FORESTGEO ARTHROPOD INITIATIVE
ANNUAL REPORT 2018

Program coordinator: Yves Basset, Smithsonian Tropical Research Institute (STRI), bassety@si.edu

I. BACKGROUND AND PARTICIPATING FORESTGEO SITES

The 'Arthropod Initiative' of the Center for Tropical Forest Science (CTFS) aims at monitoring key arthropod assemblages over long-term and studying insect-plant interactions over the network of the Forest Global Earth Observatories (ForestGEO, https://forestgeo.si.edu/research-programs/arthropod-initiative). The Initiative integrates with ongoing monitoring of plant dynamics within the ForestGEO network, causes minimum possible impact to the plots and focus on a priority set of assemblages chosen for their ecological relevance, taxonomic tractability and ease of sampling. At each participating ForestGEO site, the first years of the program are usually devoted to a 'baseline' survey. The baseline survey is followed by longer-term programs of field work and analysis, organized into two main sub-programs: monitoring, and key interaction studies. The monitoring sub-program is directed to detecting long-term changes, as reflected in priority assemblages, driven by climatic cycles, climatic change and landscape scale habitat alteration. Monitoring protocols are derived from those used during the baseline survey. The food web approach of interaction studies targets interactions between plants and specific insect assemblages, with different protocols than those used for monitoring.

So far, the Arthropod Initiative involves nine ForestGEO sites: Yasuni in Ecuador, Barro Colorado Island (BCI) in Panama, Rabi in Gabon, Khao Chong (KHC) in Thailand, Tai Po Kau (Hong Kong), Dinghushan and Xishuangbanna (XTBG) in China, Bukit Timah in Singapore and Wanang (WAN) in Papua New Guinea. At BCI, four full-time research assistants were in charge of arthropod monitoring protocols in 2018: Filonila Perez, Ricardo Bobadilla, Yacksecari Lopez and Alejandro Ramirez. The program coordinator, YB, doubled as BCI site supervisor, working at 66% FTE. The collections and staff of the ForestGEO Arthropod Initiative in Panama are based at the Tupper complex.

Most of the insect monitoring at KHC in 2018 was under the responsibility of Montarika Panmeng, Manat Reungaew, Kanyakarn Sripila and Sontaya Promchaisri. Supervision at KHC was assured by Sarayudh Bunyavejchewin, Nantachai Pongpattananurak, (Kasetsart University, Bangkok), Watana Sakchoowong (Thai National Parks Wildlife and Plant Conservation Dept) and YB (one visit of three weeks). At WAN, Richard Ctvrtecka (University of South Bohemia), Francesca Dem (Binatang Research Centre), Vojtech Novotny (Czech Academy of Sciences and University of South Bohemia) and YB (one visit of three weeks) supervised assistants Roll Liplip, Ruma Umari, Aisak Saldon, Fidelis Kimberg and Ananias Kamam, who were in charge of ForestGEO protocols. At Yasuni David Donoso (Escuela Politécnica Nacional, Quito, Ecuador) and assistants performed Winkler protocols to monitor litter ants, while Maria Fernanda Checa (Museo QCAZ de Invertebrados. Pontificia Universidad Católica del Ecuador) organized butterfly transects. Timothy Bonebrake and Chum-Lim Luk supervised butterfly monitoring at the plots of Tai Po Kau, and Dingshushan. At Xishuangbanna, Aki Nakamura (Xishuangbanna Botanical Gardens) supervised butterfly, ant, fruitfly and termite monitoring.

II. TAXONOMIC STUDIES AND DNA BARCODING

We are currently working on a revised list of the Dynastinae (rhinoceros beetles) of BCI that will be crucial for analyses of time-series for this group. Grants from the Smithsonian DNA Barcoding Opportunity and the SENACYT will allow us to barcode (results expected early 2019) species of Formicidae, Collembola, Reduviidae, Flatidae, Dynastinae, Arctiinae and Isoptera, all from BCI. David Donoso visited both STRI and the KHC insect lab in Thailand and refined ant identifications in our collections as part of our ant projects. Jan Sobotnik and Petr Stiblik (Czech University of Life Sciences, Prague) visited Panama, collected new termite material and renewed collaboration with the ForestGEO Arthropod Initiative. Jan Krecek (same institution) refined the identification of some Panamanian termites and donated a reference collection to be used in our termite project. Alejandro Ramirez is now studying closely the reduviids of BCI as part of his MSc at the University of Panama. Weeyawat Jaitrong visited our ant collections at KHC and refined some identifications. Scott Miller (NMNH, Washington) refined the identifications of many moths attacking seeds and fruits at BCI, KHC and WAN. Simon Segar (Harper Adams University, UK) organized a workshop in phylogenetical methods at the University of Panama as part of our SENACYT ant project (H. Barrios PI) and with his help we will build local phylogenies for several insect groups in 2019.

III. MONITORING: BARRO COLORADO ISLAND, KHAO CHONG AND WANANG

Year 2018 represented the tenth year of insect monitoring at BCI. So far, the BCI database contains data on 537,138 arthropods, including 2,360 species (1,756 of which with pictures, 74%) and 65,372 pinned specimens in our collections (250 drawers). Each year we collect at BCI 330 insect samples (80 light trap samples, 50 Winkler samples, 120 butterfly transects, 40 termite transects and 40 bee bait samples) and in 2018 this represented 41,604 arthropods. Field protocols represent routine work and most of our work at BCI is focused on improving our insect collections.

With the help of intern Gersey Vargas (Pontificia Universidad Javeriana – Cali, Colombia¸ scholarship SENACYT-STRI) we are currently refining the taxonomy and ecology of BCI Dynastinae, with the ultimate aim of sound analyses of time-series for this group. This project involves several colleagues, including Greg Lamarre (University of South Bohemia) who recently got funding from the Czech Grant Agency to start his laboratory at Ceske Budejovice. The "Biodiversity and Climate Change" laboratory will be closely collaborating with the ForestGEO Arthropod Initiative in 2019 and beyond, and we look forward to this exciting opportunity to increase our ability to analyze data rapidly. Meanwhile, work has progressed with the analysis of a long time-series (15 years) of alates ants and termites obtained with Malaise traps on BCI (SENACYT project) and we should have the first manuscripts ready in 2019. In particular, Constance Courville (University of Panama) worked as intern (scholarship SENACYT-STRI) on termites. Further, Candy Ramirez (University of Panama) successfully defended her MSc thesis entitled "Efecto de las variables climáticas en la fluctuación poblacional y diversidad de Arctiinae (Lepidoptera: Erebidae) en la Isla Barro Colorado en el período de 2009 a 2016, Panamá Oeste, República de Panamá". Remi Mauxion (Agro-Paris Tech, France) also successfully defended his MSc memoir entitled "An ecological study of the Papilionidae and Pieridae (Lepidoptera : Rhopalocera) of Barro Colorado Island, Panama". Congratulations to both. We are also on track with the SENACYT-funded project to test the feasibility of using DNA metabarcoding for long-term monitoring of the soil fauna (and other taxa), in collaboration with the UNAM, Mexico (J. Palacios-Vargas & G. Castano-Meneses) and the University of Guelph, Canada (M. Hajibabaei). This pilot study is using soil samples and target ants, termites and Collembola. In Panama, Marleny Rivera (University of Panama) was in charge of ant and termite identification, with the help of David Donoso, whereas our UNAM colleagues are in charge of Collembola identification.

2018 represented our eighth year of monitoring at KHC. We collected 370 insect samples (80 light trap samples, 50 Winkler samples, 120 butterfly transects, 40 termite transects and 80 McPhail samples). So far, our database includes 180,000 specimens (35,000 pinned specimens in collections) and 2,300 species. We still need to improve on processing quickly insect samples and including representative insect pictures in our database. At WAN, 2018 represented the sixth year of insect monitoring. The ForestGEO insect database contains data on 50,000 specimens, but apart from butterflies and fruitflies, few of these specimens are yet identified.

Instead of detailing statistics for each protocol performed on, for example, BCI during 2018, we present in Appendix I the full text of a paper published in *Journal of Biogeography* (please see Interaction studies). We hope that this may be of higher interest to the reader than compilation of annual indices for common species collected on BCI.

IV. INTERACTION STUDIES

The field component of our studies of insect seed and seedling predators at the three ForestGEO plot of BCI, KHC and WAN are now finished. We are currently collating all data into different databases for convenient analyses of the results. The insect seed predator databases represent over 80,000 insect records and the seedling damage database represent currently ca. 2.8 mio records. The later project monitored the survivorship of seedlings in control plots and in plots treated with insecticide, to evaluate the action of insect herbivores on seedlings (Plate I). It included sowing ca 90,000 seeds and we harvested +7,000 seedlings after 120 weeks of monitoring at the three sites. We have started analyzing the data and published our results (see Section VI, Plate I and Appendix I), but we expect that the bulk of our results should be published in 2019-2020.

