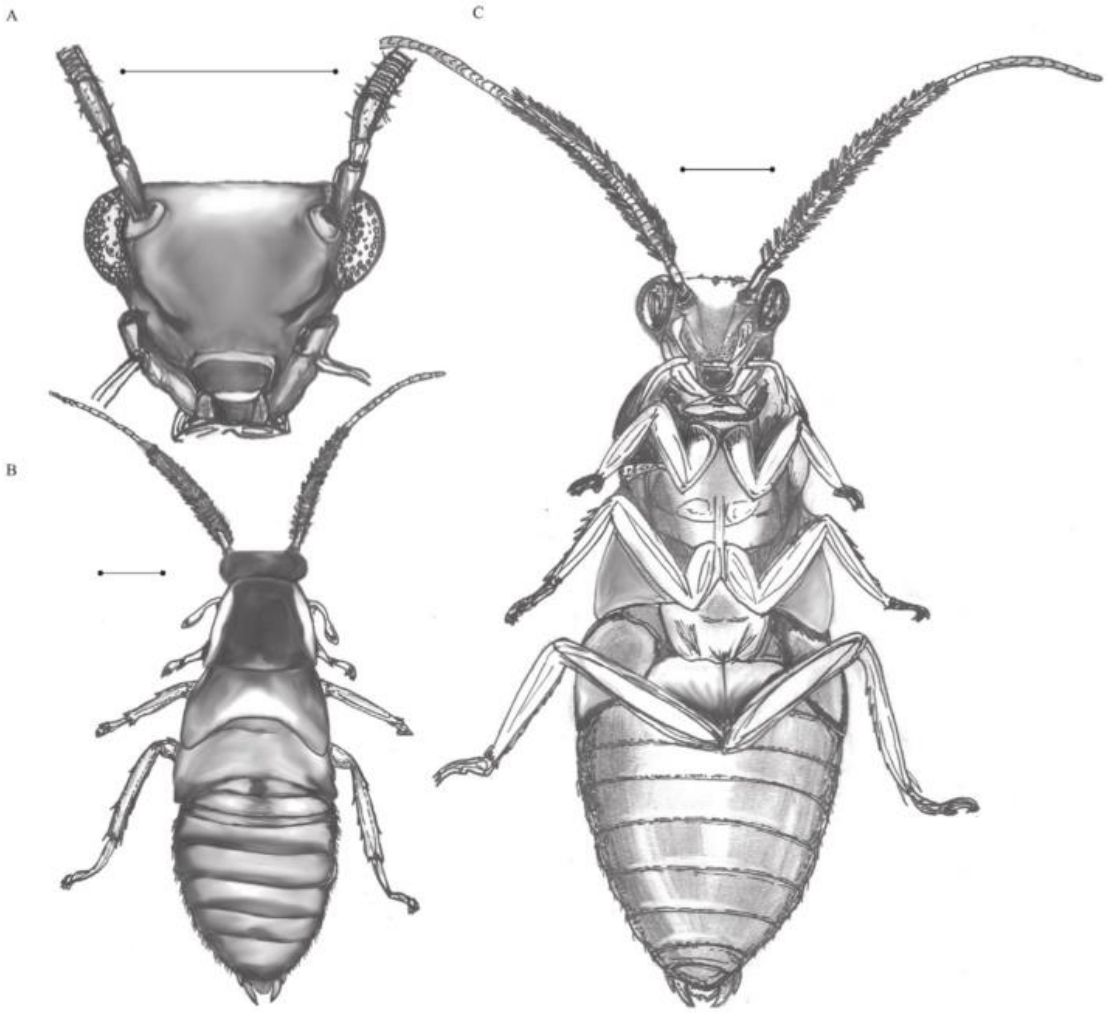
Dendroblatta litura Evangelista & Sylvain, 2016. A-B Adult female paratype. Voucher number: DEKBO0974. A Dorsal body. B Ventral body. C Male head, ventral. Voucher number: DEKBO1083. D Female head, ventral. Voucher number: DEKBO0974. C and D show the variation in the facial coloration of this species. This variation seems to be present independently of sex. E Tegmina, dorsal. Voucher number: DEKBO0689.

Figure 1 - 26 *Dendroblatta litura* Evangelista & Sylvain



Dendroblatta litura Evangelista & Sylvain, 2016. Adult male paratype. Voucher number: DEKBO0975. A Subgenital plate, ventral; with protrusions labelled (RP – right protrusion, MP – medial protrusion, LP – left protrusion). B Right hooked genital phallomere (R2; L3 of Klass 1997). C Right phallomere (R1; L1 of Klass 1997). This sclerite is placed just ventral and slightly more medial to R2. D Medial phallomere (Lvm). This sclerite is ventral and medial to R1. E Left phallomere (L1; R2 & R3 of Klass 1997). F Head, ventral. Highlighting the extent of coloration on the face. Voucher number: DEKBO1083. G Right wing with anal field folded and with major veins labeled in accordance with Rehn (1951) and Kukalova-Peck & Lawrence (2004) in parentheses. Voucher number: DEKBO0689.

Figure 1 - 27 *Calhypnorna* Saussure & Zehnter

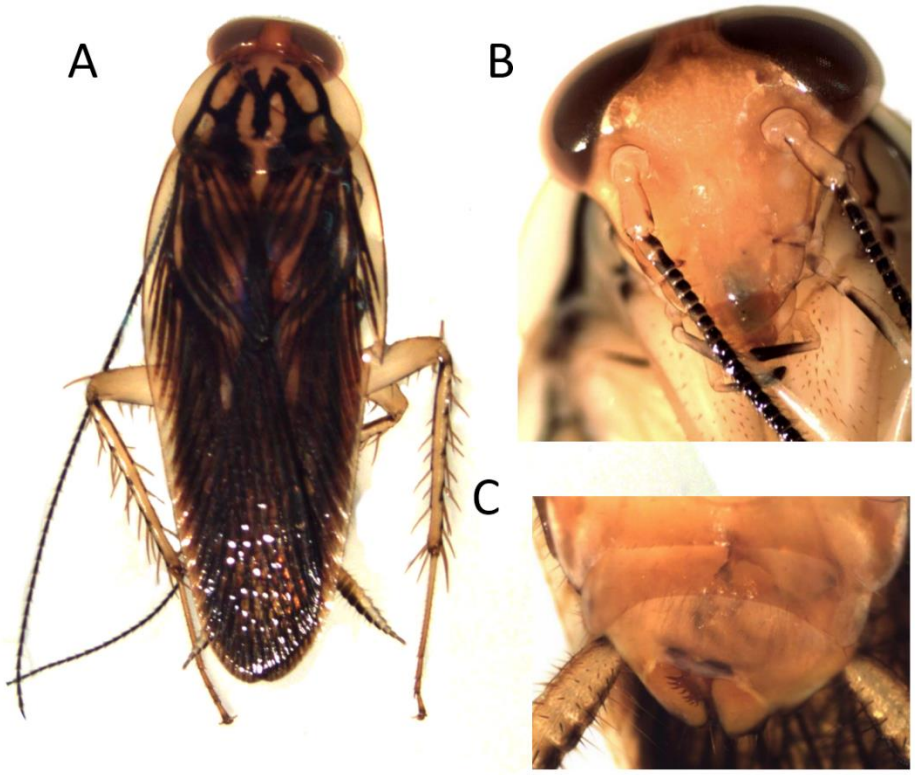


Calhypnorna sp. A Ventral view of head. B Dorsal view of body. C Ventral view of body. Scale bar = 1 mm. Illustrations contributed by Megan M. Wilson.

Figure 1 - 28 Comparison of *Calhypnorna* coloration

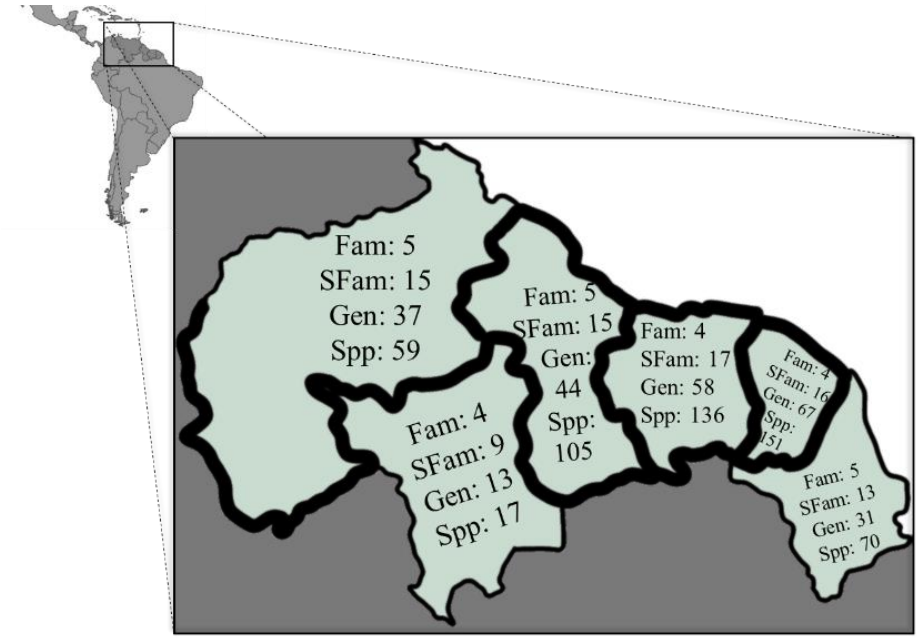
Comparison of overall body coloration of three sympatric species (Left: Ichneumonidae, Middle: *Calhypnorna* sp., Right: Reduviidae) from northern Guyana. *Calhypnorna* sp. shares the orange hind section and dark forward section with the other two insects. Additionally, the antennae of the cockroach composed of: a white band shared with the wasp; an orange band shared with the assassin bug; and a black base share among all. Photos are not to scale.

Figure 1 - 29 *Euphyllodromia amazonensis* Rocha E Silva



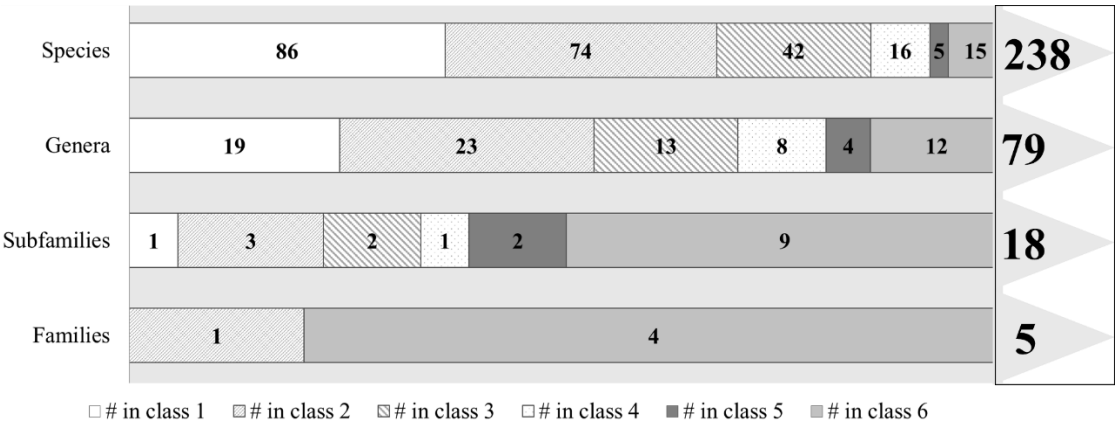
Euphyllodromia amazonensis Rocha E Silva, 1984. Adult male. Voucher number: DEIWO0173. A Dorsal body. B Head, ventral. C Male sub-genital plate.

Figure 1 - 30 Richness of cockroach fauna for Guiana Shield



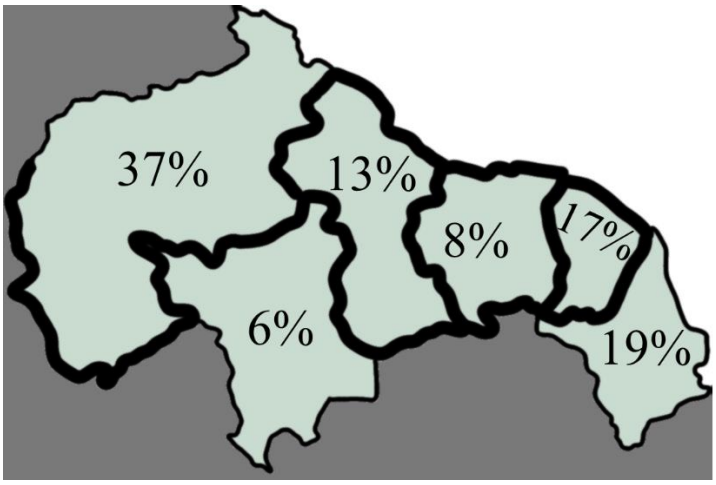
Known richness of cockroach fauna at different taxonomic levels for six regions of the Guiana Shield.

Figure 1 - 31 Extent of range of cockroaches



Extent of range for cockroach taxa. Classes represent the number of regions a taxon was present in: present in only one region – class one; present in all six regions – class 6; etc. Total number of taxa for each level shown on the right.

Figure 1 - 32 Endemicity of Guianan cockroaches



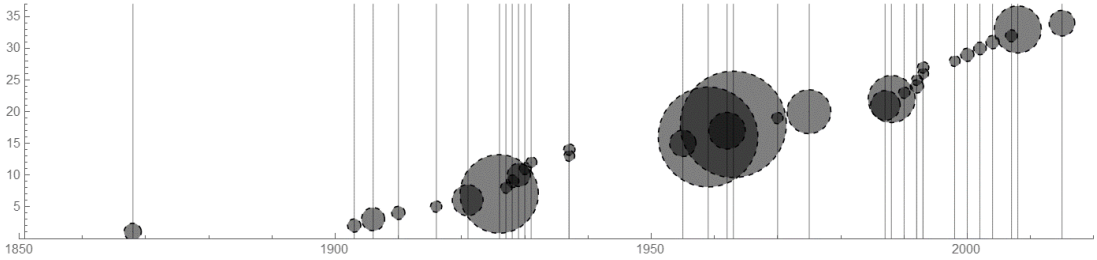
Proportion of cockroach fauna endemic to a region. Endemism is only referred to within the context of the shield.

Figure 1 - 33 Proportion of fauna shared

	Venezuela	Guyana	Suriname	French Guiana	Roraima, Bra.	Amapa, Bra.
Venezuela		0.42	0.45	0.43	0.25	0.48
Guyana	0.24		0.71	0.7	0.15	0.35
Suriname	0.2	0.55		0.81	0.11	0.32
French Guiana	0.17	0.48	0.73		0.11	0.32
Roraima, Bra.	0.88	0.94	0.88	0.94		0.94
Amapa, Bra.	0.41	0.53	0.61	0.69	0.23	

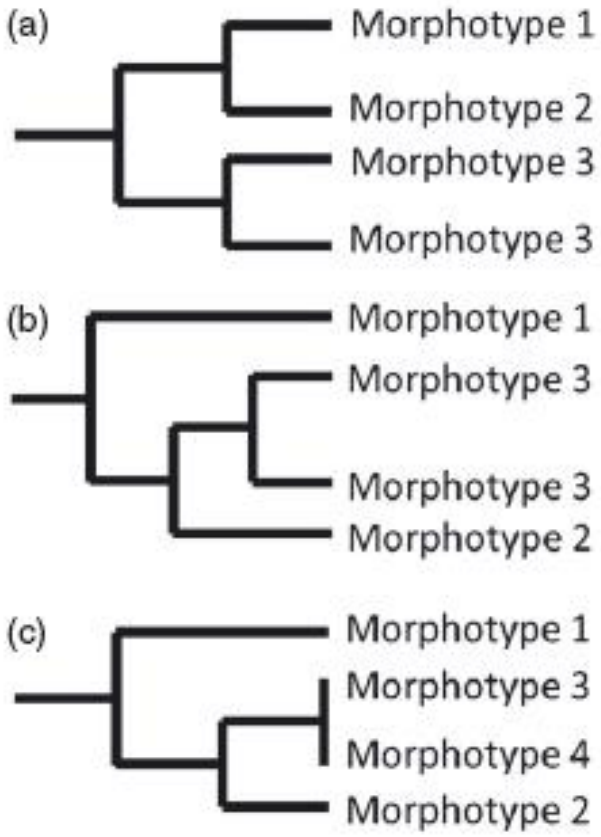
Proportion of fauna in a region (left) shared with each other region (top). Values greater than .5 are shaded by magnitude. The three central regions (Guyana, Suriname and French Guiana) have a high degree of similarity with each other.