This project was funded by the Grant Agency of the Czech Republic and results from a collaboration with Sofia Gripenberg (University of Reading), Owen Lewis (University of Oxford), Richard Ctvrtecka; Philip Butterill (University of South Bohemia) and Simon Segar (Harper Adams University). Assistants Karina Viquez, Yornelis Gonzalez, Maikol Guevara and Wessley Ferguson, (Panama), Sutipun Putnaul, A. Maprasong (Thailand), Aisak Saldon, Joel Jorry and Abraham Umari (Papua New Guinea) helped with the logistics of the project. A PhD student, Chris Dahl (University of South Bohemia), was also involved in the project.

V. FORESTGEO ARTHROPOD DATABASE

Phil Butterill (University of South Bohemia) continued to implement the new ForestGEO Arthropod database. The local version is now 100% complete and routinely used by 9 sites. We hope that the web version should be on-line in early 2019. Once the ForestGEO Arthropod database will be on-line, we plan on developing new web pages centered around the database, with links to insect programs at the participating ForestGEO sites and PIs. The database and related pages will allow, for sites interested to join the database project, to (a) conveniently and securely store their data; (b) facilitate overall analyses including data from several sites (for data owners interested in this opportunity); and (c) foster scientific collaboration via a better visibility of the ForestGEO Arthropod Initiative and release of case studies based on BCI data.

The current web pages of the ForestGEO Arthropod Initiative are at https://forestgeo.si.edu/research-programs/arthropod-initiative. The personal web page of the program coordinator is maintained at https://stri.si.edu/scientist/yves-basset.

VI. SCIENTIFIC OUTPUT

In 2018, the ForestGEO Arthropod Initiative trained, at the sites of BCI, KHC and WAN, 20 assistants (7: BCI, 6: KHC, 7: WAN); 3 interns (all at BCI); two MsSc students (BCI) and one PhD student (BCI-WAN). The work of other PhD students and researchers was also facilitated at these three sites. In 2018, we consolidated two projects implemented at BCI and another project distributed over BCI, KHC and WAN. We initiated new collaboration with colleagues interested in the ForestGEO Arthropod Initiative and we expect these new collaborations to flourish in 2019 and to lead to an increasing number of exciting publications.

Publications related to the ForestGEO Arthropod Initiative in 2018:

Basset, Y., Ctvrtecka, R. Dahl, C. Miller, S.E., Quicke, D.L.J., Segar, S.T., Barrios, H., Beaver, R.A., Brown, J.B., Bunyavejchewin, S., Gripenberg, S., Knižek, M., Kongnoo, P., Lewis, O.T., Pongpattananurak, N., Pramual, P., Sakchoowong, W. & Schutze, M. 2019. Insect assemblages attacking seeds and fruits in a rainforest in Thailand. *Entomological Science*, in press.

Basset, Y., Miller, S.E., Gripenberg, S., Ctvrtecka, R., Dahl, C., Leather, S.R. & Didham, R.K. 2019. An entomocentric view of the Janzen-Connell hypothesis. *Insect Conservation and Diversity*, 12, 1-8.

Basset, Y., Dahl, C., Ctvrtecka, R., Gripenberg, S., Lewis, O.T., Segar, S.T., Klimes, P., Barrios, H., Brown, J.W., Bunyavejchewin, S., Butcher, B.A., Cognato, A.I., Davies, S.J., Kaman, O., Knizek, M., Miller, S.E., Morse, G.E., Novotny, V., Pongpattananurak, N., Pramual, P., Quicke, D.L.J., Robbins, R.K., Sakchoowong, W., Schutze, M., Vesterinen, E.J., Wang, W.-z., Wang, Y.-y., Weiblen, G. & Wright, S.J. 2018. A cross-continental comparison of assemblages of seed- and fruit-feeding insects in tropical rainforests: faunal composition and rates of attack. *Journal of Biogeography*, ***45***, 1395-1407.

Dahl, C., Ctvrtecka, R., Gripenberg, S., Lewis, O.T., Segar, S.T., Klimes, P., Sam, K., Rinan, D., Filip, J., Lilip, R., Kongnoo, P., Panmeng, M., Putnaul, S., Reungaew, M., Rivera, M., Barrios, H., Davies, S.J., Bunyavejchewin, S., Wright, S.J., Weiblen, G.D., Novotny, V, & Basset, Y. 2019. The entomocentric classification of fruit syndromes in tropical rainforests: an inter-continental comparison. *Biotropica*, in press.

Gripenberg, S. 2018. Do pre-dispersal insect seed predators contribute to maintaining tropical forest plant diversity? *Biotropica*, **50**, 839–845.

Quicke, D. L., Čtvrtečka, R., & Butcher, B. A. A remarkable new genus of Braconini (Hymenoptera: Braconidae: Braconinae) from Papua New Guinea, reared from fallen fruit. 2018. *Journal of Asia-Pacific Entomology*, **21**, 527-530.

Other publications of the program coordinator in 2018:

Redmond, C.M., Auga, J., Bradley, G., Segar, S.T., Miller, S.E., Molem, K., Weiblen, G.D., Butterill, P.T., Maiyah, G., Hood, A.S.C., Volf, M., Jorge, L.R., **Basset, Y**. & Novotný, V. 2019. High specialization and limited structural change in plant-herbivore networks along a successional chronosequence in tropical montane forest. *Ecography*, **42**, 162-172.

Selected manuscripts in preparation related to the ForestGEO Arthropod Initiative:

The role of herbivorous insects in the regeneration dynamics of *Guazuma ulmifolia* in Panama. Submitted to *Nature Conservation.*

Inter-annual monitoring improves capture of regional tropical butterfly assemblages. Submitted to *Biotropica*

Long-term monitoring of social insects in tropical rainforests.

Calibrating biodiversity for long-term monitoring: detecting changes in assemblage composition from temporarily and spatially variable insect data.

Invasive ants in the Yasuni National Park. Where do they come from?

Host specificity and interaction networks of insects feeding on seeds and fruits in tropical rainforests.

A highly-resolved food web for insect seed predators in a species-rich tropical forest.

Host records from Tortricidae (Lepidoptera) reared from seeds and fruits in Panama.

Functional groups of rhinoceros beetles (Coleoptera, Dynastinae) in Panama.

Assemblages of tephritid fruit flies along an elevational gradient in the rainforests of Papua New Guinea.

Ant male flights in a Neotropical seasonal forest are shaped by low relative humidity and not by rainfall or moonlight

Plate I. Representative activities/items for the ForestGEO Arthropod Initiative in 2018. (1-3) Representative Dynastinae from different tribes: (1) *Cyclocephala brevis*, Cyclocephalini; (2) *Strategus aloeus*AS2, Oryctini; (3) *Megasoma elephas*, Dynastini. (4-7) Preliminary results of interaction studies including insect seed and seedling predators projects: (4) The newly described species of *Karposibracon papuensis* (Braconidae); (5) Distribution of the insect host specificity index DSI* among study sites, insect and plant families and fruits types; (6) Weekly number of seedlings alive in control (blue) and insecticide (orange) plots in Panama. (7) Picture of leaves of one of the +7,000 seedlings harvested to estimate leaf area and herbivory. (8) Changes in annual species composition for Pieridae and Papilionidae on BCI, 2009-2017 (R. Mauxion). (9) Population dynamics of three species of Pieridae and Papilonidae on BCI, 2009-2017 (R. Mauxion). (10) Population dynamics of several species of Arctiinae on BCI, 2009-2016 (C. Ramirez). (11) Petr Stiblik and Y. Basset in conversation at the STRI lab with termite material (J. Sobotnik). (12) *Incisitermes* sp., collected in Panama (J. Sobotnik).