Figure 1 - 34 History of Guianan cockroach studies



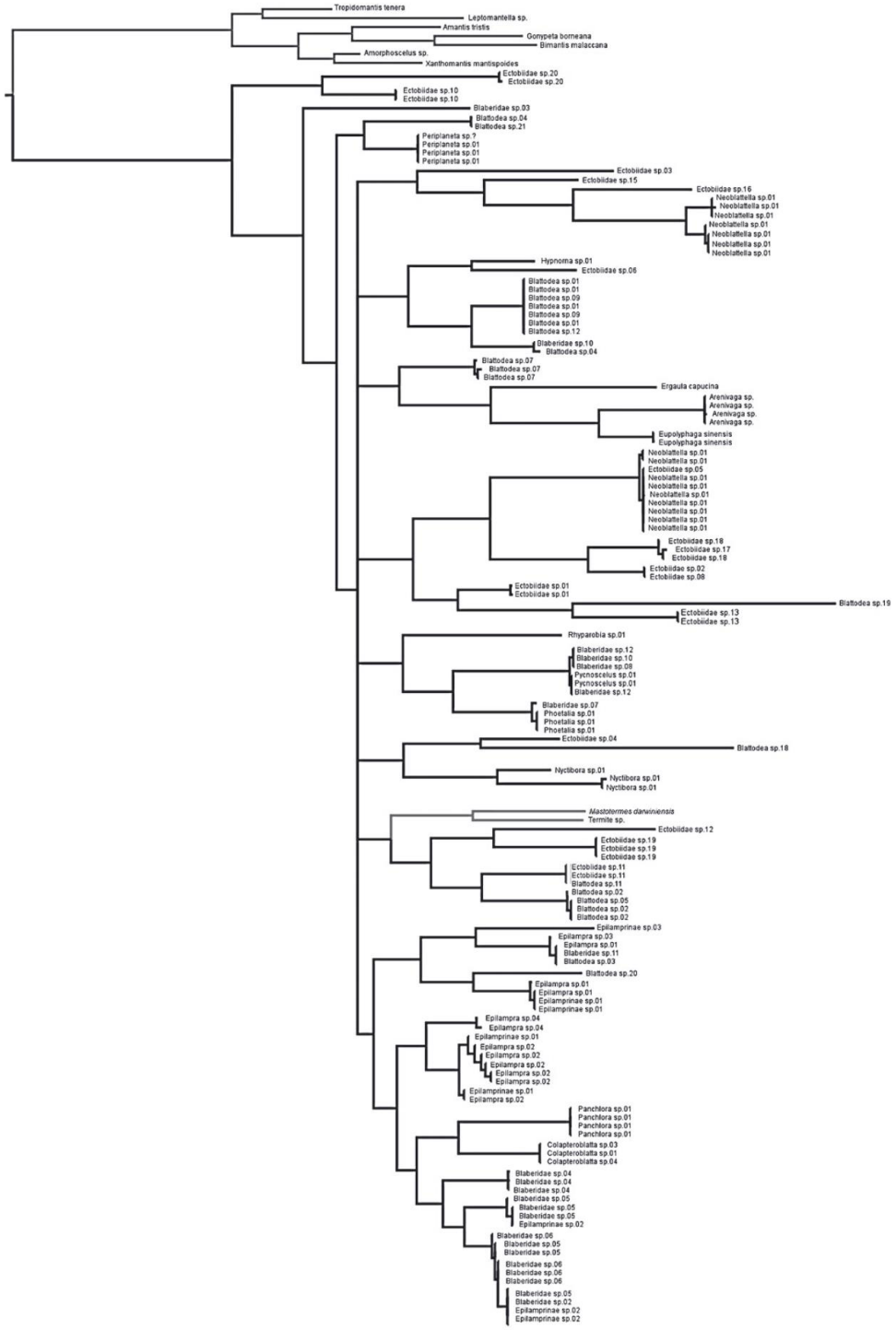
Studies contributing to the checklist of cockroaches of the Guiana Shield. The year of publication of each source plotted against the order in which they were published. The present study, the 34th, is the final circle in the top right. The radius of the circles represents the relative number of times that study is cited in the checklist.

Figure 2 - 1 Example tree analysis



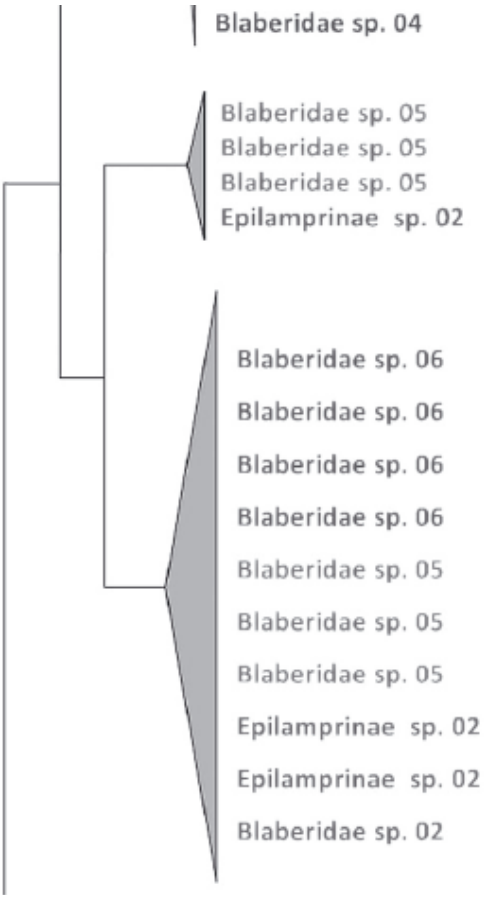
These trees partially exemplify how we analyze our tree. Tip labels indicate morphotype designations of each specimen. Branch lengths indicate genetic distance. In 1a and 1b, morphotype 3 is confirmed to be a valid species because both individuals' COI haplotype is most similar to that of its own morphotype. We also determine that morphotype 1 and 2 are separate species in both of these because they have both separate morphology and COI haplotypes. Part 1c shows that morphotypes 3 and 4 have no genetic difference between them. In this case we reexamine their morphology. For example, if all individuals of morphotype 3 are female and all individuals of morphotype 4 are male we will assume that these are actually the same species and were inappropriately split because of sexual dimorphism.

Figure 2 - 2 Maximum likelihood COI tree



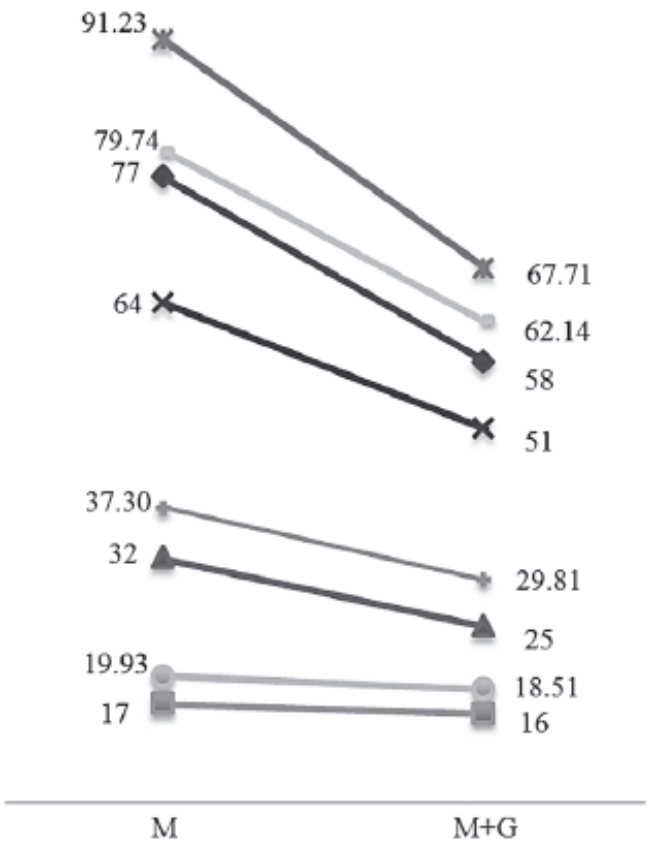
Maximum likelihood tree of the COI gene extracted from the Blattodea of Guyana and other identified cockroach, termite and mantis specimens. Consensus of 500 bootstrap replicates.

Figure 2 - 3 Partial COI tree for explanation of species delimitation



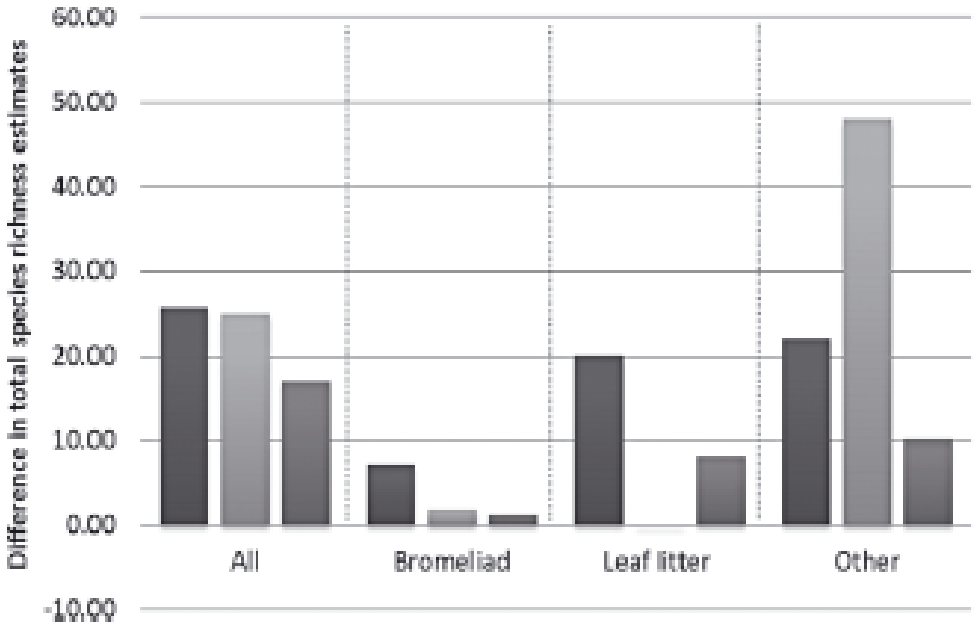
As an example of the species delimitation process we include this clade of our ML tree showing the relationships between a few Blaberids from Guyana. If we start with the taxon Blaberidae sp. 5 as a morphological type we can see that specimens of this type have non-identical COI haplotypes, indicated by the branch length separating them. Then we see that these haplotypes cannot be grouped monophyletically. The next step would be to match the morphologies of the "alien taxa", in this case Blaberidae sp. 2, sp. 6 and Epilamprinae sp. 2, with the morphology of Blaberidae sp. 5. When looking at the morphologies we determined that the type Epilamprinae sp. 2 is the only winged morph. Blaberidae sp. 5 and 6 are indistinguishable except for the shape of the subgenital plate. Blaberidae sp. 2 is much smaller than all the other types but has significant morphological similarities with all other types, despite superficial dissimilarity. Therefore we determine that the alien taxa are of compatible types and therefore one species. Blaberidae sp. 04 is a much simpler case where we have non-identical COI haplotypes but it is possible to group them monophyletically.

Figure 2 - 4 Change in total estimated richness by data type



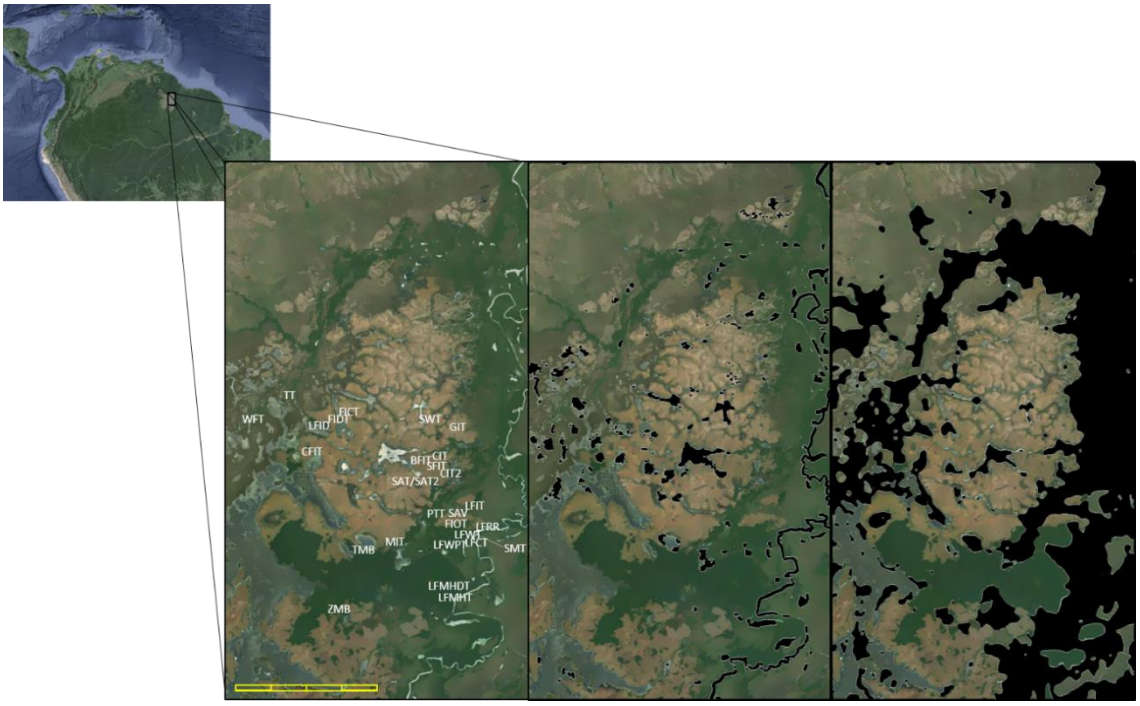
We calculated the sample richness and total estimated richness of our sampled Guyanese Blattodea and subsections of the data divided by microhabitat. We show the changed in these calculations in using two methods of species delimitation: M, morphological species delimitation; M + G phylogenetic species delimitation using both morphological and genetic data. Diamond - sample richness of full set; Large square - sample richness of bromeliads subset; Triangle - sample richness of leaf litter subset; Dark "X" - Sample richness of "other" subset; Light "X" – total estimated richness of full set; Circle – total estimated richness of bromeliad subset; "+" – total estimated richness of leaf litter subset; Small square – total estimated richness of "other" subset.

Figure 2 - 5 Differences in estimates of total richness between three methods



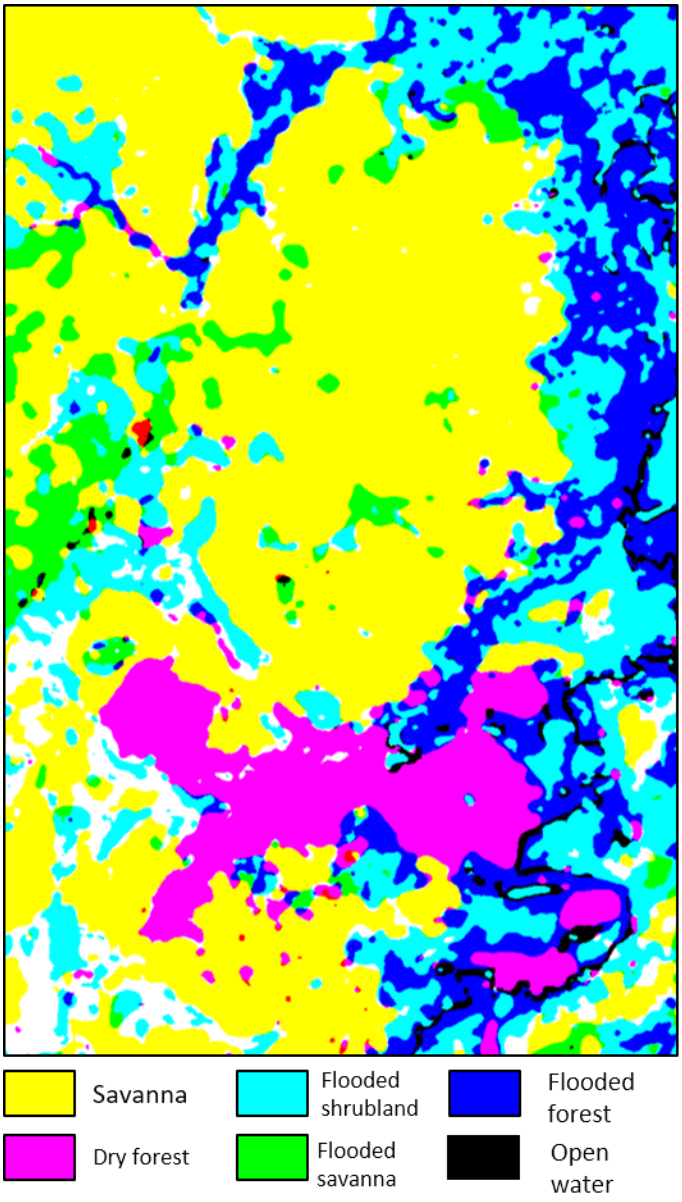
Differences in estimates of total richness between both interpretations of the data (M and M + G) as compated between three methods of calculating richness (bootstrap, unbiased Chao-1, and ACE). This is shown for the full set of cockroaches collected for three pseudo-replicate subsets divided by ecological realm from our site in Guyana. Because of unique taxon assemblages in various ecological realms, the effects of error in morphological type assignment may not vary uniformly, as can be seen here. Darkest color (left) Bootstrap; Lightest color (middle) Unbiased Chao-1; Medium color (right) ACE.

Figure 3 - 1 Karanambu Ranch, southern Rupununi, Guyana



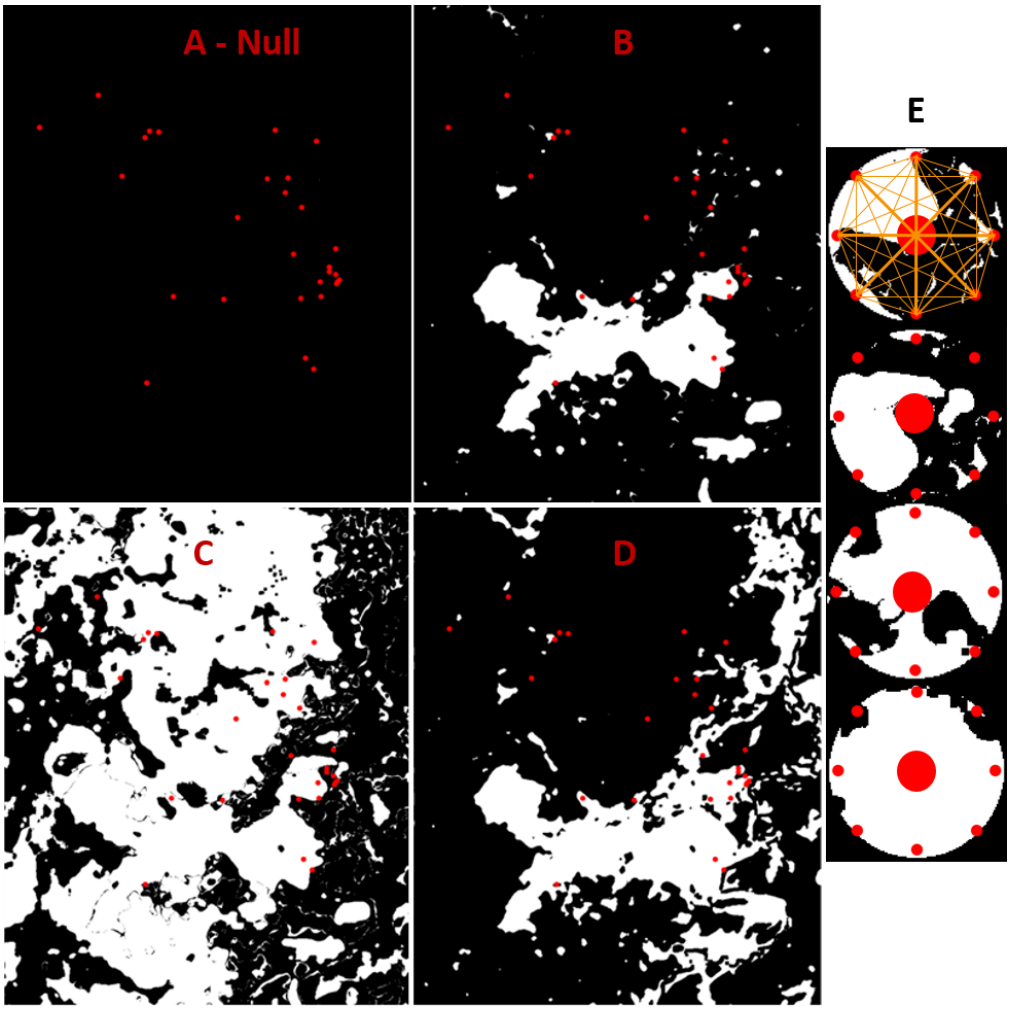
Satellite image of Karanambu Ranch in southern Rupununi, Guyana (**EarthMaps 2015**). Left: Abbreviated names of all the sites from which we used data are shown on the image. Scale bar is 4 miles total. Center: Black regions represent approximation of surface water during dry season. Right: Black regions represent approximation of surface water during the wet season. Water and flood regions approximated using satellite image analysis (see methods) and calibrated using field observations.

Figure 3 - 2 Satellite image analysis



The results of satellite image processing. Yellow regions = dry savanna, pink regions = dry forest, light blue = flooded shrubland, green regions = flooded savanna, dark blue shows flooded woodland. Red, white and black spots in represent ambiguous or uncategorized regions. Ambiguous regions were manually adjusted for the final analysis. All our sites (see figure 1) are within or bordering the crescent of woodland surrounding the central savannah. This image underrepresents some very small forest islands and thin peninsulas of forest main-land.

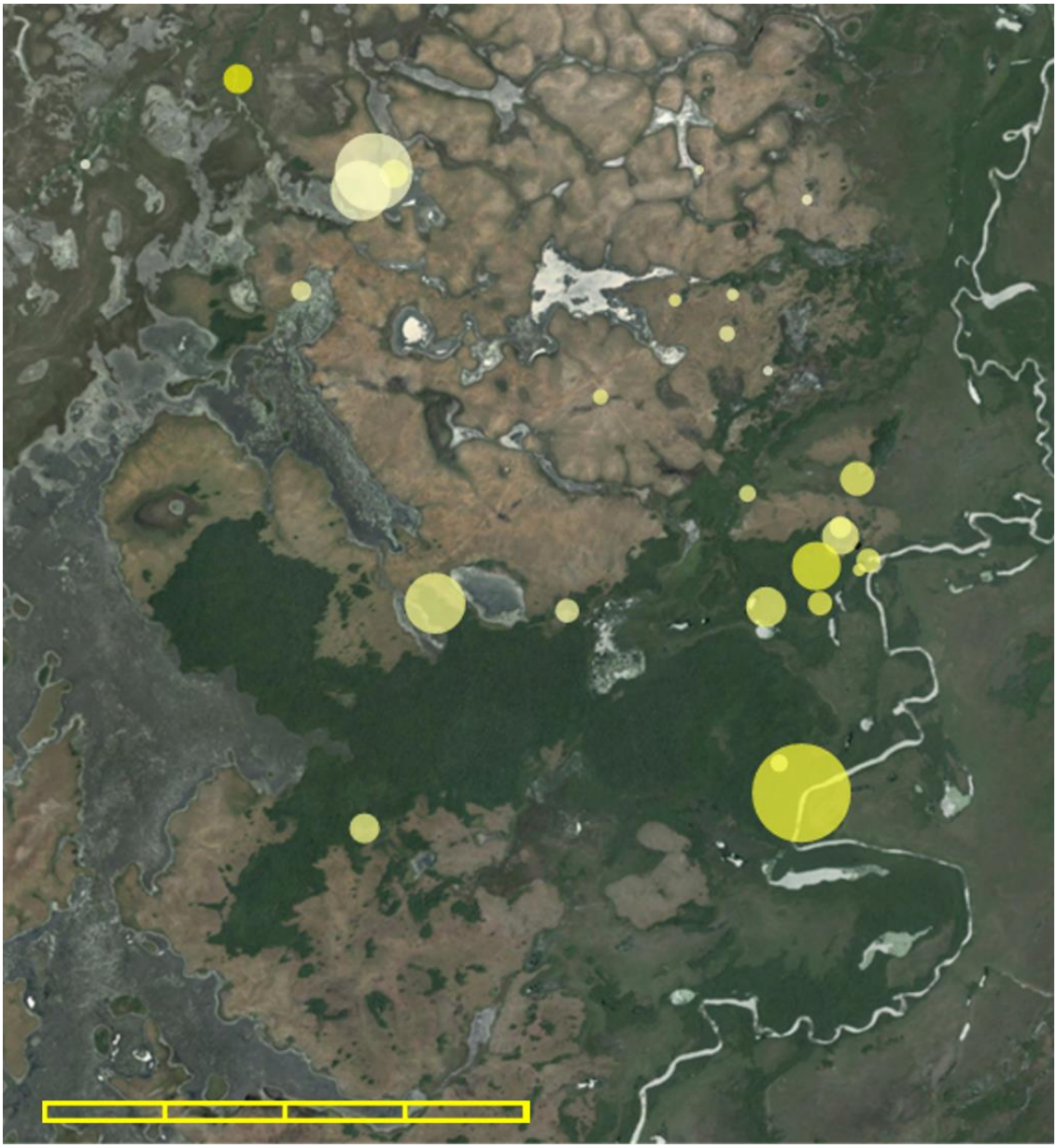
Figure 3 - 3 Landscape hypotheses



A-D. These four binary images represent four hypothetical models of permeability to dispersal. Each is shown with the collection sites mapped as red dots. A. The null model is that landscape is uniformly permeable and dispersal is affected by distance alone. B. Dry-forest model: Only dry forests are permeable and all other landscape features are uniformly impermeable to dispersal. C. Flood model: Non-flooded regions are uniformly permeable and areas that flood during the wet season are uniformly impermeable to dispersal. D. Forest model: Only forested regions, regardless of flooding, are permeable to dispersal. Savanna and open water are uniformly impermeable to dispersal. E. An example of how four sites were treated in the isolation analysis (flood model). In the image centered on each site, the cost of travel was calculated among the 9 points indicated. Dark pixels represent less permeable landscape categories and light pixels were more permeable landscape categories. The orange lines in the first image show the total number of

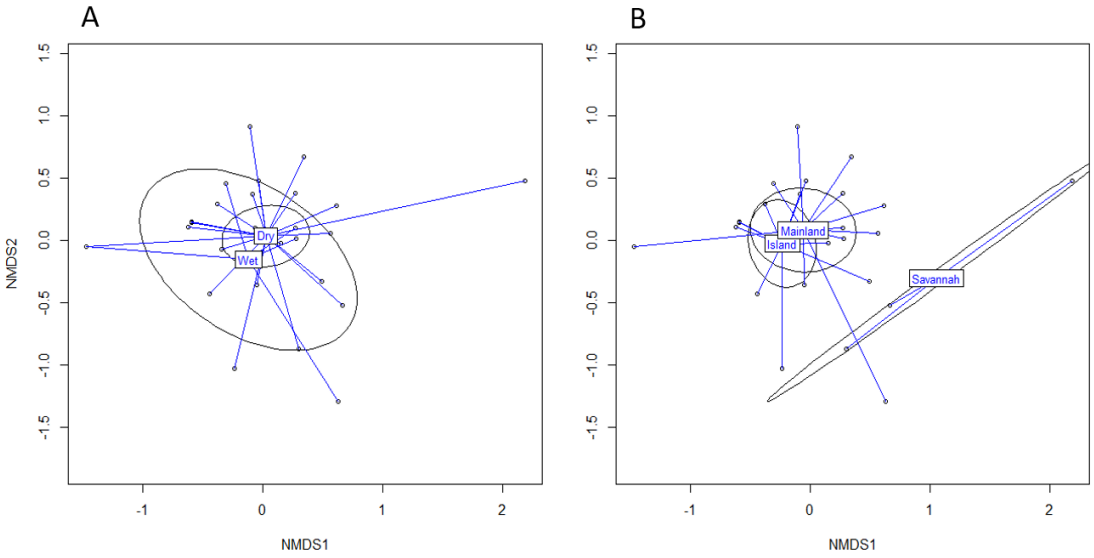
connections for which costs were calculated. The average cost of travel among these 9 points was used as a measure of isolation.

Figure 3 - 4 Overview of total cockroaches collected



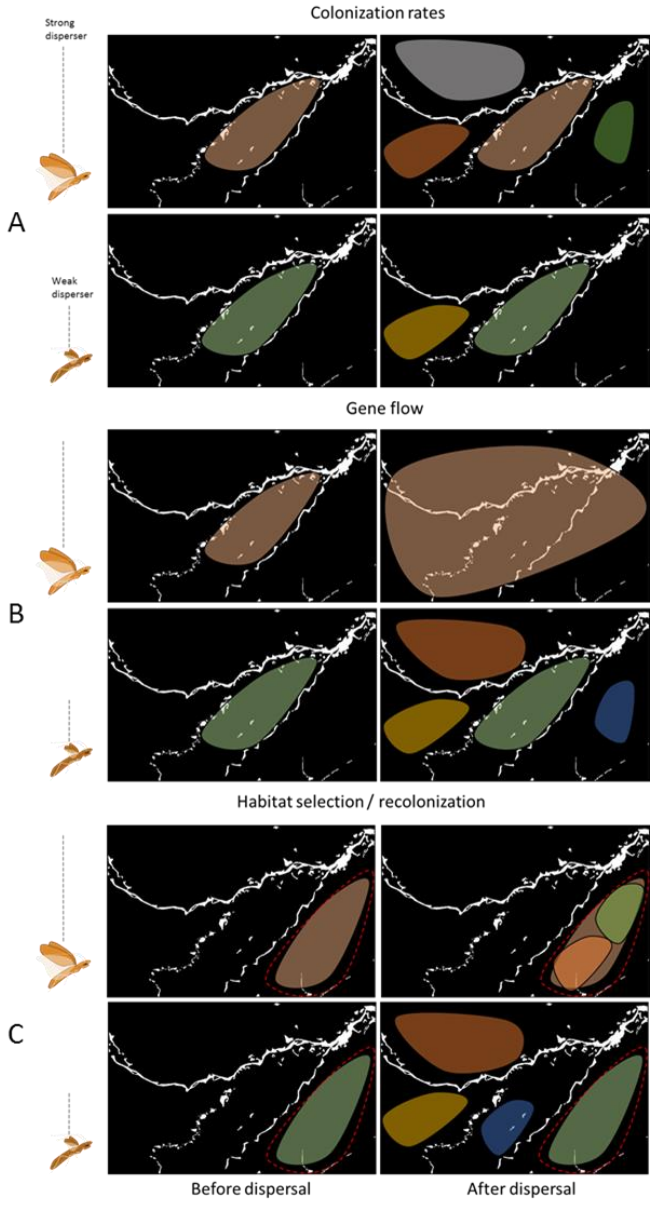
28 collection sites (circles) overlaid on the map. Circle radius relative to number of individuals collected. Circle color relative to observed species richness with yellow being the most rich and white being the least rich.