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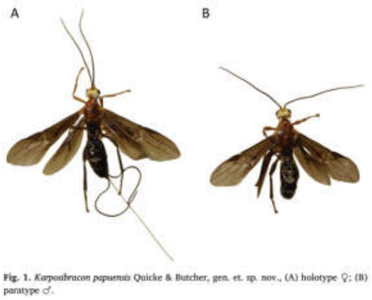

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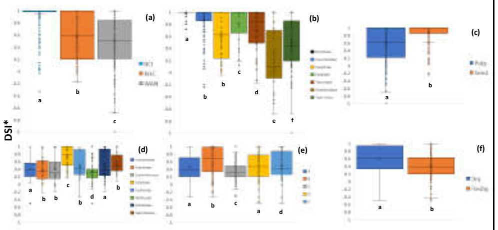

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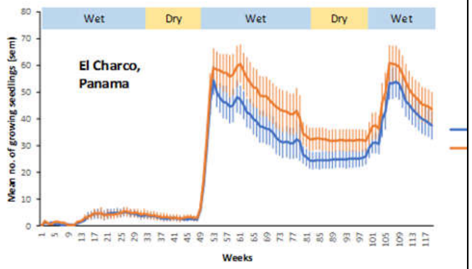

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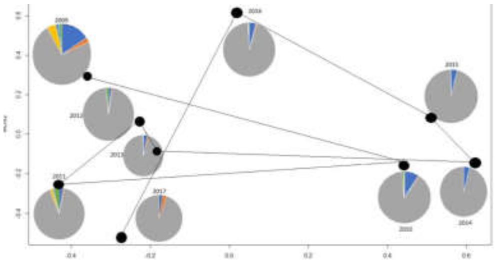

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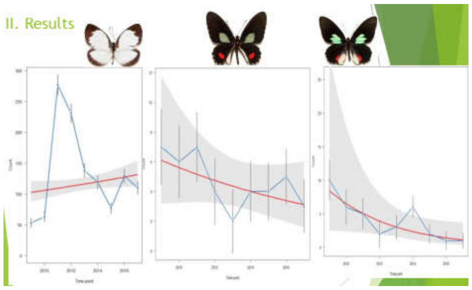

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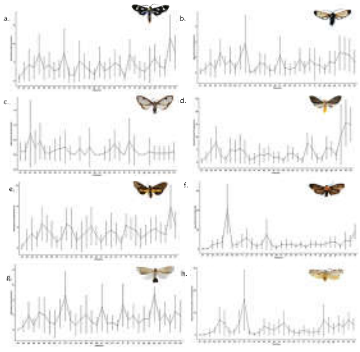

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APPENDIX I. FULL TEXT OF BASSET ET Al. (2018), PUBLISHED IN *J. BIOGEOGR.* (see next page)

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ORIGINAL ARTICLE

WILEY Journal of Biogeography

A cross-continental comparison of assemblages of seed- and fruit-feeding insects in tropical rain forests: Faunal composition and rates of attack

Yves Basset[1,2,3,4] | Chris Dahl[2,3] | Richard Ctvrtecka[2,3] | Sofia Gripenberg[5] | Owen T. Lewis[5] | Simon T. Segar[2,3] | Petr Klimes[3] | Héctor Barrios[4] | John W. Brown[6] | Sarayudh Bunyavejchewin[7] | Buntika A. Butcher[8,9] | Anthony I. Cognato[10] | Stuart Davies[11] | Ondrej Kaman[2,3] | Milos Knizek[12] | Scott E. Miller[6] | Geoffrey E. Morse[13] | Vojtech Novotny[2,3] | Nantachai Pongpattananurak[14] | Pairot Pramual[15] | Donald L. J. Quicke[8] | Robert K. Robbins[6] | Watana Sakchoowong[16] | Mark Schutze[17] | Eero J. Vesterinen[18] | Wen-zhi Wang[19,20,21] | Yun-yu Wang[19] | George Weiblen[22] | Joseph S. Wright[1]

[1]Smithsonian Tropical Research Institute, Balboa, Ancon, Panamá
[2]Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic
[3]Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic
[4]Maestria de Entomologia, Universidad de Panamá, Panama City, Panama
[5]Department of Zoology, University of Oxford, Oxford, UK
[6]National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
[7]Research Office, Department of National Parks, Wildlife and Plant Conservation, Bangkok, Thailand
[8]Integrative Ecology Laboratory, Department of Biology, Faculty of Science, Chulalongkorn University, Pathumwan, Bangkok, Thailand
[9]Center of Excellence in Entomology: Bee Biology, Diversity of Insects and Mites, Chulalongkorn University, Pathumwan, Bangkok, Thailand
[10]Department of Entomology, Michigan State University, East Lansing, MI, USA
[11]Center for Tropical Forest Science-Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Washington, DC,USA
[12]Forestry and Game Management Research Institute, Jíloviště, Czech Republic
[13]Biology Department, University of San Diego, San Diego, CA, USA
[14]Department of Forest Biology, Faculty of Forestry, Kasetsart University, Bangkok, Thailand
[15]Department of Biology, Faculty of Science, Mahasarakham University, Kantharawichai District, Maha Sarakham, Thailand
[16]Forest Entomology Group, Department of National Parks, Wildlife and Plant Conservation, Chatujak, Bangkok, Thailand
[17]School of Earth, Environmental & Biological Sciences, Queensland University of Technology, Brisbane, QLD, Australia
[18]Department of Agricultural Sciences & Department of Biology, University of Helsinki, Helsinki, Finland
[19]State Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China
[20]Guizhou Academy of Testing and Analysis, Guiyang, China
[21]Forensic Science Services of Yunnan Endangered Species Scientific Commission, Kunming, China
[22]Bell Museum and Department of Plant and Microbial Biology, University of Minnesota, St. Paul, MN, USA

Correspondence
Yves Basset, Smithsonian Tropical Research Institute, Balboa, Ancon, Panamá.
Email: bassety@si.edu

Abstract

Aim: Insects feeding on seeds and fruits represent interesting study systems, potentially able to lower the fitness of their host plants. In addition to true seed eaters, a suite of insects feed on the fleshy parts of fruits. We examined the likelihood of

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community convergence in whole insect assemblages attacking seeds/fruits in three tropical rain forests.

Location: Three ForestGEO permanent forest plots within different biogeographical regions: Barro Colorado Island (Panama), Khao Chong (Thailand) and Wanang (Papua New Guinea).

Methods: We surveyed 1,186 plant species and reared 1.1 ton of seeds/fruits that yielded 80,600 insects representing at least 1,678 species. We assigned seeds/fruits to predation syndromes on the basis of plant traits relevant to insects, seed/fruit appearance and mesocarp thickness.

Results: We observed large differences in insect faunal composition, species richness and guild structure between our three study sites. We hypothesize that the high species richness of insect feeding on seeds/fruits in Panama may result from a conjunction of low plant species richness and high availability of dry fruits. Insect assemblages were weakly influenced by seed predation syndromes, both at the local and regional scale, and the effect of host phylogeny varied also among sites. At the driest site (Panama), the probability of seeds of a plant species being attacked depended more on seed availability than on the measured seed traits of that plant species. However, when seeds were attacked, plant traits shaping insect assemblages were difficult to identify and not related to seed availability.

Main conclusions: We observed only weak evidence of community convergence at the intercontinental scale among these assemblages. Our study suggests that seed eaters may be most commonly associated with dry fruits at relatively dry tropical sites where fleshy fruits may be less prevalent.

KEYWORDS
convergence, guild structure, pulp eater, seed predator, seed rain, seed syndrome, species richness

1 | INTRODUCTION

Convergent evolution (or convergent phenotypic evolution: Mahler, Weber, Wagner, & Ingram, 2017) refers to the independent evolution of similar traits in different lineages resulting from strong selective pressures. Convergence is also recognized in ecological assemblages, and community convergence may be defined as the similarity in community structure or physiognomy of assemblages of co-occurring plants or animals resulting from comparable physical and biotic selective pressures (Bittleston, Pierce, Ellison, & Pringle, 2016; Samuels & Drake, 1997; Schluter, 1986; Smith & Wilson, 2002). Hence, community (or ecological) convergence can be sought in terms of (1) search for similarities in patterns of biodiversity and community structure, including species richness, relative abundance distributions, occurrence of trophic guilds, or (2) convergence in the characters of the species present (Korňan, Holmes, Recher, Adamík, & Kropil, 2013; Segar, Pereira, Compton, & Cook, 2013; Smith & Wilson, 2002). In this contribution, we focus on the former aspect of community convergence.

Several mechanisms have been proposed to explain community convergence. First, the likelihood of convergence may be driven by ecological opportunity, which may be based on what resources are in excess and can be easily employed (Agrawal, 2017). Second, biotic filtering, mostly based on species interactions, can result in community-level convergence (Smith & Wilson, 2002). Eventually, communities may reach similar ecological structure through different phylogenetic structures. In this case, empty niches are filled through a combination of colonization by pre-adapted species and/or niche shifts by resident lineages (Gillespie, 2004; Segar et al., 2013). Segar et al. (2013) demonstrated this mechanism for intercontinental fig wasps assemblages.

Of particular interest are examples of community convergence involving assemblages developing on different continents but under similar environmental conditions (Samuels & Drake, 1997). Community convergence on different continents has been reported for a variety of plant communities (Samuels & Drake, 1997) and vertebrate taxa. For the latter, convergence was observed with regard to morphology (fishes: Winemiller, 1991; birds: Ricklefs & Travis, 1980; mammals: Mares, 1993) or species richness (fishes: Irz et al., 2007; birds: Schluter, 1986). Yet, convergence is often evidenced at rather coarse levels, such as guilds (a group of species that exploit the same class of resources in a similar way: Root, 1973), as opposed to finer levels of scale such as species composition (Korňan et al., 2013; Samuels & Drake, 1997). One explanation may be that environmental conditions may determine the types of available niches and, therefore, the functional groups that can fill them, while species compositions within functional groups are influenced stochastically by the history of species arrivals (Fukami, Bezemer, Mortimer, & Putten, 2005).

It has been repeatedly demonstrated that assemblages of invertebrates, particularly arthropods, are rather different from those of vertebrates or plants, as including finer-grained patch sizes and geographical distributions, more complex seasonal and successional sequences, and more rapid generation turnover (Kremen et al., 1993). As a consequence, community convergence is more likely in vertebrates than invertebrates, because the latter are generally more closely tied to the specifics of their resources (Samuels & Drake, 1997). Nevertheless, convergence in arthropod communities has been observed in series reflecting island colonization (Gillespie, 2004), secondary succession (Hendrix, Brown, & Dingle, 1988), habitat restoration (Watts, Clarkson, & Didham, 2008), or in assemblages submitted to intense interspecific competition for patchy and ephemeral food resource, such as dung beetles (Inward, Davies, Pergande, Denham, & Vogler, 2011).

Convergent evolution of phytophagous insects is indicated, for example, by resistance to plant toxins, such as cardiac glycosides (Petschenka, Wagschal, Tschirnhaus, Donath, & Dobler, 2017). In contrast, lack of community convergence appears to be common in many phytophagous insect communities. This may result from host plants being sufficiently biochemically and structurally different to prevent certain modes of feeding or from interspecific competition being too weak to induce convergence (Lawton, 1984). One notable exception includes assemblages of highly specific fig wasps and their parasitoids enclosed in fig syconia. Segar et al. (2013) confirmed intercontinental community convergence in guild proportionality for these assemblages and predicted that similar examples could be observed for bounded communities with well-defined resource units, such as insect herbivores feeding on fruits.

Insects feeding on seeds and fruits represent tractable study systems for studying community convergence. In addition to true seed predators, a suite of insects (notably Diptera and Lepidoptera) feed on the fleshy parts of fruits (Ctvrtecka, Sam, Miller, Weiblen, & Novotny, 2016). The study of these insect assemblages can provide important information on how insect assemblages are structured in hyperdiverse tropical communities. Yet, we know very little about the basic biology and ecology of insect herbivores in tropical rain forests, with, specifically, only a handful of studies documenting whole assemblages of seed/fruit feeders (Ctvrtecka, Sam, Brus, Weiblen, & Novotny, 2014; Ctvrtecka et al., 2016; Nakagawa et al., 2003; Sam et al., 2017).

Following the results of Segar et al. (2013), we ask whether intercontinental convergence in discrete and specialist communities could be generalized to insects feeding on seeds and fruits in different tropical rain forests. While the barriers to community membership are weaker for seed- and fruit-feeding insects, these communities are still bounded. Because of the high diversity and phylogenetic extent of these assemblages (see Results), we took a simplistic approach in testing for differences in insect variables most likely to reflect community convergence, such as species richness and guild proportionality. Our general objectives were to test whether assemblages of insects feeding on seeds/fruits in three representative rain forests within different biogeographical regions (Neotropical, Oriental and Australian) converged towards predictable patterns of community structure influenced by plant phylogeny and/or plant functional traits (“seed predation syndromes,” see methods).

We specifically aim at answering three key questions, derived from mechanistic hypotheses from the literature on plant–insect interactions (reviews in Strong, Lawton, & Southwood, 1984; Lewinsohn, Novotny, & Basset, 2005):

1. Are the community attributes of insect assemblages feeding on seeds/fruits (abundance, higher taxonomic composition, guild structure and species richness) similar, both at local and intercontinental scales, and when controlling for plant phylogeny? Further, can plant and seed traits predict the characteristics of these insect assemblages? The classic defence and plant apparency theory postulates that the breadth of an herbivore’s diet depends on the apparency and mode of defence of its food–plant (Feeny, 1976). Under this hypothesis, the species richness of seed/fruit predator assemblages is expected to be similar for sets of host plants with particular functional traits, irrespective of plant family, provided that host traits are reasonably independent of plant phylogeny. The defence theory has been modified several times and is now part of a framework of three syndromes of plant defence, including (1) tolerance/escape, (2) low nutritional quality and (3) high nutritional quality and defence (Agrawal & Fishbein, 2006). Considering the antagonism between seeds and seed predators, fleshy fruits may represent an analogy with the tolerance/escape syndrome, as they are quickly dispersed by frugivores, while dry fruits (achenes) may be more likely to be nutritious but well defended against seed predators. If community convergence exists in assemblages of insects feeding on seeds/fruits, then we would expect community attributes to be influenced by seed predation syndromes (see Methods), including fruit fleshiness, and to be similar across locations.
2. Do rare tree species support less abundant, less diverse or functionally distinct seed/fruit-feeding insect assemblages than common tree species? The encounter frequency and resource concentration hypotheses state that more widespread or more locally abundant tree species may support a more abundant and richer herbivore fauna (Kelly & Southwood, 1999; Root, 1973). These hypotheses likewise predict differences in the species richness of seed/fruit feeder assemblages supported by rare and common host trees. Further, if community convergence exists at continental scale, we would at least expect similarity in some of the community attributes between insect assemblages feeding on

seeds/fruits of common tree species, as resources may be easily exploited in this case (Agrawal, 2017).

3. Are seed predation rates lower in forests of higher floristical diversity, do these rates vary among plant families, and can they be predicted from plant and seed traits? Plant resource in floristically diverse tropical forests may be difficult to track for insect herbivores and result in relatively low host specificity in these forests (Novotny et al., 2002). As abundant and specialized insect feeders are responsible for most of plant damage (Coley & Barone, 1996), we predict lower seed predation rates in floristically more diverse forests and/or within more diverse plant families. If the likelihood of community convergence depends to some extent on the ease of tracking resources (Agrawal, 2017), then we would also expect plant species richness to be one of the key factors shaping similarities in insect assemblages feeding on fruits/seeds.

2 | MATERIALS AND METHODS

2.1 | Study sites

Our study sites are three ForestGEO lowland rain forest plots (Anderson-Teixeira et al., 2014), located in different biogeographical regions (Table S1). These sites are detailed in Anderson-Teixeira et al. (2014), salient characteristics of the vegetation plots are also summarized in Table S1 and in Appendix S1, and maps can be consulted at http://www.forestgeo.si.edu/. Neotropical: Barro Colorado Island (BCI) is a 1,500 ha island created by the opening of the Panama Canal in 1914. The 50 ha plot is located in the centre of the island, which is a biological reserve. Oriental: the 24-ha plot at Khao Chong (KHC) is located in the protected forest of the Khao Ban Thad Wildlife Sanctuary in Southern Thailand. Australian: the 50-ha plot is located within the 10,000 ha Wanang Conservation Area in Papua New Guinea (WAN).

2.2 | Plant surveys

Field methods were similar for all study sites. Plant surveys spanned 3–4 years at each site (Table S1). During the first study year at each site, we surveyed seeds and fruits of locally abundant tree, shrub and liana (more rarely herb) species. During subsequent study years, we restricted our sampling effort to 10 plant families, which represented the most common families at each plot (eight families were common to all sites, two other families were well represented locally). We refer to these families as focal families and they included at all plots: Annonaceae, Arecaceae, Euphorbiaceae, Fabaceae, Lauraceae, Meliaceae, Rubiaceae, Sapindaceae; at BCI: Bignoniaceae, Clusiaceae; at KHC: Ebenaceae, Phyllanthaceae; at WAN: Myristicaceae, Myrtaceae. Unless specified, results are detailed for all host plant species. Seeds and fruits collected on plants or freshly fallen (without apparent decomposition) were surveyed within and/or near permanent plots (from an area <1,500 ha corresponding to the smallest study area, BCI). Rearing sample units included clusters of conspecific seeds/fruits of similar size collected from the same trees. We targeted as many individuals as possible for each plant species, typically >5. These sample units were weighted (fresh weight) and stored in individual plastic pots (details in Table 1 and Appendix S1).