Figure 3 - 5 Nonmetric multidimensional scaling (NMDS) analysis



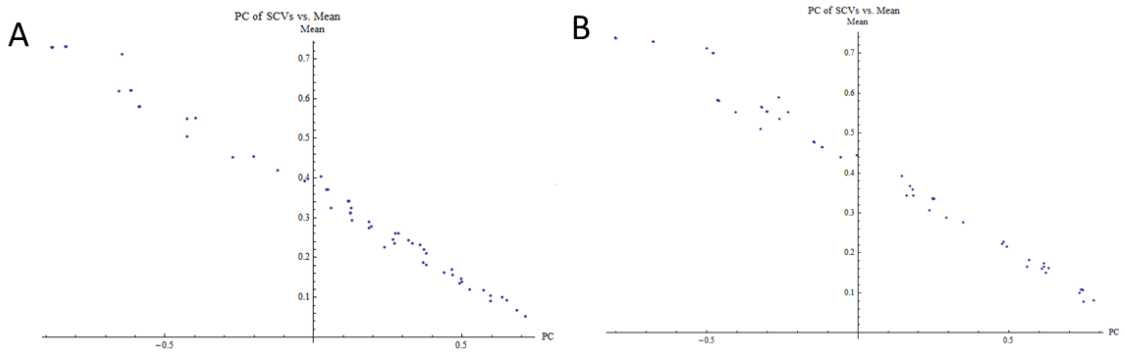
Cockroach assemblage NDMS with environmental factor names plotted at their centroids' positions. A. Dry forests and (Dry) and flooded forests (Wet) in NMDS space with 95% confidence intervals plotted (ellipses). There are no significant differences between assemblage compositions among flooded (Wet) or non-flooded (Dry) sites (n=27, R^2= 0.217, p = 0.719). B. Island forests, mainland forests, and savanna assemblages all plotted in NMDS space. Forest islands and mainlands showed no difference in species (n=24, R^2 = 0.033, p=0.478). However, savanna assemblages were significantly different from forest species assemblages (n=27, R^2=0.210, p=0.009).

Figure 4 - 1 Illustration of three hypothetical mechanisms of range evolution



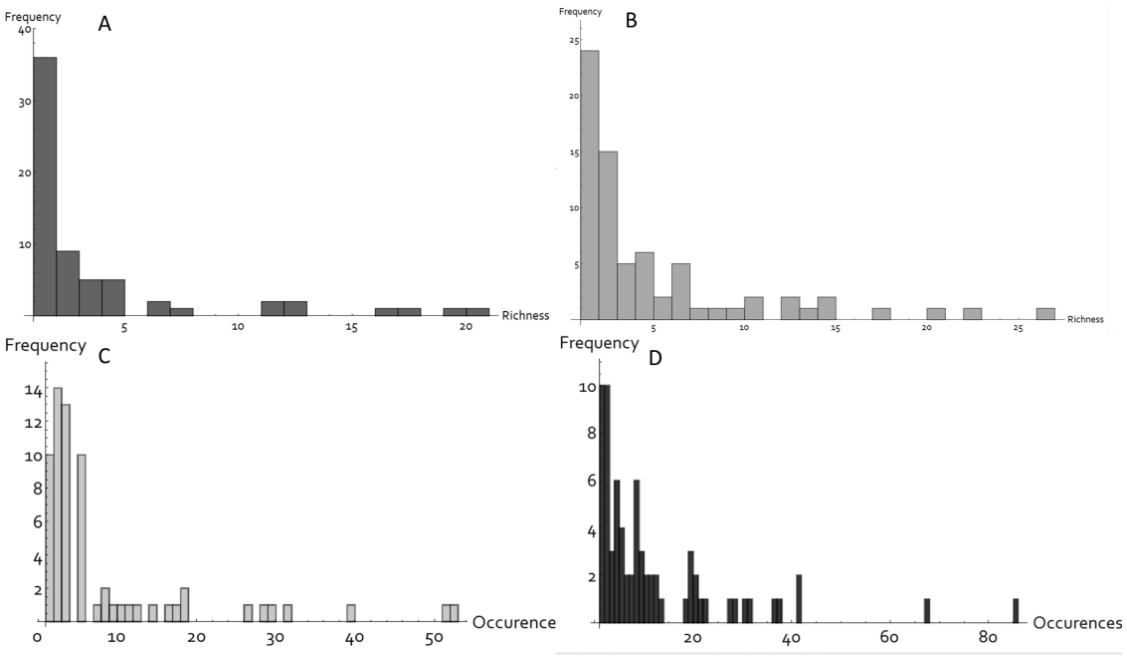
In each part, we illustrate two hypothetical dispersing taxa (one strong disperser and one weak) and how their dispersal ability may affect their range evolution. In most cases the dispersal event occurs along with speciation. In the maps, white are waterways that we treat as boundaries, the top waterway being a larger boundary. A. If dispersal ability affects the rate of colonizing new areas, then strong dispersers will not be limited by large boundaries where weak dispersers are limited by them. This predicts that the weak dispersers will be more clustered together. B. On evolutionary time scales the large boundaries become surmountable by both taxa, but gene flow is maintained in the strong disperser. The independent movement of ranges that results from speciation in the weak disperser allows the ranges to spread out randomly. This predicts that we will see weak dispersers will be more spread apart. C. Dotted red line indicates a more "ideal" habitat. If initial colonization rates and speciation rates are equal, strong dispersers are more likely to end up in the "ideal" habitat. This predicts that weak dispersers are more spread apart.

Figure 4 - 2 Relationship of principal component to spatial clustering values



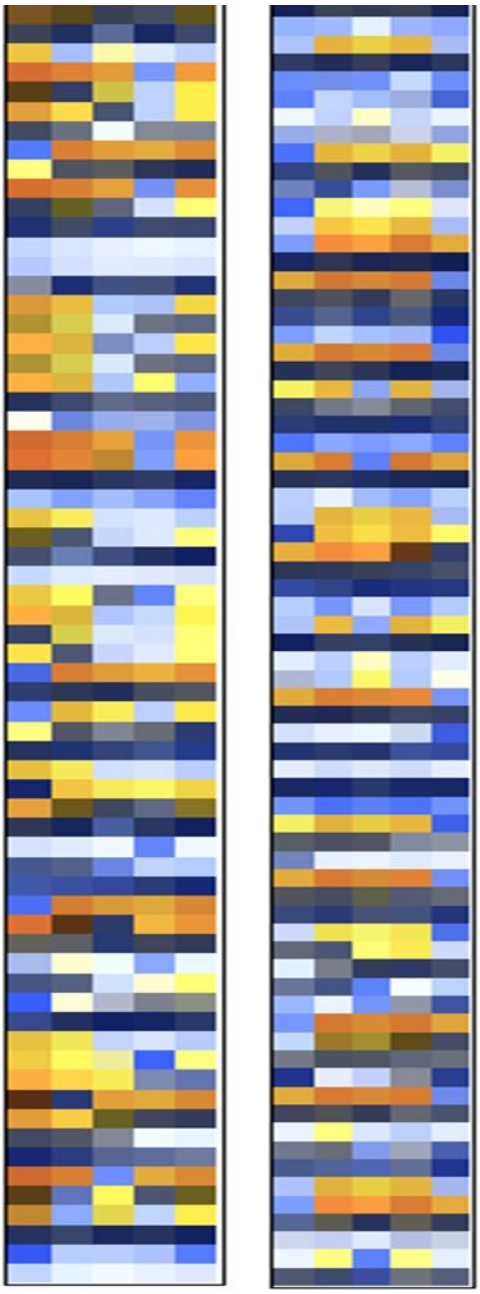
Relationship of principal component to spatial clustering values. First principal component (PC) of all probability values against the mean probability values for each genus in (A) Blaberoidea and (B) Anisoptera. The PC correlates highly with the mean probability with higher PCs corresponding to lower probabilities. The best fit linear model of this relationship highly supports this (A: m = -.42, R^2 = .98; B: m = -.42, R^2 = .99). Since lower probabilities can be interpreted as deviance from random range distributions we can interpret the PCs as having a direct relationship with range spread: the higher the PC the more spread in space the ranges are.

Figure 4 - 3 Frequency distribution of faunal data



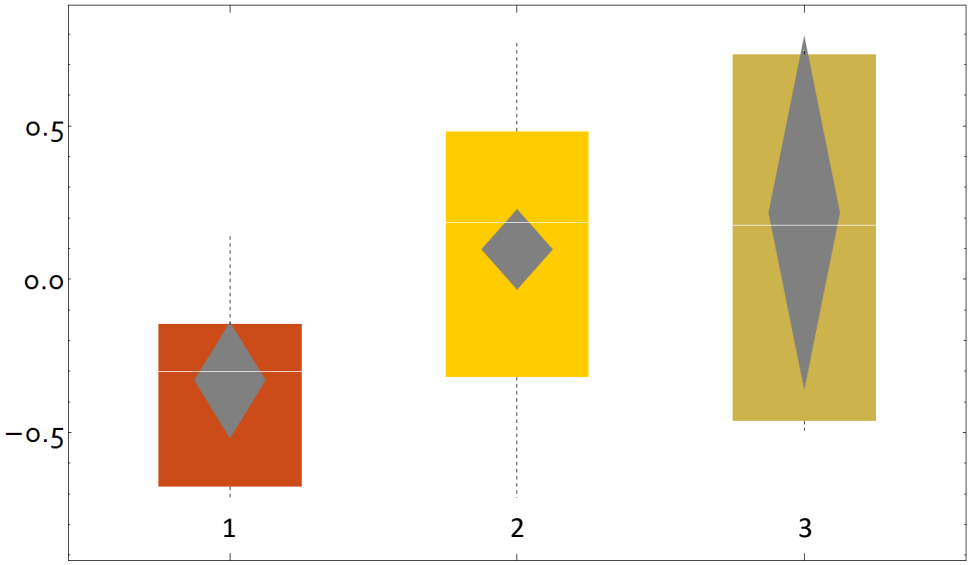
Frequency distribution of faunal data. Distributions of the frequency of (A, B) richness and (C, D) regional occurrences among genera in (A,C) Blaberoidea and (B, D) Anisoptera.

Figure 4 - 4 Distribution of relative range clustering



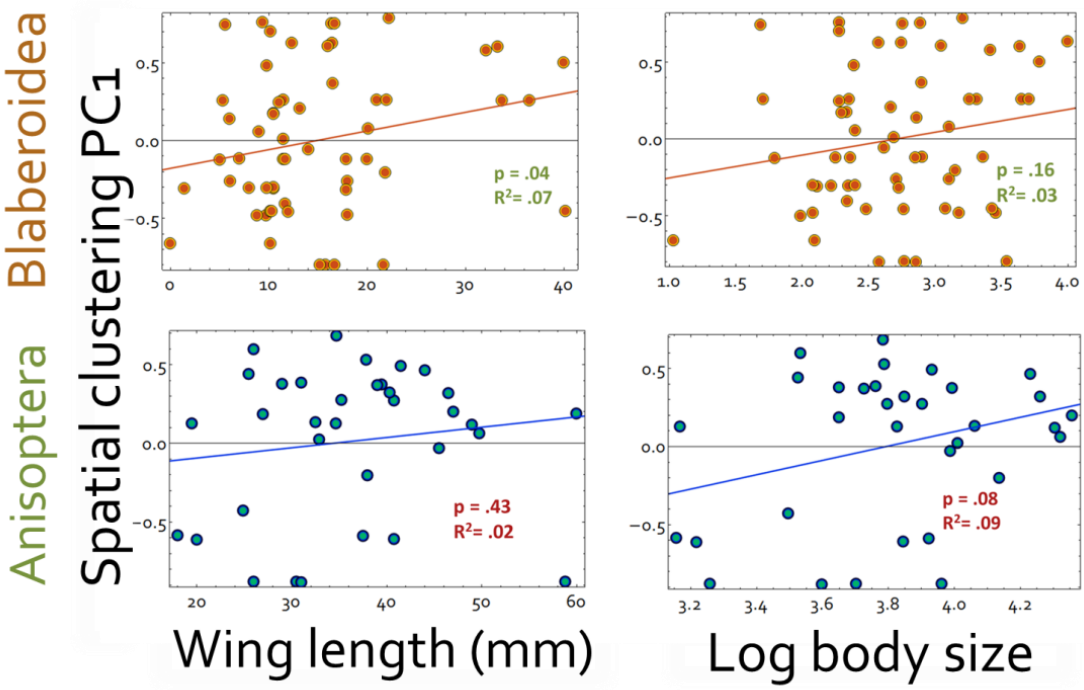
Heat table showing the distribution of relative range clustering (probabilities) among (A) Blaberoidea and (B) Anisoptera in the Guiana shield. Each row represents one genus with each column representing each region. Cooler colors (blues) represent values closer to 0 and warmer colors (reds) representing values closer to 1.

Figure 4 - 5 Range clustering by wing state



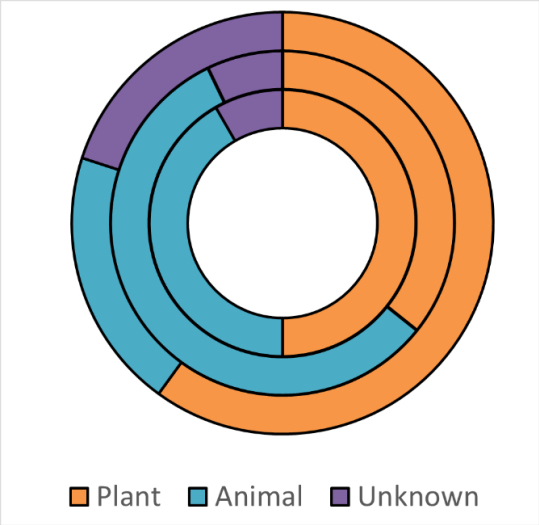
Wing state of Blaberoid cockroach genera (1 = apterous and brachypterous (n=12); 2 = macropterous with no expanded apical field (n=45); 3 = macropterous + expanded apical field (n=6)) against principal component of spatial clustering values (PC). Diamonds show mean confidence intervals, white line represents median value, colored bar represents 95% of the data and the dotted lines represent the remaining 5%. Higher PC can be interpreted as the ranges of the species within a genus being more clustered and lower PC means that they are more rarified or spread out. Here we can see that genera lacking morphology for functional flight are more spread out in space (p=.009, F=5.2).

Figure 4 - 6 Dispersal ability metrics against spatial clustering in Anisoptera and Blaberoidea



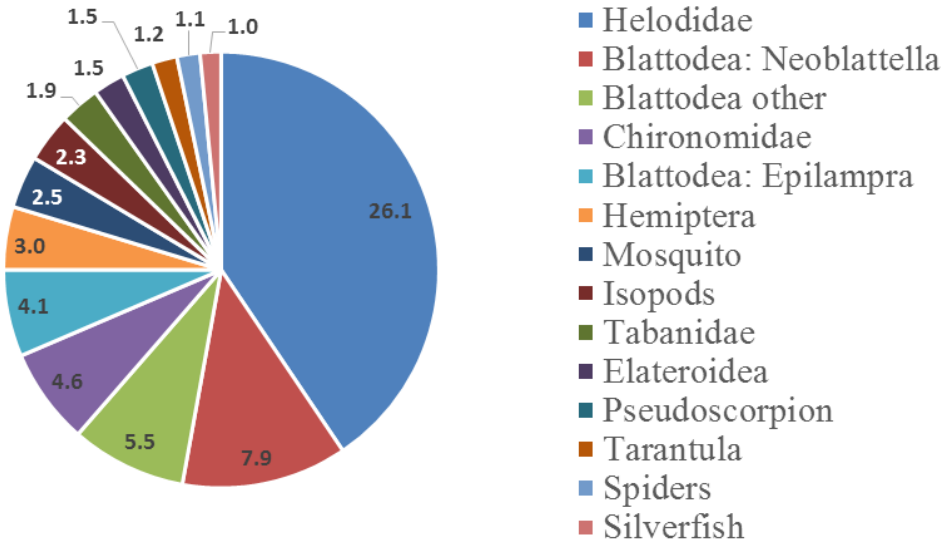
Dispersal ability metrics against spatial clustering in Anisoptera and Blaberoidea. (A, B) Blaberoidea and (C, D) Anisoptera are shown and includes (A, C) wing length in millimeters and (B, D) Log[body length in millimeters]. Sample sizes are (A, B) n = 62, (C) n = 34 and (D) n = 33. Line shows best fit linear regression. Higher PC means the ranges of the species within that genus are more clustered and lower PC means that they are more rarified or spread out. Most of the data show weak or unsupported relationships between morphological features for dispersal and spatial clustering.