2.3 | Insect rearing and processing

Rearing pots were stored under semi-natural conditions in covered but ventilated sheds under the forest canopy. They were checked twice weekly, and any emerging insect was collected, preserved, mounted and then identified with the assistance of taxonomists (see Table S2) and/or with molecular techniques. We obtained DNA Cytochrome c oxidase subunit I (COI, "DNA barcode") sequences from legs of representative insect specimens, and we used Barcode Index Numbers (BINs) derived from insect sequences to delineate species (Ratnasingham & Hebert, 2013). Data were deposited in different Barcode of Life projects (details in Appendix S1).

Insects reared from seeds/fruits were assigned to the following guild categories, inspired from Moran and Southwood (1982): seed eaters (coded as SE: larva feeding mostly on seed tissue), pulp eaters (PU: larva feeding mostly on mesocarp tissue), scavengers (SC: larva feeding mostly on decaying matter), fungal feeders (FU: larva feeding mostly on fungi) and parasitoids (PA: larva feeding on insect hosts). Guild assignment was done mostly at the familial or subfamilial level, but in some case at the generic or specific level, as indicated in Table S2 and Appendix S1.

2.4 | Measurement of plant traits and rates of seed attack

Host plants were identified and a suite of plant traits was determined as far as possible for each plant species, including plant lifeform (tree, shrub, liana, herb, palm), seed syndrome, species abundance (no. of stems or basal area in vegetation plots), seed rain, seed fresh mean weight and mean length, and rates of seed attack (see below). Seeds and fruits exhibit a diversity of morphological and ecological features, which may represent important determinants of host use in seed- and fruit-feeding insect taxa. We selected eight putative seed predation syndromes (in analogy with "flower syndromes": Barth, 1981) on the basis of (1) plant traits particularly relevant to insects (Janzen, 1969; Ramírez & Traveset, 2010); and (2) previous comparisons of the distribution of seed/fruit categories at our three study sites (C. Dahl et al., unpubl. data). Each plant species was assigned a seed syndrome on the basis of seed/fruit appearance (fleshiness and dehiscence), number of seeds per fruit and measurement of mesocarp thickness (Table 2). Beside host chemistry and odour, these traits represent important variables for ovipositing female insects and the developing larvae (Díaz-Fleischer, Papaj, Prokopy, Norrbom, & Aluja, 2000; Messina, 1984). This classification of seed syndromes is compared elsewhere with other systems used in botany (based on morphology and mode of dispersal) and in vertebrate zoology (frugivory) (C. Dahl et al., unpubl. data). Seed rain was estimated using weekly censuses of litter traps (Wright, Calderón,

TABLE 1 Salient characteristics of plant traits and insect variables measured across sites (BCI: Barro Colorado Island, KHC: Khao Chong, WAN: Wanang). Means are reported with standard errors in brackets. Differences between means are tested by Kruskal–Wallis tests (significantly different groups indicated by different letters, Dwass-Steel post hoc tests), differences between proportions by chi-square tests. Details about study sites and plant samples are reported in Table S1

Variable	BCI	KHC	WAN	*p*
Plant traits (average per plant species)				
Average no. of stems per tree species per ha	13.02 (2.80)	7.97 (1.06)	9.17 (1.02)	.065
Average basal area per tree species per ha (m^{-2} × ha^{-1})	0.133 (0.02)^a	0.087 (0.01)^b	0.052 (0.01)^c	<.001
Average seed rain per tree species (dry g × m^{-2} × yr^{-1})	0.53 (0.139)^a	0.009 (0.005)^b	0.015 (0.004)^b	<.001
Average seed fresh weight (g)	25.6 (5.0)^a	18.3 (3.1)^a	11.4 (1.3)^b	<.001
Average seed length (mm)	39.7 (2.4)^a	28.0 (1.1)^b	22.3 (0.9)^c	<.01
Average no. of seed eaters reared per seed	0.12 (0.03)^a	0.23 (0.14)^b	0.10 (0.04)^a	<.001
Apparent rate of seed attack (% seed attacked)	5.4 (0.43)^a	9.4 (0.89)^b	12.5 (0.98)^b	<.001
Apparent rate of seed attack (%)—10 focal plant families	6.1 (0.77)^a	10.1 (1.33)^b	12.2 (1.33)^b	.013
Insect samples:				
Total number of insects reared	27,610	17,555	35,434	—
Total number of insects reared—10 focal plant families	12,736	8,851	24,033	—
Proportion of samples with insects reared (%)	29.4	59.4	51.2	<.001
Proportion of samples with seed eaters reared (%)	12.6	10.9	12.7	.141
Mean insects reared per sample	2.6 (0.15)^a	7.6 (0.55)^b	7.5 (0.39)^b	<.001
Mean seed eaters reared per sample	1.17 (0.11)	1.08 (0.19)	1.07 (0.13)	.15
Mean seed eaters reared per attacked sample	9.3 (0.82)	9.8 (1.62)	8.5 (0.95)	.15
Mean insects reared per seed	0.51 (0.04)^a	1.71 (0.16)^b	0.53 (0.04)^a	<.001
Mean insects reared per g weight	0.23 (0.09)^a	0.11 (0.01)^b	0.08 (0.01)^c	<.001

TABLE 2 Number of individual insects reared from different seed syndromes, detailed for each study site (BCI: Barro Colorado Island, KHC: Khao Chong, WAN: Wanang). Sum refer to the total of insect reared, SE % to percentage of seed eaters and AT% to mean percent apparent rate of attack (standard error in bracket)

	BCI			KHC			WAN		
Seed syndrome[a]	Sum	*SE %*	AT%	Sum	*SE %*	AT%	Sum	*SE %*	AT%
A. Drupe (one seed per fruit)									
A1. Fleshy drupe									
A1.1 Fleshy drupe with thick mesocarp (>5 mm)	1125	32.2	12.5 (0.96)	1293	4.0	11.8 (1.7)	7676	12.4	11.5 (1.06)
A1.2 Fleshy drupe with thin mesocarp (<5 mm)	5655	62.1	10.5 (0.63)	3388	8.6	9.2 (0.96)	7092	10.0	11.1 (0.82)
A2. Non-fleshy drupe									
A2.1 Non-fleshy drupe with thick mesocarp (>5 mm)	1424	30.1	13.1 (1.23)	275	5.5	12.1 (3.19)	2844	24.1	17 (2.07)
A2.2 Non-fleshy drupe with thin mesocarp (<5 mm)	2748	51.6	11.6 (0.84)	1735	12.4	18.4 (2.59)	1116	31.1	17 (2.72)
B. Fleshy or non-fleshy fruit with multiple seeds									
B1 Fleshy indehiscent fruit with multiple seeds	3834	48.0	7.1 (0.69)	6388	7.2	14.6 (1.18)	5930	18.5	14.3 (1.22)
B2 Non-fleshy dehiscent fruit with multiple seeds (dehiscence typically across multiple axes)	7239	21.7	8.6 (0.55)	593	3.9	9.3 (2.2)	9665	2.5	8.4 (0.89)
C. Dry fruit/seed, often winged									
C1 Dry winged seed that do not develop in capsule	521	49.7	7.3 (0.86)	436	40.4	16 (2.11)	29	0	1.3 (1.25)
C2 Multiple dry seeds (with or without wings) that do develop in capsule/pod (opening across one axis)	4766	33.4	7.6 (0.51)	1654	22.2	28.7 (4.34)	462	3.7	32.2 (6.16)

[a] Recombined categories for some analyses: drupes = A1.1, A1.2, A2.1, A2.2; "fleshy fruits" = A1.1, A1.2, B1; "dry fruits" (achenes) = A2.1, A2.2, B2, C1, C2.

Hernandéz, & Paton, 2004; Appendix S1). Rates of seed attack may be derived with different approaches. Here, we consider an entomocentric view including, for each plant species, either the average number of seed eaters reared per seed or the percentage of seed attacked. The former has been identified as a critical factor for seed germination (Nakagawa et al., 2003), and we refer to the latter as the “apparent rate of seed attack.” Average values for most plant traits at the community level (i.e. average for all plant species surveyed) are detailed in Table 1.

2.5 | Statistics: question (1)

For answering this question, our analyses aimed at evaluating differences in insect community structure between our study sites. Differences in insect variables suggest lack of community convergence, while a high similarity does not necessarily indicate community convergence. Sampling effort, either expressed as the number of seeds collected or the weight of samples, was significantly different between sites (Table S1). To account for this situation, our analyses considered average proportions within samples, rarefaction or expressed insect variables per unit seed or unit g fresh weight, for comparisons among study sites (see Appendix S1 for details). To compare insect faunal composition and species richness, we considered the following taxa, which were well studied, represented 48% of the total material collected and were also observed as important seed/fruit feeders in other tropical community studies (Ctvrtecka et al., 2016; Ramírez & Traveset, 2010): Bruchinae, Scolytinae, Curculionidae others than Scolytinae (Coleoptera), Tortricidae, Pyralidae (Lepidoptera), Stratiomyidae, Tephritidae (Diptera) and Braconidae (Hymenoptera). We evaluated differences across sites with Kruskal–Wallis tests, after a logit transformation (Warton & Hui, 2011). Faunal similarity was estimated with the Morisita-Horn index calculated with the “vegan” library of the R-language (Oksanen et al., 2011), separately for each main guild on the basis of the abundance of insect families at each site. We tested for differences in the distribution of insect guilds across seed syndromes and sites with contingency analysis.

To evaluate the possible existence of clusters formed by insect guilds and seed syndromes, we performed correspondence analyses (CA) for each site on the matrices of the abundance of the main insect guilds (seed eaters, pulp eaters, fungal feeders, scavengers, parasitoids) ordered by plant species (all plant species surveyed, 264, 237 and 257 species for BCI, KHC and WAN, respectively). These and other multivariate analyses (see below) were performed with Canoco 5.04 (ter Braak & Smilauer, 2012). We compared species richness (measurements of species diversity or evenness are less relevant in this context) for these same insect groups among study sites by computing rarefaction and extrapolation sampling curves of species richness with the R package “iNEXT” (Hsieh, Ma, & Chao, 2016). We considered the following datasets for comparing insect groups: all plant data available, data restricted to the 10 plant focal families and data restricted to BINs. We also compared total species richness separately for each study site and seed syndrome, with all plant data. With the same software, we calculated an estimated asymptotic species richness (Hsieh et al., 2016).

We tested the influence of plant and seed traits on insect assemblages as follows. First, we estimated the phylogenetic relationships between our focal host species using the software package Phylomatic (Webb & Donoghue, 2005; details in Appendix S1). We used a variance partitioning approach (Dray, Legendre, & Peres-Neto, 2006) to quantify the contribution of our explanatory variables (plant traits) and host phylogeny to structuring the composition of insect communities across plant hosts at each site, using Canonical Correspondence Analysis (CCA; details in Appendix S1). We used the following plant traits for each plant species: life-form, seed syndrome, seed type (as binary trait dry or fleshy), weight and length, and number of seeds per fruit. To obtain a balanced design, the analyses were restricted to the 10 focal plant families and to host species for which all measured variables were available. The representation of phylogeny through eigenvectors does not always capture phylogenetic structure fully (Freckleton, Cooper, & Jetz, 2011). Hence, we tested the influence of seed traits on insect community structure (i.e. presence of species) using a more explicit phylogenetic comparative framework: binomial Phylogenetic Linear Mixed Models (PGLMMs) (Ives & Helmus, 2011). Insect presence (response variable) was modelled using separate models for the traits: fruit length, number of seeds, fresh fruit weight and seed type (fixed explanatory variables), while including insect and host species identities as random effects. We included phylogenetic covariation as an additional random effect. We used the R package “pez” (Pearse et al., 2015) to construct PGLMMs (fitting models using restricted maximum likelihood; see Appendix S1).

2.6 | Statistics: question (2)

Common and rare tree species were defined as belonging to the first and last quartiles of abundance, respectively (Gaston, 1994), within each ForestGEO plot (vegetation data, Appendix S1). We compared the average abundance (all insects and seed eaters), species richness (rarefaction method as previously) and guild structure of all insects (proportion of individuals) reared from tree species belonging to the first and last quartile of abundance in vegetation plots. We tested for differences in guild structure in common tree species between different sites with contingency analysis.

2.7 | Statistics: question (3)

To evaluate differences in seed attack rates, we used the logit transformation (cf. above) to transform the apparent rate of seed attack and tested the significance of factors site and seed syndrome in a two-way ANOVA. We performed a similar analysis with log transformed abundance of seed eaters reared per unit seed. For each site, we analysed the statistical relationship between all continuous independent variables included in the multivariate analyses and the dependent variable presence/absence of seed eaters reared from all plant species surveyed (1/0), using quasibinomial generalized linear models (GLMs). We controlled for the phylogenetically non-independent data points as explained in Appendix S1. Further when seeds were attacked, we quantified the influence of continuous independent variables on three dependent variables (average number of seed eaters per unit seed, apparent rate of seed attack and number of species of seed eaters reared), using phylogenetic path analysis

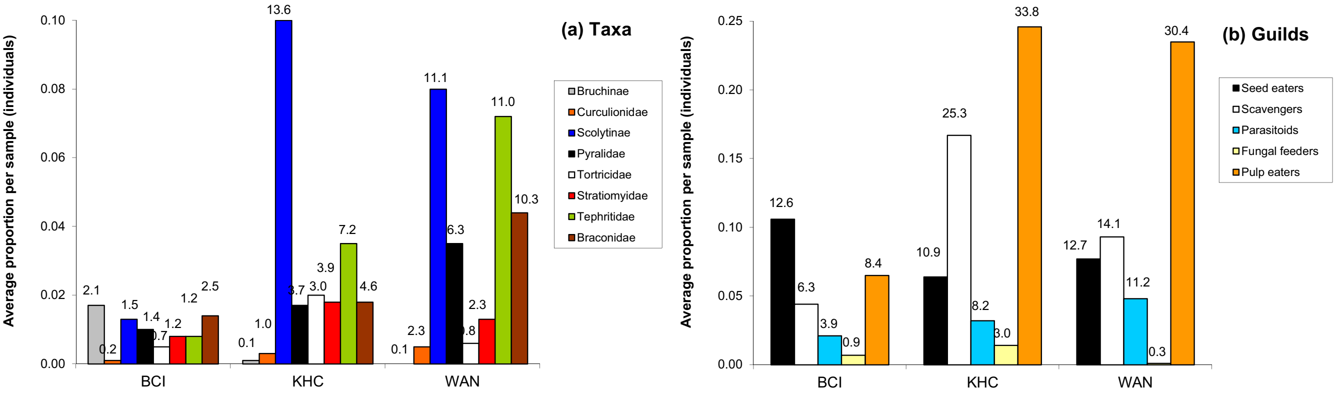

FIGURE 1 Plot of the average proportion of individuals of insect (a) taxa and (b) guilds reared per sample (all samples considered) for each study site. For taxa and guilds, proportions of particular taxa/guilds across sites are all significantly different (Kruskal–Wallis tests, all with $p < .05$). Figures above bars indicate, for each site, the percentage of samples in which a taxon or guild was present. Note that because values are averaged across all samples, proportions are rather small

(PPA; Gonzalez-Voyer & von Hardenberg, 2014). The procedure and the assumptions of the models, which were calculated with the R package "phylopath" (van der Bijl, 2017), are detailed in Appendix S1 and Figure S1. Eventually, to evaluate the possible effect of plant species richness on seed attack, we considered (1) the results of the GLMs described above, with the number of confamilial species for each plant species included as independent variable; and (2) the relationship between the number of confamilial plant species and the average percentage of seed attack per plant genus at each study site. In this case, considering plant genera instead of plant species reduced the possible effects of host phylogeny on the independence of data points.

3 | RESULTS

3.1 | Differences in the composition, guild structure and species richness of insect assemblages

At the three sites, 1,163 kg of seeds/fruits were reared, which yielded 80,600 insects representing at least 1,678 species reared from 1,186 plant species (Tables 1 and S1). Details about the salient differences between study sites in terms of plant and insect variables are further reported in Appendix S2. Average proportions per sample of particular taxa or guilds were all significantly different across sites (Figures 1, S2), with sometimes higher taxa absent at particular sites (Table S2). Generally, the highest faunal similarity was recorded between KHC and WAN (Table S3). Most insect reared were assigned to pulp eaters (present in 8%–34% of samples), scavengers (6%–25%) and seed eaters (11%–13%), and this general pattern was similar across sites and when restricting the data to the 10 focal plant families (Figures 1 and S2). Seed eaters overall represented 44.3% of all insects reared at BCI, whereas this percentage was only 14.2% and 14.3% at KHC and WAN, respectively. These general patterns were broadly similar for data restricted to 10 plant families, but with notable exceptions for the Curculionidae (Figure S2).