Figure C - 1 Diets of some common Guyanese cockroaches



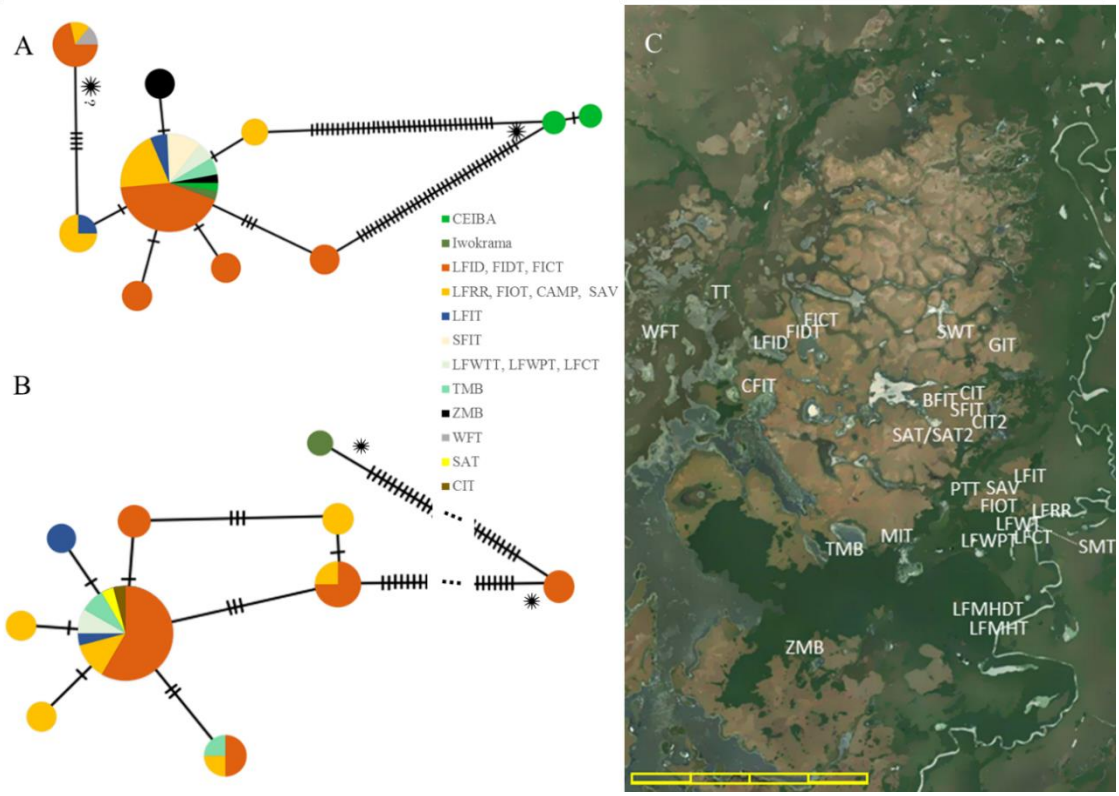
Diets of the some common species at CEIBA Biological station and Kamuni creek in Madewini Guyana.
Inner circle: *Xestoblatta berenbaumae* (n= 7).
Middle circle: *Ischnoptera galibi* (n=11).
Outer circle: *Neoblattalla* spp. (n=8).

Figure C - 2 Bromeliad insect communities in northern Guyana



Bromeliad insect communities in northern Guyana. From a sampling of N bromeliads we reconsitruct the typical bromeliad community. In a bromeliad of typical size (mean number of bracts) we calculated the mean abundance of different insect species in that bromeliad. Other than Helodidae beetle larvae, cockroaches were the most abundant insects found in bromeliads. Specific identification of which species these consisted of is unknown, because the vast majority were juveniles. Finally, the average body length of the resident cockroaches is much higher than both the abundant Helodids and Chironimids, leading us to believe that cockroaches are extremely important in these bromeliad eecosystems.

Figure C - 3 Mitochondrial haplotype networks of Ischnoptera galibi and other Ischnoptera



Two minimum spanning haplotype networks of *Ischnoptera* mitochondrial genes. A – B. Circles are individual haplotypes from mitochondrial genes. Circle size is proportional to number of individuals contained in each haplotype. Lines indicate relationships among haplotypes with tick marks indicated the number of changes separating those haplotypes. Haplotypes in main part of network are from *Ischnoptera galibi*. Asterisks denote lines leading to other species of *Ischnoptera*. A. COI haplotype network (n = 55). B. COII haplotype network (n=40). Dashed line abbreviates many changes along the branch. C. Map of Karanambu region of the Rupununi with site names overlaid. CEIBA and Iwokrama are not shown on the map due to the extreme geographic distances of these sites from Karanambu. Haplotype diversity among *Ischnoptera galibi* is not geographically localized but widely distributed across all sites. For an extreme example, an individual from CEIBA and one from Iwokrama share an identical COI haplotype with multiple individuals from Karanambu (although contamination is possible). This indicates that *Ischnoptera galibi* is likely a strong disperser and savanna, flood zones, or forest do not impeded gene flow among populations in this species.

APPENDIX II

TABLES

Table 1 - 1 Checklist of the Blattodea s.s. of the Guiana Shield

Checklist of species from 8 regions of the Guiana Shield. ? = Record with a non-specific locality, and thus unconfirmed in this region. o = Presence record from published literature. + = new record from this paper. Amaz VEN = Amazonas Venezuela, Bolivar VEN = Bolivar Venezuela, Del Ama VEN = Delta Amacuro Venezuela, Rora BRA = Roraima Brazil, GUY = Guyana, SUR = Suriname, FG = French Guiana, Ama BRA = Amapa Brazil.

Taxon			***Amaz VEN***	***Bolivar VEN***	***Del Ama VEN***	***Rora BRA***	***GUY***	***SUR***	***FG***	***Ama BRA***	***Source***
Blaberidae											
Blaberinae											
Blaberus	*atropos*	(Stoll, 1813)	?	?	?		o				(Bruijning, 1959; Hebard, 1929; Perez, 1988; Princis, 1963; Princis and Kevan, 1955; Walker, 1868)
	colosseus	(Illiger, 1801)					o		o		(Bonfils, 1987; Princis, 1963; Hebard, 1916)
	craniifer	Burmeister, 1838					o		o		(Princis, 1963; Gutierrez and Perez-Gelabert, 2000)
	discoidalis	Serville, 1838		o							(Princis, 1963; Perez, 1988; Princis and Kevan, 1955; Gutierrez and Perez-Gelabert, 2000)

	giganteus	(Linnaeus, 1758)				o	o	o	o	(Bonfils, 1975; Bruijning, 1959; Gutierrez and Perez-Gelabert, 2000; Hebard, 1926, 1921b; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963; Princis and Kevan, 1955; Rocha e Silva Albuquerque and Gurney, 1962; Walker, 1868)
	latissimus	(Herbst, 1786)					o			(Princis, 1963)
	parabolicus	Walker, 1868					o			(Bruijning, 1959; Princis, 1963)
Eublaberus	*distanti*	(Kirby, 1903)				o	o	o	o	(Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963)
	posticus	(Erichson, 1848)				o	o	o		(Bruijning, 1959; Hebard, 1926, 1929; Princis, 1963; Princis and Kevan, 1955; Rehn, 1906)
	marajoara					o				(Bruijning, 1959; Evangelista et al. 2016; Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963)
	sulzeri	(Guerin-Meneville, 1857)					o			(Princis, 1963)
Hormetica	*laevigata*	Burmeister, 1838	o							(Perez, 1988)
	marmorata	(Saussure, 1869)	?	?	?					(Bonfils, 1987; Perez, 1988; Princis, 1963)

Lucihormetica	*verrucosa*	(Brunner von Wattenwyl, 1865)	?	?	?						(Perez, 1988; Hebard, 1929; Princis, 1963)
Neorhicnoda	*maronensis*	(Hebard, 1921)					o	o	o		(Bonfils, 1975; Bruijning, 1959; Evangelista et al. 2015; Grandcolas, 1992b; Hebard 1921b, 1926; Princis, 1963)
Paradicta	*rotunda*	Grandcolas, 1992							o		(Grandcolas, 1992b)
Phoetalia	*circumvagans*	(Burmeister, 1838)	o	o	o	o	o	o	o	o	(Princis, 1963)
	pallida	(Brunner von Wattenwyl, 1865)	o	o	o	o	o	o	o	o	(Baaren et al., 2002; Bruijning, 1959; Princis, 1963; Princis and Kevan, 1955)
Sibylloblatta	*pustulata*	(Hebard, 1929)	?	?	?						(Bonfils, 1987; Perez, 1988)
Epilamprinae											
Colapteroblatta	*bordoni*	Bonfils, 1987		o							(Bonfils, 1987)
	surinama	(Saussure, 1868)					o	o			(Princis, 1963; Roth, Gutierrez, 1998; Evangelista et al., 2015)
Dryadoblatta	*mira*	Rehn, 1937	o								(Bonfils, 1987; Perez, 1988; Princis, 1963; Rehn, 1937a)
Epilampra	*abdomennigrum*	(De Geer, 1773)					o	o	o		(Bonfils, 1975; Bruijning, 1959; Hebard, 1921b, 1926, 1929; Princis, 1963; Princis and Kevan, 1955; Rehn, 1903; Shelford, 1910)
	amapae	Rocha e Silva Albuquerque & Gurney, 1962								o	(Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)

azteca	Saussure, 1868	o				o	o		(Bonfils, 1975, 1987; Bruijning, 1959; Hebard, 1921b, 1926; Perez, 1988; Princis, 1963; Princis and Kevan, 1955)
bromeliacea	Princis, 1965				o				(Princis, 1963)
carsevennae	Bonfils, 1975						o		(Bonfils, 1975)
colorata	Rocha e Silva Albuquerque & Gurney, 1962				o			o	(Evangelista et al. 2016; Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
conferta	Walker, 1868							o	(Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
conspersa	Burmeister, 1868					o	o	o	(Bruijning, 1959; Hebard 1921b, 1926; Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
crossea	Saussure, 1864					o	o		(Bonfils, 1975; Bruijning, 1959; Hebard 1921b, 1926; Princis, 1963)
egregia	Hebard, 1926					o	o		(Bonfils, 1975; Bruijning, 1959; Princis, 1963)
fusca	Brunner von Wattenwyl, 1865	?	?	?	o	o			(Bruijning, 1959; Perez, 1988; Princis, 1963; Rehn, 1906)

grisea	(De Geer, 1773)		o	o	o	o	(Baaren et al., 2002; Bonfils, 1975; Bruijning, 1959; Hebard, 1921b, 1926; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963; Rehn, 1903, 1906; Rocha e Silva Albuquerque and Gurney, 1962; Shelford, 1910; Walker, 1868)
guianae	Hebard, 1926		o	o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
maculicollis	(Serville, 1838)		o		o		(Hebard, 1921b; Rehn, 1906)
opaca	Walker, 1868	?	o	o	o	o	(Bonfils, 1975; Bruijning, 1959; Hebard, 1926, 1929; Pellens and Grandcolas, 2008; Perez, 1988; Rocha e Silva Albuquerque and Gurney, 1962; Roth, 1970; Walker, 1868)
sagitta	Hebard, 1929					o	(Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
sodalis	Walker, 1868	o	o	o	o	o	(Bonfils, 1975; Bruijning, 1959; Evangelista et al. 2015; Hebard, 1926; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963)
substrigata	Walker, 1868	o				o	(Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963; Roth, 1970; Rocha e Silva

											Albuquerque and Gurney, 1962; Shelford, 1910)
	taira	Hebard, 1926						o	o	o	(Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963)
Galiblatta	*cribrosa*	Hebard, 1926						o	o		(Bruijning, 1959; Hebard, 1926)
Notolampra	*punctata*	Saussure, 1862						o	o	o	(Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962)
Phoraspis	*pellucens*	(Thunberg, 1826)						o			(Princis, 1963; Shelford, 1910)
Oxyhaloinae											
Nauphoeta	*cinerea*	(Olivier, 1789)	o	o	o	o	o	o	o	o	(Princis, 1963)
Rhyparobia	*maderae*	(Fabricius, 1781)	o	o	o	o	o	o	o	o	(Bonfils, 1987; Bruijning, 1959; Hebard, 1926; Perez, 1988; Princis and Kevan, 1955)
Panchlorinae											
Achroblatta	*luteola*	(Blanchard, 1843)					o	o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
Panchlora	*aurora*	Hebard, 1926					o	o	o		(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Princis, 1963)
	bidentula	Hebard, 1916	o					o	o		(Bonfils, 1975; Bonfils, 1987; Bruijning, 1959; Hebard, 1926;

										Perez, 1988; Princis, 1963; Princis and Kevan, 1955)
dumicola	Rocha e Silva Albuquerque & Gurney, 1962								o	(Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
exoleta	Burmeister, 1838	?	?	?					o	(Pellens and Grandcolas, 2008; Perez, 1988; Rocha e Silva Albuquerque and Gurney, 1962)
fraterna	Saussure & Zehntner, 1893					o	o			(Bruijning, 1959; Hebard, 1929; Princis, 1963)
hebardi	Princis, 1951					o	o	o		(Bonfils, 1975; Princis, 1963)
maracaensis	Lopes & Oliveira, 2000				o					(Pellens and Grandcolas, 2008)
nivea	(Linnaeus, 1758)	o	o	o	o	o	o	o	o	(Bonfils, 1975; Bruijning, 1959; Hebard 1921b, 1926, 1929; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963; Princis and Kevan, 1955; Walker, 1868)
peruana	Saussure, 1864					o				(Rehn, 1906)
regalis	Hebard, 1926						o	o	o	(Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962)
thalassina	Saussure & Zehntner, 1893	o	o						o	(Bonfils, 1987; Pellens and Grandcolas, 2008; Perez, 1988)

	viridis	(Fabricius, 1775)					o				(Gutierrez and Perez-Gelabert, 2000; Rehn, 1906)
Pycnoscelinae											
Proscratea	*complanata*	(Perty, 1832)						o	o		(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Princis, 1963)
Pycnoscelus	*surinamensis*	(Linnaeus, 1758)	o	o	o	o	o	o	o	o	(Bonfils, 1987; Bruijning, 1959; Hebard, 1926; Perez, 1988; Princis, 1963; Princis and Kevan, 1955; Rehn, 1906)
Zetoborinae											
Lanxoblatta	*emarginata*	(Burmeister, 1931)					o	o	o		(Bruijning, 1959; Hebard 1921b, 1926; Princis, 1963)
Phortioeca	*nimbata*	(Burmeister, 1838)						o	o		(Bruijning, 1959; Hebard 1921b, 1926; Princis, 1963)
Schizopilia	*fissicollis*	(Serville, 1838)						o	o		(Bruijning, 1959; Hebard, 1921b, 1926; Princis, 1963; Rehn and Hebard 1927; Shelford, 1910)
	neblinensis	Lindemann, 1971	o								(Beccaloni, 2007; Bonfils, 1987)
Schultesia	*nitor*	Grandcolas, 1991							o		(Baaren et al., 2002; Grandcolas, 1990)
Thanatophyllum	*akinetum*	Grandcolas, 1991					o		o		(Evangelista et al. 2015; Grandcolas, 1990)
Tribonium	*guyanense*	Grandcolas, 1993							o		(Grandcolas, 1993b)
Zetoborella	*gemmicula*	Hebard, 1921						o	o		(Bruijning, 1959; Hebard 1921b, 1926; Princis, 1963)
Blattidae											