When all three study sites were considered together, it was apparent that a high relative proportion of Bruchinae and of seed eaters were reared from dry fruits (categories B2, C1 and C2, see Ramírez & Traveset, 2010), whereas a high relative proportion of Tephritidae and scavengers were reared from fleshy fruits (Figure S3; see Copeland, Luke, & Wharton, 2009). The highest and lowest relative proportion of seed eaters reared originated from categories C1 and A1.1-B2, respectively. The distribution of insect guilds across seed syndrome categories was significantly non-uniform within each site (BCI, $\chi^2 = 5{,}589.6$; KHC, $\chi^2 = 1{,}695.3$; WAN, $\chi^2 = 3{,}935.8$; all with $p < .001$), but appeared more resembling when comparing KHC and WAN data than when comparing BCI data with other sites (Figure 2). The proportion of plant species with dry fruits was higher at BCI (Table S1), but seed eaters were reared from a variety of syndrome categories, not just dry fruits (Table 2). This was confirmed by the large spread of insect guilds across seed syndrome categories, with no obvious clusters around guilds (CA, Figure S4). The distributions of insect guilds within syndrome categories were significantly non-uniform across sites, even when only drupes were considered

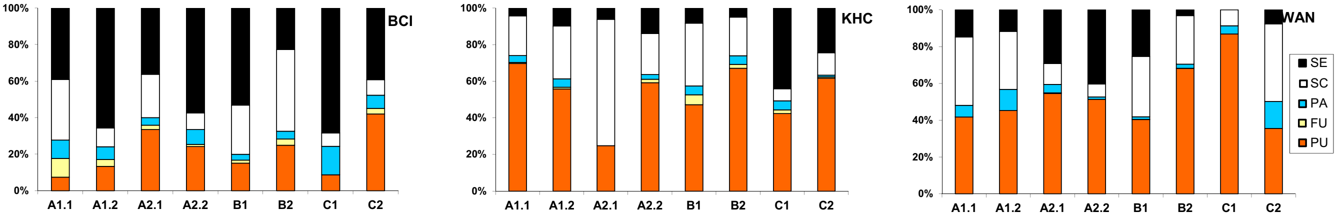

FIGURE 2 Proportion of the number of individuals reared from each seed syndrome category, detailed for each guild and each study site

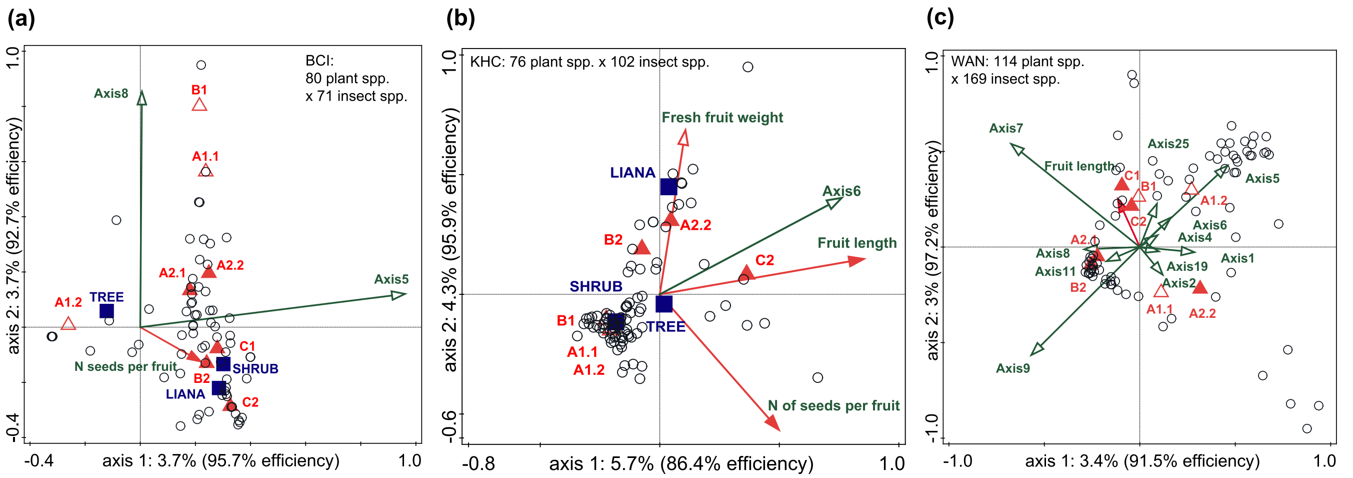

FIGURE 3 Plot of the variance in composition of insect species (circles; singletons excluded from analyses) explained by significant ecological variables (plant traits) and plant phylogeny in the first and second canonical axes of the CCA for (a) BCI, (b) KHC and (c) WAN. Continuous variables are coded as red vectors with closed arrows, factorial predictors as symbols. For the later, plant life-form is coded as blue squares, centroids of seed syndromes as red triangles (empty = fleshy fruits, solid = dry fruits). Plant phylogenetic axes are coded as green vectors with open arrows. The matrix sizes (plant species × insect species) and % of variability explained by each axis and their efficiency are indicated in the plots

(χ^2 = 7,639.2, p < .001), fleshy fruits (χ^2 = 9,308.4, p < .001) or dry fruits (χ^2 = 3,781.5, p < .001; Figure 2, Table 2).

Overall insect species richness reared from samples followed the series BCI (total number of species observed = 1,178/number of species of seed eaters = 311) >WAN (462/77 spp.) > KHC (378/60 spp.). Rarefaction and asymptotic estimators indicated that BCI was the most species-rich site when considering all data and BINs. For the 10 focal species, species richness at BCI and WAN appeared to be similar (Figure S5). For seed syndromes surveyed with relatively high sample size, insect species accumulated faster on dry seeds/fruits at BCI (C2 > B2 > A1.2), whereas this pattern was opposite at KHC (B1 > A1.2 > C2) and WAN (A1.2 > A1.1 > B2; Figure S6).

3.2 | Influence of plant traits and phylogeny

The proportion of overall variance in insect faunal composition that was explained by all the explanatory variables in the CCAs was significant and relatively consistent (12.6%–18.7% after excluding singletons; Table S4), with seed syndrome, seed length and number of seeds, as best explanatory variables (Figure 3). However, the effects of host phylogeny (both overall and exclusive after controlling for plant traits) were much more variable among sites, ranging from 3.2% (BCI) to 72% (WAN) (Table S4). The results using binary occurrence of insect species (PGLMM) mirrored the multivariate CCAs but also confirmed the difficulty to predict insect faunal composition with plant traits. Seed type (dry/fleshy) did not influence faunal composition for any site. Still, fresh fruit weight had a significant positive relationship with the response variable for KHC (Table S5).

3.3 | Insect assemblages on rare and common tree species

Significantly more insects and seed eaters were reared from rare tree species than from common tree species at BCI (Mann–Whitney test, U = 30.87, p > .001 and U = 6.26, p = .012, respectively, n1 = 1044, n2 = 66; Figure 4). This pattern was opposite at WAN for seed eaters (U = 4.54, p = 0.033, n1 = 1036, n2 = 55) but not significant for all insects (U = 0.67, p = .41). At KHC, neither the abundance of all insects nor of seed eaters was significantly different between common and rare trees (U = 0.08, p = .78 and U = 0.06, p = .81, respectively, n1 = 392, n2 = 57; Figure 4). The rate of species accumulation was difficult to compare between common and rare trees, because of the relatively small sample of the latter, but extrapolations suggested that common tree species accumulated more species than rare tree species at all study sites (Figure S7a). The guild structure of common tree species was significantly non-uniform between study sites (χ^2 = 3721.6, p < .001; Figure S7b). Further, the guild structure of insects reared from common and rare tree species was similar at KHC and WAN, but the proportion of seed eaters vs. other insects was significantly non-uniform across these tree categories at BCI (Fisher exact test, p < .001; Figure S7b).