Blattinae											
Blatta	*orientalis*	Linnaeus, 1758	o	o	o	o	o	o	o	o	(Princis, 1963)
Neostylopyga	*rhombifolia*	(Stoll, 1813)	o	o	o	o	o	o	o	o	(Perez, 1988; Princis, 1963)
Pelmatosilpha	*guianae*	Hebard, 1926						o	o	o	(Baaren et al., 2002; Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Rehn 1930)
	lata	Hebard, 1929					o	o			(Bruijning, 1959; Hebard, 1929; Princis, 1963; Rehn, 1930)
	macu	Rehn, 1930								o	(Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
	miranha	Rehn, 1930								o	(Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
Periplaneta	*americana*	(Linnaeus, 1758)	o	o	o	o	o	o	o	o	(Bruijning, 1959; Hebard, 1926; Princis, 1963; Perez, 1988; Princis and Kevan, 1955)
	australiasiae	(Fabricius, 1775)	o	o	o	o	o	o	o	o	(Bruijning, 1959; Hebard, 1926; Princis, 1963; Perez, 1988; Princis and Kevan, 1955; Rocha e Silva Albuquerque and Gurney, 1962)
	brunnea	Burmeister, 1838	o	o	o	o	o	o	o	o	(Bruijning, 1959; Hebard, 1921b, 1926; Perez, 1988; Princis, 1963; Princis and Kevan, 1955)

Polyzosteriinae											
Eurycotis	*blattoides*	Hebard, 1926					o	o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
Corydiidae											
Corydiinae											
Eulissosoma	*stygia*	Hebard, 1926						o	o		(Hebard, 1926)
Holocompsinae											
Holocompsa	*nitidula*	(Fabricius, 1781)	o	o	o	o	o	o	o	o	(Bruijning, 1959; Hebard, 1921b, 1926; Princis, 1963; Princis and Kevan, 1955; Rehn, 1906)
Latindiinae											
Buboblatta	*geijskesi*	Bruijning, 1959						o			(Bruijning, 1959; Princis, 1963)
Latindia	*dohrniana*	Saussure & Zehntner, 1894	?	?	?	?	?	o	o	?	(Bruijning, 1959; Hebard, 1921b, 1926; Princis, 1963)
Tiviinae											
Melestora	*fusca*	Rocha e Silva Albuquerque, 1964	o								(Bonfils, 1987; Perez, 1988)
Oulopteryx	*dascilloides*	Hebard, 1921						o	o		(Bruijning, 1959; Hebard, 1921b, 1926; Princis, 1963)
Sphecophila	*polybiarum*	Shelford, 1907							o		(Bruijning, 1959; Hebard, 1921b, 1926)
Ectobiidae											
Anaplectinae											
Anaplecta	*analisignata*	Rehn, 1916								o	(Pellens and Grandcolas, 2008)

balachowskyi	Bonfils, 1975				o		(Bonfils, 1975)
bivittata	Brunner von Wattenwyl, 1865	o				o	(Bonfils, 1987; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962)
guianae	Bruijning, 1959			o			(Bruijning, 1959)
hemiscotia	Hebard, 1920					o	(Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
jari	Rocha e Silva Albuquerque, 1966					o	(Pellens and Grandcolas, 2008)
lateralis	Burmeister, 1838	o					(Bonfils, 1987; Perez, 1988; Princis, 1963)
maronensis	Hebard, 1921			o	o	o	(Bruijning, 1959; Hebard 1921b; Pellens and Grandcolas, 2008)
minutissima	(De Geer, 1773)			o	o		(Bruijning, 1959; Hebard, 1926)
parviceps	(Walker, 1868)		o	o	o	o	(Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008)
pluto	Hebard, 1926			o	o		(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Princis, 1963)
poecila	Hebard, 1926	o	o	o	o	o	(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963; Rocha e

								Silva Albuquerque and Gurney, 1962)
	pulchella	Rehn, 1906		o	o	o	o	(Bruijning, 1959; Hebard 1921b; Pellens and Grandcolas, 2008; Rehn, 1906)
	pygmaea	Bruijning, 1959			o			(Bruijning, 1959; Princis, 1963)
	subsignata	Hebard, 1926	o		o	o	o	(Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962)
	suffusa	Hebard, 1926		o	o	o	o	(Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962)
Maraca	*fossata*	Hebard, 1926	o		o	o		(Bruijning, 1959; Hebard, 1926; Perez, 1988; Princis, 1963)
Attaphilinae								
Attaphila	*aptera*	Bolivar, 1905			o			(Bruijning, 1959; Princis, 1963)
Blattellinae								
Anisopygia	*decora*	Hebard, 1926		o		o		(Bruijning, 1959; Evangelista et al. 2015; Hebard, 1926)

Blattella	*germanica*	(Linnaeus, 1767)	o	o	o	o	o	o	o	o	(Bonfils, 1987; Perez, 1988; Princis, 1963; Princis and Kevan, 1955)
Cahita	*insignis*	(Hebard, 1926)							o		(Bruijning, 1959; Hebard, 1926; Rehn, 1937a)
Chromatonotus	*coloratus*	Rocha e Silva Albuquerque, 1964	o								(Perez, 1988)
	infuscatus	(Bruner, 1906)	o								(Bonfils, 1987; Princis, 1963; Princis and Kevan, 1955)
	notatus	(Brunner von Wattenwyl, 1893)						o	o		(Bonfils, 1975, 1987; Bruijning, 1959; Hebard, 1926; Princis, 1963)
Dasyblatta	*charpentierae*	Bonfils, 1975							o		(Bonfils, 1975)
	maldonadoi	Rocha e Silva Albuquerque, 1964	o								(Bonfils, 1987; Perez, 1988; Princis, 1963)
	stylata	Bonfils, 1975							o		(Bonfils, 1975)
	thaumasia	Hebard, 1921					o	o			(Bonfils, 1975; Bruijning, 1959; Evangelista et al. 2016; Princis, 1963)
	warei	Evangelista & Mendoza, 2016					o				(Evangelista et al. 2016)
Eudromiella	*bequaerti*	Rehn, 1932	o								(Bonfils, 1987; Perez, 1988; Princis, 1963)
	chopardi	Hebard, 1926						o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
	inexpectata	(Rehn, 1906)					o		o		(Bruijning, 1959; Hebard, 1926, 1929; Princis, 1963; Rehn, 1906)

	maroni	Hebard, 1926				o		(Bruijning, 1959; Hebard, 1926)
Ischnoptera	*atrata*	Hebard, 1916			o			(Princis, 1963; Hebard, 1916)
	castanea	Saussure, 1869	o				o	(Bonfils, 1987; Pellens and Grandcolas, 2008; Perez, 1988; Rocha e Silva Albuquerque and Gurney, 1962)
	clavator	Rehn, 1918					o	(Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
	galibi	Hebard, 1926			o	o	o	(Bonfils, 1975; Bruijning, 1959; Evangelista et al. 2016; Hebard, 1926)
	hercules	Rehn, 1928			o	o		(Bruijning, 1959; Princis, 1963; Rehn, 1928)
	neoclavator	Rocha e Silva Albuquerque, 1964	o					(Bonfils, 1987; Perez, 1988; Princis, 1963)
	ocularis	Saussure, 1873					o	(Beccaloni, 2007)
	paramacca	Hebard, 1926			o	o	o	(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Princis, 1963)
	rehni	Hebard, 1926			o	o	o	o	(Bonfils, 1975, 1987; Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962)
	rufa	(De Geer, 1773)			o	o			(Bruijning, 1959; Gutierrez and Perez-Gelabert, 2000;

								Princis and Kevan, 1955; Rehn, 1903)
	stygia	Hebard, 1926	o		o	o	o	(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962)
Pseudomops	*affinis*	(Burmeister, 1838)			o	o	o	(Bruijning, 1959; Hebard, 1926, 1929; Pellens and Grandcolas, 2008; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962; Walker, 1868)
	angustus	Walker, 1868	o					(Bonfils, 1987; Perez, 1988; Princis, 1963)
	brunneri	(Saussure, 1869)			o	o		(Bruijning, 1959; Hebard, 1929; Princis, 1963)
	crinicornis	(Burmeister, 1838)			o			(Rehn, 1906)
	luctuosus	(Saussure, 1868)			o	o	o	(Bruijning, 1959; Hebard, 1926; Princis, 1963)
	oblongatus	(Linnaeus, 1758)			?	o	o	(Bonfils, 1975; Bruijning, 1959; Princis, 1963; Walker, 1868)
Xestoblatta	*agautierae*	Grandcolas, 1992			o		o	(Evangelista et al. 2015; Grandcolas, 1992a)
	amaparica	Rocha e Silva Albuquerque & Gurney, 1962	o				o	(Bonfils, 1987; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963; Rocha e Silva

							Albuquerque and Gurney, 1962)
	carbuncula	Grandcolas, 1992				o	(Grandcolas, 1992a)
	castanea	Hebard, 1926			o	o	(Bruijning, 1959; Hebard, 1926; Princis, 1963)
	cavicola	Grandcolas, 1992				o	(Grandcolas, 1992a)
	jygautieri	Grandcolas, 1992				o	(Grandcolas, 1992a)
	micra	Hebard, 1921		o			(Princis, 1963)
	nourragui	Grandcolas, 1992				o	(Grandcolas, 1992a)
	nyctiboroides	(Rehn, 1906)		o		o	(Bruijning, 1959; Hebard, 1926; Princis, 1963; Rehn, 1906)
	berenbaumae	Evangelista et al. 2015		o			(Evangelista et al. 2015)
	surinamensis	Bruijning, 1959		o	o	o	(Bonfils, 1975; Bruijning, 1959; Evangelista et al. 2016; Princis, 1963)
Nyctiborinae							
Megaloblatta	*insignis*	(Serville, 1838)			o	o	(Bruijning, 1959; Hebard, 1926; Princis, 1963)
Nyctibora	*brunnea*	(Thunberg, 1826)	o			o	(Bonfils, 1975; Perez, 1988; Hebard 1921b)
	dichropoda	Hebard, 1926		o	o	o	(Evangelista et al. 2015; Hebard, 1926; Princis, 1963)

	latipennis	Burmeister, 1838		o	o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963; Rehn, 1906; Walker, 1868)
	tenebrosa	Walker, 1868		o	o	o	o	(Bonfils, 1975, 1987; Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963; Walker, 1868)
Paramuzoa	*alsopi*	Grandcolas, 1993				o		(Grandcolas, 1993a)
Paratropes	*elegans*	(Burmeister, 1838)		o	o	o	o	(Bruijning, 1959; Hebard, 1921b; Pellens and Grandcolas, 2008; Princis, 1963; Rehn, 1906; Rocha e Silva Albuquerque and Gurney, 1962; Walker, 1868)
	phalerata	(Erichson, 1848)		o	o	o		(Bruijning, 1959; Hebard, 1929; Princis, 1963; Princis and Kevan, 1955)
Pseudischnoptera	*lineata*	(Olivier, 1789)			o	o		(Princis, 1963; Hebard, 1921b, 1926; Rehn and Hebard, 1927)
Pseudophyllodromiinae								
Amazonina	*conspersa*	(Brunner von Wattenwyl, 1865)	o	o	o	o	o	(Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Perez, 1988; Princis, 1963)
	impuctata	Rocha e Silva Albuquerque, 1995	o					(Bonfils, 1987; Perez, 1988; Princis, 1963)

	lanei	Rocha e Silva Albuquerque, 1962	o				o	(Pellens and Grandcolas, 2008; Perez, 1988; Rocha e Silva Albuquerque and Gurney, 1962)
	platystylata	(Hebard, 1921)		o	o	o		(Bruijning, 1959; Perez, 1988; Hebard, 1921b, 1929)
Arawakina	*frontalis*	Hebard, 1926		o		o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
Calhypnorna	sp.	Saussure & Zehntner, 1893		o				(Evangelista et al. 2015)
Cariblatta	*personata*	Rehn, 1916				o		(Bruijning, 1959; Hebard, 1926)
Cariblattoides	*gruneri*	Bonfils, 1975				o		(Bonfils, 1975)
	guyanensis	Bonfils, 1975				o		(Bonfils, 1975)
	sinnamariensis	Bonfils, 1975				o		(Bonfils, 1975)
Ceratinoptera	*picta*	Brunner von Wattenwyl, 1865			o	o		(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Princis, 1963; Princis and Kevan, 1955)
Chorisoneura	*albonervosa*	Rehn, 1916			o	o		(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Princis, 1963)
	barticae	Hebard, 1921		o	o	o		(Bonfils, 1975; Bruijning, 1959; Hebard 1921b, 1926; Princis, 1963)
	cistelina	(Walker, 1868)			o	o		(Bonfils, 1975; Bruijning, 1959; Hebard, 1926)
	elegantula	Hebard, 1926			o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)

fuscipennis	Hebard, 1920		o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
galibi	Hebard, 1926		o	o		(Bonfils, 1975; Bruijning, 1959)
gatunae	Hebard, 1921		o	o		(Bruijning, 1959; Hebard, 1926; Perez, 1988; Princis, 1963)
gracilis	(Saussure, 1862)	o	o			(Bruijning, 1959; Princis, 1963; Rehn, 1906)
guianae	Hebard, 1921	o	o	o		(Bruijning, 1959; Hebard 1921b, 1926)
heydei	Bruijning, 1959		o			(Bruijning, 1959; Princis, 1963)
inversa	Hebard, 1926	o	o	o	o	(Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963)
lata	Rehn, 1916		o	o		(Bonfils, 1975; Bruijning, 1959; Hebard 1921b, 1926)
multivenosa	Saussure, 1869			o		(Beccaloni, 2007)
parishi	Rehn, 1918	o	o	o		(Bruijning, 1959; Hebard, 1926; Perez, 1988; Princis, 1963)
splendida	Hebard, 1926	o	o	o		(Bonfils, 1975; Bruijning, 1959; Hebard, 1926, 1929; Princis, 1963)
strigifrons	Hebard, 1926		o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
stylata	Hebard, 1926	o	o			(Bruijning, 1959; Hebard, 1926; Princis, 1963)
surinama	Saussure, 1868		o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)

	vitrifera	(Walker, 1868)		o	o	o		(Bruijning, 1959; Hebard, 1926, 1929)
	vivida	Rocha e Silva Albuquerque & Gurney, 1962					o	(Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
Dendroblatta	*callizona*	Rehn, 1928		o	o			(Princis, 1963; Princis and Kevan, 1955; Bruijning, 1959; Rehn, 1928)
	cnephaia	Hebard, 1926			o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
	insignis	Hebard, 1926			o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
	litura	Evangelista & Sylvain, 2016		o				(Evangelista et al. 2016)
Doradoblatta	*coppenamensis*	Bruijning, 1959			o			(Bruijning, 1959; Princis, 1963)
Euphyllodromia	*amazonensis*	Rocha e Silva, 1984		o				(Evangelista et al. 2016)
	atropos	Rehn, 1928		o	o	o		(Bonfils, 1975; Bruijning, 1959; Princis, 1963; Rehn, 1928)
	aurora	Rehn, 1932				o	o	(Bonfils, 1975; Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
	chopardi	Hebard, 1921	o	o		o	o	(Bruijning, 1959; Hebard 1921b; Pellens and Grandcolas, 2008; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962)

elegans	(Shelford, 1907)						o	o	(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Rehn, 1928; Rocha e Silva Albuquerque and Gurney, 1962)
fasciatella	(Saussure, 1868)				o	o			(Bruijning, 1959; Hebard, 1929; Princis, 1963; Rehn, 1906)
hystrix	(Saussure, 1869)	?	?	?					(Bonfils, 1987; Perez, 1988; Princis, 1963; Hebard, 1929)
literata	(Burmeister, 1838)				o	o	o	o	(Bruijning, 1959; Hebard 1921b, 1926; Pellens and Grandcolas, 2008; Princis, 1963; Walker, 1868)
marowijnensis	Bruijning, 1959					o			(Bruijning, 1959; Princis, 1963)
obscura	(Saussure, 1873)				o				(Rehn, 1906)
pavonacea	(Rehn, 1903)				o	o	o	o	(Bonfils, 1975; Bruijning, 1959; Pellens and Grandcolas, 2008; Princis, 1963; Rehn, 1903, 1906; Rocha e Silva Albuquerque and Gurney, 1962)
prona	(Rehn, 1906)				o				(Bruijning, 1959; Princis, 1963; Rehn, 1906)
variegata	(Walker, 1868)					o	o	o	(Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963; Rocha e

								Silva Albuquerque and Gurney, 1962)
Imblattella	*litosoma*	(Hebard, 1926)			o	o	o	(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962)
Leuropeltis	*atopa*	Hebard, 1921				o		(Bruijning, 1959; Hebard 1921b, 1926)
	gurneyi	Rocha e Silva Albuquerque, 1964	o					(Bonfils, 1987; Perez, 1988; Princis, 1963)
Lophoblatta	*arawaka*	Hebard, 1929		o	o			(Bonfils, 1975, 1987; Bruijning, 1959; Perez, 1988; Princis, 1963; Princis and Kevan, 1955; Hebard, 1929)
	brevis	Rehn, 1937	o	o	o			(Bruijning, 1959; Perez, 1988; Princis, 1963; Rehn, 1937b)
	pellucida	(Burmeister, 1838)			o	o	o	(Pellens and Grandcolas, 2008; Princis, 1963)
Macrophyllodromia	*nigrigena*	Hebard, 1926		o	o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
Nahublattella	*aristonice*	Hebard, 1926			o	o		(Bonfils, 1975; Hebard, 1926; Princis, 1963)
	incompta	(Hebard, 1926)				o		(Bonfils, 1975; Bruijning, 1959; Hebard 1926)
Neoblattella	*adspersicollis*	(Stål, 1860)					o	(Bruijning, 1959; Hebard 1921b; Pellens and Grandcolas, 2008; Rocha e

								Silva Albuquerque and Gurney, 1962)
	binodosa	Hebard, 1926			o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
	elegantula	Rocha e Silva Albuquerque, 1964	o					(Perez, 1988; Princis, 1963; Lopes and Oliveira 2004)
	guianae	Hebard, 1929		o		o	o	(Bonfils, 1975; Hebard, 1929; Lopes and Oliveira, 2004; Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
	longior	Hebard, 1926			o	o		(Bruijning, 1959; Hebard, 1926; Lopes and Oliveira, 2004; Princis, 1963)
	nodipennis	Hebard			o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)
	picta	Rocha e Silva Albuquerque & Gurney, 1962					o	(Pellens and Grandcolas, 2008; Rocha e Silva Albuquerque and Gurney, 1962)
	poecilops	Hebard, 1926			o	o		(Bruijning, 1959; Hebard, 1926; Lopes and Oliveira, 2004; Princis, 1963)
	titania	(Rehn, 1903)		o	o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963; Rehn 1903)
	unifascia	Hebard, 1926				o		(Bruijning, 1959; Hebard, 1926; Lopes and Oliveira, 2004; Princis, 1963)
Plectoptera	*pulicaria*	Saussure & Zehntner, 1893			o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963)

Riatia	*distincta*	(Hebard, 1926)						o	o		(Bruijning, 1959; Hebard, 1926)
	fulgida	(Saussure, 1862)					o	o			(Bruijning, 1959; Rehn, 1906; Princis, 1963)
	orientis	(Hebard, 1926)	o				o	o	o		(Bruijning, 1959; Hebard, 1926; Princis, 1963; Perez, 1988; Princis and Kevan, 1955)
	stylata	(Hebard, 1926)						o	o		(Bonfils, 1975; Bruijning, 1959; Hebard, 1926)
	variegata	Rocha e Silva Albuquerque & Aguiar, 1976	o								(Perez, 1988)
	venezuelana	Rocha e Silva Albuquerque, 1964	o								(Perez, 1988; Princis, 1963)
Sciablatta	*galibi*	Hebard, 1926							o		(Bruijning, 1959; Hebard, 1926)
	poecila	Hebard, 1921					o		o		(Bruijning, 1959; Hebard, 1921b; Princis, 1963)
Supella	*longipalpa*	(Fabricius, 1798)	o	o	o	o	o	o	o	o	(Bonfils, 1987; Bruijning, 1959; Hebard, 1929; Perez, 1988; Princis, 1963; Princis and Kevan, 1955)
Tairella	*carinatifrons*	Hebard, 1926						o	o		(Hebard, 1926; Princis, 1963)
Trioblattella	*callosoma*	(Hebard, 1926)					o		o	o	(Bonfils, 1975; Bruijning, 1959; Hebard, 1926; Pellens and Grandcolas, 2008; Princis, 1963; Rocha e Silva Albuquerque and Gurney, 1962)

Lamproblattidae

Lamproblattinae

Lamproblatta	*albipalpus*	Hebard, 1919	?	?	?		o	(Hebard, 1931; Pellens and Grandcolas, 2008; Princis and Kevan, 1955; Rehn, 1930; Rocha e Silva Albuquerque and Gurney, 1962)
	ancistroides	Rehn, 1930	?	?	?	o		(Evangelista et al. 2016; Perez, 1988; Princis, 1963)

Table 1 - 2 Allometry of some Guyanese cockroaches

Allometry of new records of cockroaches from Guyana reported in the text. All values are lengths reported in millimeters. NA – refers to specimens which are damaged and therefore cannot be measured or refer to specimens for which the listed measurement does not apply. Specimens with asymmetrical styli have lengths of both right (R.) and left (L.) styli given. When possible, broken specimens had relevant measurements estimated (est.) by piecing together damaged parts or extrapolating visually.

Morphological feature			*Eublaberus distanti* Adult ♂ DEKBO0843	*Neorhicnoda maronensis* Adult ♂ DECBA0615	*Colapteroblatta surinama* Adult ♂ DECBA0703	*Colapteroblatta surinama* Adult ♀ DECBA1810	*Epilampra opaca* Adult ♂ DECBA1845	*Epilampra opaca* Adult ♀ DECBA1847	*Epilampra sodalis* Adult ♀ DECBA0401	*Thanatophyllum akinetum* Adult ♂ DECBA0611
Head	Greatest width		6.5	4.5	3.0	3.4	3.3	3.8	5.0	3.8
	Medial length		7.5	5.4	3.1	3.4	3.1	4.5	5.5	3.8
Pronotum	Greatest width		17.5	12.9	6.0	6.5	6.0	8.0	10.0	10.0
	Medial length		11.0	8.8	4.7	4.5	4.6	6.5	7.8	7.0
Leg	Front	Femur	6.0	5.0	2.2	2.2	3.0	3.5	4.8	4.0
		Tibia	2.8	2.2	1.4	1.6	2.0	2.5	2.5	2.2
	Middle	Femur	9.5	6.3	2.3	2.7	4.5	5.5	5.6	5.0
		Tibia	7.0	4.5	1.8	1.9	4.0	4.0	5.5	4.9
	Hind	Femur	10.0	6.7	3.1	2.7	5.8	6.0	7.0	5.8
		Tibia	13.0	8.5	3.7	3.4	7.9	9.2	10.0	8.0
Cerci length			3.0	1.5	0.6	0.5	3.0	2.2	3.3	1.2
Styli length			0.8	0.5	0.3	NA	0.5	NA	NA	NA
Tegminal length			39.5	NA	10.0	2.0	20.0	24.5	28.0 (est.)	22.0
Total body length			43.5	34.0	15.7	19.3	20.5	25.0	31.0	26.0

Table 1 – 2 continued

Morphological feature			*Anaplecta parviceps* Adult ♂ DECBA1843	*Anisopygia decora* Adult ♀ DEKBO0504	*Ischnoptera atrata* Adult ♂ DECBA2153	*Ischnoptera atrata* Adult ♂ DEKBO0594	*Xestoblatta agautierae* Adult ♂ DEKBO0827	*Xestoblatta agautierae* Adult ♀ DEKBO0826	*Nyctibora dichropoda* Adult ♂ DECBA0302	*Chorisoneura inversa* Adult ♂ DECBA1782	*Dendroblatta callizona* Adult ♀ DECBA0805	*Calhypnorna* sp. Juvenile DECBA1802
Head	Greatest width		1.0	1.8	3.1	3.5	2.6	2.4	4.9	1.6	2.4	1.5
	Medial length		1.1	1.9	3.8	4.2	3.3	3.0	6.0	1.5	2.8	1.3
Pronotum	Greatest width		1.6	3.9	5.9	6.7	5.0	5.3	11.0	2.9	4.9	1.7
	Medial length		1.1	2.4	4.0	4.8	3.4	3.8	6.0	1.8	3.0	1.6
Leg	Front	Femur	1.0	1.8	3.1	3.0	2.8	3.1	6.0	1.5	2.8	1.1
		Tibia	0.7	1.0	2.2	2.0	1.7	2.0	4.0	1.0	1.9	0.7
	Middle	Femur	1.4	2.2	4.0	3.8	3.5	4.0	7.6	?	3.4	1.4
		Tibia	1.2	1.8	4.1	3.6	3.4	3.5	7.0	?	2.8	1.0
	Hind	Femur	NA	2.5	5.2	4.3	4.0	4.6	9.0	2.3	4.3	1.4
		Tibia	NA	2.9	6.0	6.1	6.0	5.1	12.0	2.7	4.6	1.3
Cerci length			NA	1.6	3.6	3.0	2.3	2.3	7.0	1.6	3.3	0.6
Styli length			0.1	NA	0.6 (L.) 0.9 (R.)	0.5 (L.) 0.7 (R.)	NA	NA	2.0 (L.) 1.2 (R.)	0.6	NA	0.2
Tegminal length			3.7	1.3	22.0	21.8	10.0	10.0	36.0	7.4	9.8	NA
Total body length			4.7	8.9	21.8	21.3	17.0 (est.)	15.0	37.0	7.8	13.8	7.3

Table 1 – 2 continued

Morphological feature			*Lamproblatta ancistroides*		*Eublaberus marajoara*	*Epilampra colorata*		*Dasyblatta thaumasia*			*Euphyllodromia amazonensis*	*Xestoblatta surinamensis*			
			Adult ♀	Adult ♂	Adult ♀	Adult ♀	Adult ♂	Adult ♂	Adult ♀	Adult ♀	Adult ♀	Adult ♀		Adult ♂	
			DEIWO 0279	DEIWO 0470	DEKBO 1034	DEIWO 0301	DEIWO 0190	DEKBO 0706	DEKBO 1308	DEKBO 0514	DEIWO 0173	DEIWO 0441	DEIWO 0449	DEIWO 0457	DEIWO 0497
Head		Greatest width	3.0	3.1	6.0	3.5	3.0	2.1	1.8	2.0	2.9	2.9	3.0	3.0	2.5
		Medial length	5.5	3.7	7.1	3.8	3.0	2.6	2.0	2.7	2.3	3.6	4.0	3.5	3.4
Pronotum		Greatest width	7.0	5.8	14.5	6.5	5.0	3.1	3.3	2.3	3.9	5.5	6.0	5.5	6.0
		Medial length	6.0	3.6	10.5	5.0	4.0	2.5	2.1	3.0	2.6	3.1	4.0	4.0	4.0
Leg	Front	Femur	3.7	3.5	7.1	3.1	3.0	2.2	2.1	2.1	2.5	3.9	4.1	3.9	4.0
		Tibia	3.2	2.7	4.0	2.0	1.8	1.0	1.1	1.5	1.9	2.8	2.9	2.9	2.3
	Middle	Femur	5.5	4.0	9.0	4.0	3.8	3.5	2.5	2.9	2.3	5.1	5.2	5.1	5.3
		Tibia	5.0	3.4	6.1	4.5	3.5	2.5	2.4	3.0	2.9	5.0	5.0	4.5	4.6
	Hind	Femur	6.5	5.0	9.0	5.0	4.1	4.9	3.0	3.5	3.0	6.2	5.9	6.0	5.6
		Tibia	7.0	6.0	10.0	7.0	6.5	4.1	3.5	3.8	4.0	8.0	8.0	8.0	7.9
		Cerci length	3.2	2.9	2.5	2.0	2.0	3.0	2.0	NA	2.5	3.1	3.0	3.1	3.3
		Tegminal length	N/A	N/A	31.3	20.0	16.0	9.9	10.0	10.4	10.1	18.2	20.0	19.0	18.5
		Total body length	25.0	16.8	33.0	22.0	18.1	10.0 (est.)	11.1	NA	10.5	18.1	19.2	17.9	20.0

Table 1 - 3 Allometry of *Dasyblatta warei*

All measurements in millimeters. The abdomen of the male specimen is not connected to its body so total body length was estimated (est.) based on the two parts.

Morphological feature			*Dasyblatta warei* Adult ♂ DECBA0907	*Dasyblatta warei* Adult ♀ DECBA1803
Head	Greatest width		1.8	1.5
	Medial length		2.0	2.1
Pronotum	Greatest width		2.4	2.5
	Medial length		1.9	2.2
Leg	Front	Femur	1.8	1.7
		Tibia	1.5	1.2
	Middle	Femur	2.1	2.4
		Tibia	2.9	2.4
	Hind	Femur	3.4	2.9
		Tibia	2.9	3.0
Cerci length			1.6	1.1
Tegminal length			9.0	2.1
Total body length			9.2 (est)	8.5

Table 1 - 4 Allometry of *Ischnoptera galibi*

Allometric data for *Ischnoptera galibi* Hebard. All measurements in millimeters. Some specimens were damaged, in which case the measurement could not be completed (NA) or had to be estimated (est.). Given the large number of specimens we measured we summarize our measurements as average values +/- their standard deviation.

Morphological feature			*Ischnoptera galibi*				
			Adult ♂ (Avg. from Karanambu) DEKBO 0345, DEKBO 0351, DEKBO 0344, DEKBO 0259	Adult ♀ (Avg. from Karanambu) DEKBO 0342, DEKBO 0343, DEKBO 0482, DEKBO 1534	Adult ♂ (Avg. from CEIBA) DECBA2210, DECBA2212	Adult ♂ (Avg. from CEIBA) DECBA2211, DECBA2019	Adult ♂ (Iwokrama) DEIWO 0120
Head		Greatest width	1.8 +/-0.22	1.5 +/-0.04	1.5 +/-0.05	1.6 +/-0.05	1.5
		Medial length	2.2 +/-0.22	2.0 +/-0.07	2.0 +/-0.05	2.1 +/-0.05	1.9
Pronotum		Greatest width	2.9 +/-0.14	2.9 +/-0.08	3.0 +/-0.00	3.1 +/-0.05	2.9
		Medial length	1.8 +/-0.35	2.1 +/-0.04	2.0 +/-0.00	2.0 +/-0.00	1.8
Leg	Front	Femur	1.9 +/-0.09	2.0 +/-0.08	2.0 +/-0.00	2.2 +/-0.15	1.6
		Tibia	1.4 +/-0.52	1.1 +/-0.05	1.1 +/-0.05	1.2 +/-0.15	1.1
	Middle	Femur	2.1 +/-0.05	2.2 +/-0.18	2.3 +/-0.30	2.3 +/-0.25	2.1
		Tibia	2.0 +/-0.04	2.1 +/-0.05	2.3 +/-0.20	2.4 +/-0.25	2.0
	Hind	Femur	2.6 +/-0.29	2.7 +/-0.15	2.8 +/-0.15	2.4 +/-0.15	2.4
		Tibia	3.0 +/-0.07	3.2 +/-0.11	3.1 +/-0.05	3.4 +/-0.25	3.0
		Cerci length	1.5 +/-0.10	1.9 +/-0.09	2.0 +/-0.05	1.8 +/-0.35	1.7
		Tegminal length	9.0 +/-0.54	8.2 +/-0.16	8.7 +/-0.20	9.0 +/-0.00	8.2
		Total body length	9.8 +/-0.64	8.9 +/-0.51	9.3 +/-1.30	8.3 +/-0.00	8.5 (est)

Table 1 - 5 Allometry of *Xestoblatta berenbaumae*

Allometry of *Xestoblatta berenbaumae*. All values are lengths reported in millimeters.

Morphological feature			*Xestoblatta berenbaumae* sp. n.										
			Adult ♂ (HT)	Adult ♂	Adult ♂	Adult ♂	Adult ♂	Adult ♂	Adult ♂	Adult ♀	Adult ♀	Adult ♀	Adult ♀
			DECBA2109	DECBA1967	DECBA0801	DECBA1958	DECBA2182	DECBA2092	DECBA2039	DECBA1787	DECBA1974	DECBA1793	DECBA2074
Head	Greatest width		2.7	3.0	3.0	2.9	3.0	2.8	2.9	3.1	3.0	3.0	3.1
	Medial length		3.6	3.8	3.8	3.8	3.9	3.5	3.6	4.0	4.0	4.0	3.7
Pronotum	Greatest width		5.3	6.0	6.0	5.6	4.9	5.3	5.3	5.9	4.7	5.9	4.1
	Medial length		4.0	4.0	4.4	4.0	4.5	4.0	4.0	4.8	5.9	4.3	5.6
Leg	Front	Femur	3.0	3.5	4.0	4.0	3.3	3.2	4.0	3.0	3.6	3.5	3.0
		Tibia	2.0	2.0	2.5	2.0	2.5	2.0	2.4	2.0	2.6	2.3	2.0
	Middle	Femur	4.0	4.5	4.2	4.0	4.7	4.0	4.8	4.2	4.3	4.4	4.2
		Tibia	3.8	3.7	4.0	4.0	3.7	4.0	4.4	4.0	4.0	3.8	4.0
	Hind	Femur	4.9	5.0	5.0	4.5	5.0	4.8	5.4	5.7	5.0	4.9	5.0
		Tibia	6.0	6.1	6.0	5.6	6.0	6.1	6.0	6.2	6.1	6.0	6.3
Cerci length			2.8	3.0	NA	2.3	2.5	3.2	3.0	3.0	2.8	2.4	NA
Tegminal length			13.5	14.0	14.0	14.0	13.3	14.0	13.8	10.1	10.0	10.0	9.2
Total body length			NA	NA	NA	17.5	15.4	16.0	18.0	18.7	17.0	18.2 (est.)	NA

Table 1 - 6 Allometry of *Dendroblatta litura*

Allometric data for *Dendroblatta litura*. All measurements in millimeters. Some specimens were damaged, in which case the measurement could not be completed (NA) or had to be estimated (est.). Given the large number of specimens we also summarized our measurements as average values +/- their standard deviation in the two right-most columns.

			Dendroblatta litura sp. nov.								
Morphological feature			Adult ♀	Adult ♀	Adult ♀	Adult ♀	Adult ♂	Adult ♂	Adult ♂	Adult ♀	Adult ♂
			DEKBO1507	DEKBO1506	DEKBO0963	DEKBO0974	DEKBO1515	DEKBO1083	DEKBO0975	Average +/- Std. Dev.	Average +/- Std. Dev.
Head	Greatest width		2.1	2.5	2.3	2.5	2.5	2.5	2.2	2.3 +/-0.17	2.4 +/-0.14
	Medial length		3.0	2.5	2.5	2.5	2.4	2.8	2.3	2.6 +/-0.22	2.5 +/-0.22
Pronotum	Greatest width		4.3	5.0	4.5	5.0	4.5	4.5	4.1	4.7 +/-0.31	4.4 +/-0.19
	Medial length		4.5	4.0	2.5	2.5	2.8	2.9	2.6	3.4 +/-0.89	2.8 +/-0.12
Leg	Front	Femur	3.0	3.0	2.8	2.9	2.2	2.6	2.5	2.9 +/-0.08	2.4 +/-0.17
		Tibia	1.6	1.5	1.5	1.7	1.7	1.9	1.6	1.6 +/-0.08	1.7 +/-0.12
	Middle	Femur	NA	3.3	3.0	3.0	3.0	3.5	3.0	3.1 +/-0.12	3.2 +/-0.24
		Tibia	NA	3.8	3.4	2.7	2.8	2.8	3.0	3.3 +/-0.45	2.7 +/-0.09
	Hind	Femur	3.6	3.5	3.5	3.6	3.7	NA	3.2	3.6 +/-0.05	3.5 +/-0.25
		Tibia	4.5	4.3	4.1	4.3	4.5	NA	4.4	4.3 +/-0.14	4.5 +/-0.05
Cerci length			n/a	2.4	3.0	2.5	2.6	3.0	3.1	2.6 +/-0.26	2.9 +/-0.22
Tegminal length			11.0	10.0	11.0	10.9	12.0	13.3	12.2	10.7 +/-0.42	12.5 +/-0.57
Total body length			12.0	9.0	12 (est)	12.1	10.9	12.0	12.5	11.0 +/-1.44	11.8 +/-0.67

Table 1 - 7 Neotropical regions of the highest cockroach richness

The ten regions of the Neotropics with the highest known cockroach richness per unit area.

Region	Size (mi^2)	# of spp.	spp/mi^2	Source
Rio de Janiero, Brazil	16871	169	0.0100	(Pellens and Grandcolas 2008)
French Guiana	32253	151	0.0047	-
Panama	29118	118	0.0041	(Beccaloni 2007)
Costa Rica	19730	72	0.0036	(Beccaloni 2007)
Hispaniola	29530	86	0.0029	(Perez-Gelabert 2008)
Continental Ecuador	46444	114	0.0025	(Vidlicka 2013)
Suriname	63039	136	0.0022	-
Cuba	42426	85	0.0020	(Gutierrez 1995)
Amapa, Brazil	55141	70	0.0013	-
Guyana	83000	105	0.0013	-

Table 1 - 8 Predicted distributions of some Guianan cockroaches

Recorded (o and +) and projected (p) presences of cockroaches from the Guiana Shield. VEN – Combined data from Amazonas, Bolivar and Delta Amacuro Venezuela; GUY – Guyana; SUR – Suriname; FG – French Guiana; Rora BRA – Roraima, Brazil. Amapa BRA – Amapa, Brazil. Projected occurrences are expectations of species presence based on confirmed presence in neighboring regions. Data used to determine this is taken from the checklist (Table 1) and other sources (see Table 1-1 for citations for these species).

Taxon		***VEN***	***GUY***	***SUR***	***FG***	***Amapa BRA***	***Rora BRA***
Blaberidae							
Blaberinae							
Blaberus	*colosseus*	p	o	p	o		
	craniifer	p	o	p	o		
Epilamprinae							
Epilampra	*azteca*	o	p	o	o		
	colorata		o	p	p	o	
	maculicollis		o	p	o		
Thanatophyllum	*akinetum*		o	p	o		
Panchlorinae							
Panchlora	*bidentula*	o	p	o	o		
Ectobiidae							
Anaplectinae							
Anaplecta	*subsignata*	o	p	o	o	o	
Maraca	*fossata*	o	p	o	o		
Blattellinae							
Anisopygia	*decora*		o	p	o		

Cahita	*insignis*	p	p	p	o		
Chromatonorus	*notatus*	p	p	o	o		
Eudromiella	*inexpectata*		o	p	o		
Xestoblatta	*nyctiboroides*		o	p	o		
	agautierae		o	p	o		
Pseudophyllodromiinae							
Arawakina	*frontalis*		o	p	o		
Chorisoneura	*gatunae*	p	p	o	o		
Euphyllodromia	*chopardi*		o	p	o	o	o
Neoblattella	*guianae*		o	p	o	o	
Sciablatta	*poecila*		o	p	o		
Trioblattella	*callosoma*		o	p	o	o	

Table 2 - 1 Abundance profile of cockroaches by data type

A summary of the abundance profile for the data on cockroaches collected in Madewini and Kamuni Creek, Guyana. This also shows subsections of the data divided by specimens found in any of three ecological habits. Abbreviations M – refer to a morphological interpretation of species, M+G – refers to an interpretation of species using both morphological and genetic data and Δ – refer to the difference between M and M + G.

				Number of Species in ecological division...		
	Species	Singletons	Doubletons	Bromeliad	Leaf litter	Other
M	77	33	13	17	32	44
M+G	58	23	7	16	25	37
Δ	19	10	6	1	7	7

Table 3 - 1 Collection site information at Karanambu

The 28 total sites at Karanambu ranch that we sampled with beer traps. Out categorization of each of the sites habitat type is shown in the three right columns.

	Name	Latitude	Longitude			
1	BFIT	3.781367	-59.332044	Island	Dry	Forest
2	FICT	3.796253	-59.365899	Island	Dry	Forest
3	CFIT	3.782501	-59.377316	Island	Dry	Forest
4	FIDT	3.796561	-59.368546	Island	Dry	Forest
5	LFID	3.794465	-59.370007	Island	Dry	Forest
6	GIT	3.793314	-59.315881	Island	Dry	Forest
7	LFIT	3.760319	-59.309800	Island	Dry	Forest
8	MIT	3.74465	-59.345129	Island	Dry	Forest
9	FIOT	3.753338	-59.311881	Island	Dry	Forest
10	SFIT	3.777472	-59.325753	Island	Dry	Forest
11	LFCT	3.745473	-59.314412	Mainland	Dry	Forest
12	LFMHT	3.723154	-59.316731	Mainland	Dry	Forest
13	LFMHDT	3.726706	-59.319408	Mainland	Dry	Forest
14	LFRR	3.750611	-59.308656	Mainland	Dry	Forest
15	TMB	3.745455	-59.361107	Mainland	Dry	Forest
16	LFWT	3.750033	-59.314906	Mainland	Dry	Forest
17	LFWPT	3.745099	-59.320891	Mainland	Dry	Forest
18	WFT	3.797514	-59.403478	Mainland	Dry	Forest
19	ZMB	3.718842	-59.369498	Mainland	Dry	Forest
20	CIT	3.782078	-59.325057	Mainland	Flood	Forest
21	CIT2	3.773007	-59.320732	Mainland	Flood	Forest
22	PTT	3.7585278	-59.3232222	Mainland	Flood	Forest
23	SMT	3.7494722	-59.3096944	Mainland	Flood	Forest

24	TT	3.807592	-59.384875	Mainland	Flood	Forest
25	Sav	3.754519	-59.311922	NA	Dry	Savanna
26	SAT	3.769875	-59.340875	NA	Dry	Savanna
27	SAT2	3.7711111	-59.3420278	NA	Dry	Savanna
28	SWT	3.796748	-59.329108	NA	Dry	Savanna

Table 3 - 2 Taxa collected at Karanambu

Each species collected at Karanambo EcoLodge, their taxonomic affiliation and observed raw abundances.

	Family	Subfamily	Species	Individuals collected from beer traps	Beer traps on savanna	Beer traps forest islands	Beer traps flooded sites
1	Anaplectidae	Anaplectinae	*Anaplecta pygmaea*	2	1	0	0
2	Anaplectidae	Anaplectinae	*Anaplecta* sp. cf *suffusa*	1	0	0	1
3	"Ectobiidae"	"Pseudophyllodromiinae"	*Cariblatta* sp. 2	44	24	8	11
4	"Ectobiidae"	"Pseudophyllodromiinae"	*Dendroblatta* sp.	2	0	1	1
5	"Ectobiidae"	"Pseudophyllodromiinae"	*Dendroblatta litura*	7	0	1	3
6	"Ectobiidae"	"Pseudophyllodromiinae"	Undet. Sp. 1	6	1	4	1
7	"Ectobiidae"	Blattellinae	*Chromatonotus notatus*	11	0	1	2
8	"Ectobiidae"	Blattellinae	*Dasyblatta thaumasia*	2	0	0	1
9	"Ectobiidae"	Blattellinae - Ischnopterini	*Ischnoptera atrata/hercules*	127	0	5	3
10	"Ectobiidae"	Blattellinae - Ischnopterini	*Ischnoptera galibi*	527	16	402	8
11	"Ectobiidae"	Blattellinae - Ischnopterini	*Ischnoptera rufa*	1	1	0	0
12	"Ectobiidae"	Blattellinae - Ischnopterini	*Ischnoptera* sp. cf. *rehni*	18	1	1	1
13	"Ectobiidae"	Blattellinae - Ischnopterini	*Ischnoptera* sp. 1	9	0	0	9
14	"Ectobiidae"	Blattellinae - Ischnopterini	*Xestoblatta agautierae*	232	2	107	54
15	Blaberidae	Epilamprinae	*Epilampra opaca/substrigata*	69	0	26	1
16	Blaberidae	Epilamprinae	*Epilampra* sp. 1	2	0	1	0
17	Blaberidae	Epilamprinae	*Epilampra* sp. 3	1	0	0	0
			Total	**1061**	**46**	**557**	**96**

Table 3 - 3 Mantel test results

Mantel test explaining cockroach assemblage variation. We compared pairwise cockroach community dissimilarity values among sites with a pairwise habitat dissimilarity matrix (Euclidean difference) and a pairwise geographic distance matrix. “n” indicates sample size in number of sites. Matrix correlation values are Pearson’s product-moment correlation coefficients. We did 10,000 random permutations per test. The results show that both geographic distance and forest vs. savanna explain differences in the cockroach communities across the landscape. The total habitat dissimilarity treatment uses total habitat dissimilarity in all categories except geographic distance. This was the best model next to forest vs. savanna alone. To ensure that our habitat dissimilarities were not being informed by autocorrelation with geographic distance, we also performed a partial Mantel test to correct for geographic distance, which gives the same result.

	Mantel			***Partial Mantel***		
	n	***Matrix correlation***	***p - value***	***n***	***Matrix correlation***	***p - value***
Geographic distance	27	0.185*	0.024	27	-	-
Habitat dissimilarity (dry or flooded)	27	0.153	0.086	27	0.170	.067
Habitat dissimilarity (forest island or mainland)	24	-0.027	0.634	24	-0.043	0.760
Habitat dissimilarity (forest or savanna)	27	0.224*	0.045	27	0.252*	0.031
Habitat dissimilarity (total)	27	0.269*	0.005	27	0.290*	0.003

Table 3 - 4 Isolation community analysis

Results of a linear model comparing isolation measures of each site using three different landscape models (dry forest model, flood model, and forest model). Isolation values for each site (under the assumptions of the landscape model) are compared to the community of that site. The table reports P-values and R2 values for all trends, omitting those P-values >0.05. The forest model strongly explains variation in total community diversity and the richness of Ischnopterini.

	Observed abundance	Observed richness	Shannon diversity	Simpson evenness	Observed Ischnopterini richness	Ischnopterini abbundance
Forests	-	-	2.E-03	-	4.E-04	-
Dry forests	-	-	-	-	-	-
Flood	-	-	-	-	-	-
Forests * dry forests	-	-	-	-	-	-
Forests * flood	-	-	-	-	-	-
Dry forest * flood	0.039	-	-	-	0.038	-
Forests * dry forest * flood	-	-	0.020	-	-	-
Model R^2	0.33	0.31	0.55	0.41	0.58	0.26

Table 3 - 5 Isolation species analysis

Results of a linear model comparing isolation measures of each site from three different landscape models to species information. Isolation values for each site (under the assumptions of the landscape model) are compared to the Log transformed abundances for each species. The table reports P-values and R2 values for all trends, omitting those P-values >0.05. The model fit from 25-80% of total variation when probable trends were found. The abundance of *Ischnoptera* sp. cf. *rehni* is the best fit with the forest model, or even better with a combination of the dry forest and flood model. Similarly, isolation from savanna and waterways (forest model) is a likely model for explaining distribution of *Ischnoptera atrata/hercules*, and *Epilampra opaca/substrigata*.

	Anaplecta sp. cf. *suffusa*	*Anaplecta pygmaea*	*Undet. Sp. 1*	*Cariblatta* sp. 2	*Chromatonotus notatus*	*Dasyblatta thaumasia*	*Dendroblatta* sp.	*Epilampra opaca/substrigata*	*Epilampra* sp. 1	*Epilampra* sp. 3	*Ischnoptera atrata/hercules*	*Ischnoptera* sp. cf *rehni*	*Ischnoptera rufa*	*Ischnoptera galibi*	*Ischnoptera sp. 1*	*Dendroblatta litura*	*Xestoblatta agautierae*
Forests	-	-	0.047	-	-	-	-	0.001	-	-	2.E-06	2.E-05	-	-	-	-	-
Dry forests	-	-	-	-	-	-	-	-	0.045	-	-	-	-	-	-	-	-
Flood	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Forests * dry forests	-	-	-	-	0.014	-	-	-	0.017	-	-	0.016	-	0.016	-	-	-
Forests * flood	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dry forest * flood	-	-	-	-	-	-	-	0.003	-	-	-	5.E-06	-	-	-	-	-
Forests * dry forest * flood	-	-	-	-	-	-	-	-	-	-	-	-	-	0.022	-	-	-
Model R^2	0.11	0.27	0.28	0.29	0.44	0.04	0.14	0.64	0.41	0.26	0.73	0.80	0.09	0.47	0.11	0.34	0.33