3.4 | Rates of seed attack

Overall, apparent rates of seed attack at all study sites averaged 8.5 ± 0.7% per plant species (1,144 plant species considered). However, apparent rate of seed attack, both for all plants surveyed and for the focal 10 plant families, was significantly different and followed the series WAN>KHC>BCI (Table 1). The average number of seeds eaters reared per seed was also significantly different and followed the series KHC>BCI>WAN (Table 1). BCI had the lowest percentage of plant species attacked (by any insect guild) to plant species surveyed (64.1%), followed by KHC (71.3%) and WAN (77.4%). Apparent percent seed attack was high for C2 syndromes at KHC and WAN (Table 2). When seeds were attacked, the abundance of seed eaters per seed was significantly different both between sites and seed syndromes (two-way ANOVA, Table S6). This pattern

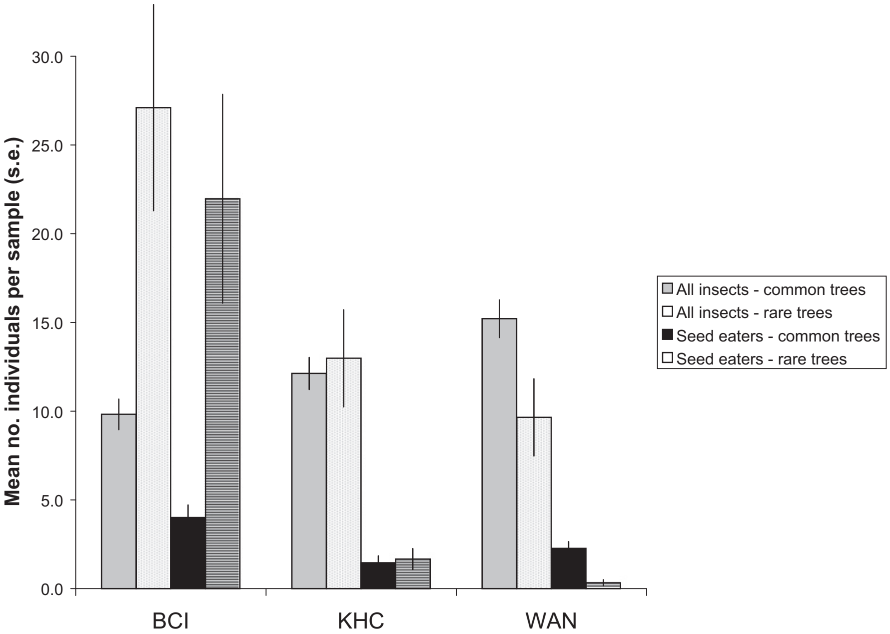

FIGURE 4 Abundance of all insects and seed eaters (means and *SE*) on common and rare tree species at each study site

was similar when considering the apparent rate of seed attack, with a stronger effect of seed syndrome than site (Table S6).

At BCI, 14% of the variance in the probability of rearing seed eaters (related to rates of seed attack, see Methods) from all plant species surveyed could be explained by the basal area of plant species and the seed rain (Table 3). At KHC, 17% of the variance could be explained by basal area, fruit length and the sum of seeds collected, whereas at WAN only 9% of the variance was explained by the number of confamilial species, the abundance in the plot and the sum of seeds collected (Table 3). The results were largely similar once the effect of phylogeny had been controlled for, but some variables no longer had explanatory power (such as basal area and number of confamilial species), suggesting a degree of phylogenetic conservatism (Table S7). When seeds were attacked, it was difficult to evidence direct paths in the PPAs to the dependent variables, as models were not significant for BCI and KHC (Table S8). For Wanang, the number of seeds per fruit had a direct positive path to the average number of seeds eaters reared per unit seed (Figure S8a), none of the independent variables influenced directly apparent rate of seed attack (Figure S8b), and only sampling effort had some direct and relatively large influence on the number of seed eaters reared (Figure S8c).

TABLE 3 Results of stepwise binary logistic regression describing the probability of rearing seed eaters for all plant species surveyed. Models are detailed separately for each study site (*SD*: standard error; *t*: *t*-value; Pr(>|t|): probability; R^2: coefficient of determination; *n*: number of plant species). For similar analyses controlling for the effect of host plant phylogeny, see Table S7

Model/ Parameter	Estimate	*SD*	*t*	Pr(>|t|)	R^2	*n*
BCI	—	—	—	—	.140	204
Constant	−0.434	0.185	−2.340	.020	—	—
Basal area	0.050	0.024	2.096	.037	—	—
Seed rain	1.313	0.653	2.011	.046	—	—
KHC	—	—	—	—	.167	156
Constant	−2.608	0.449	−5.810	.000	—	—
Basal area	0.058	0.030	1.917	.057	—	—
Fruit length	0.035	0.010	3.496	.001	—	—
Sum of seeds collected	0.003	0.001	2.879	.005	—	—
WAN	—	—	—	—	.086	240
Constant	−0.831	0.288	−2.889	0.004	—	—
No. of confamilial species	0.012	0.008	1.543	.124	—	—
Abundance in plot	0.000	0.000	1.453	.148	—	—
Sum of seeds collected	0.001	0.000	2.550	.011	—	—

As indicated previously, the influence of the number of confamilial species was non-existent or weak in explaining the probability of rearing seed eaters from plant species (Table 3). Further, when plant species were attacked, there was no significant linear relation (or any notable nonlinear relation) between the number of confamilial plant species and the average percentage of seed attack per plant genus at BCI ($F_{1,183}$ = 0.51, p = .48), at KHC ($F_{1,109}$ = 0.23, p = .64) or at WAN ($F_{1,104}$ = 2.53, p = .12).

4 | DISCUSSION

4.1 | Synopsis of salient results

Most of observed differences in our study system contrast BCI to other sites. BCI has a relatively low plant species richness, with a high proportion of shrubs and lianas and a high proportion of dry fruits. Basal area per plant species is high, as is the average seed weight, seed length and seed rain per plant species. A high proportion of seed eaters was reared from BCI samples. However, a low proportion of seed samples yielded insects (this may be partly due to the small size of BCI samples), apparent rate of seed attack was low, and less plant species were attacked at BCI than at other sites. With reference to the questions formulated in the Introduction, our study indicated that (1) significant differences in insect assemblages exist at the study sites but it was difficult to predict the characteristics of these assemblages with plant and seed traits, including seed predation syndromes and fruit fleshiness. (2) Seeds of rare trees were more likely to be attacked than those of common trees only at BCI. Guild proportionality in insect assemblages on common tree species was not conserved between sites. (3) Rates of seed attack were not particularly low at the two floristically diverse sites and, within plant families, floristic richness had little apparent effects on rates of seed attack. As such, these results suggest only weak community convergence of these insect assemblages at the intercontinental scale.

4.2 | Intercontinental comparison of insect assemblages feeding on seeds/fruits

As far as we are aware our study represents the first intercontinental comparison with similar protocols of insect assemblages attacking seeds/fruits in tropical rain forests. Overall, it indicated large differences in insect faunal composition, species richness and guild structure between the three study sites (question 1). These patterns were similar when we restricted our dataset to the 10 focal plant families. Still, it can be argued that all insect guilds were represented at the three study sites and that the main guilds were also reared from all seed syndromes. This observation can be interpreted as partial convergence (Korňan et al., 2013) in guild structure of the phylogenetically distinct insect assemblages at the three study sites.

However, the predictive power of seed syndromes was relatively weak. At BCI, where the availability of dry fruits was high, nearly 45% of insects reared were seed eaters, whereas this proportion was <15% at KHC and WAN. In contrast, pulp eaters were proportionally better represented at KHC and WAN than at BCI. Further, at BCI dry seeds/fruits accumulated faster insect species than fleshy seed/fruits. In addition, the distribution of guilds appeared rather distinct for each category of seed syndromes. We conclude that for coarse functional comparison of insect assemblages between sites, the most distinctive dichotomy among our categories of seed syndromes is probably dry vs. fleshy fruits, although this variable cannot explain fine insect composition, which is best explained by seed syndromes. This suggests that insect community convergence, either on dry or fleshy fruits, must be rather weak, if it exists at all. Gripenberg et al. (2018) showed that seed polyphenols on BCI are more influenced by the host successional stage (pioneer vs. shade-tolerant tree species) than by plant apparency (height of tree). It is conceivable that insect communities feeding on seed/fruits may also be more likely to convergence according to their host successional status. However, data were lacking in this study to accurately score the successional status of many plant species.

Still, several studies reported higher damage on dry fruits than on fleshy fruits (Ctvrtecka et al., 2014; Janzen, 1969; Wright, 1990). Our results partially support the hypothesis that the pulp of fleshy fruits may, in addition to being a reward for vertebrates disseminating fruits (Gautier-Hion, 1990), also act as protection from the attack of specific seed eaters (Bolmgren & Eriksson, 2010). Specific adaptations may be required for insect ovipositing within or near the seed or for the insect larvae to reach the seed and start its development there in the presence of an abundant pulp (Wright, 1990). This certainly warrants further studies examining insect damage on different seed syndromes.

There were also overall differences between sites in the relative proportion of variance in insect faunal composition explained by plant traits and phylogeny. Our CCA and PGLMM results suggest that seed syndromes were important in shaping insect communities at BCI, while some seed traits were more important at KHC, and plant phylogeny represented the best predictor in this regard at WAN. This high influence of phylogeny at WAN was probably due to closely related plants hosting more similar insect communities, while at BCI and KHC plant traits were more important in shaping insect communities and independently of plant phylogeny. Apart from seed syndromes, seed length and number of seeds per fruit appeared to influence most significantly the composition of insect assemblages. Ctvrtecka et al. (2016) reported that fruits attacked by Diptera are significantly larger than fruits attacked by Coleoptera and Lepidoptera. Other studies likewise reported a positive effect of seed size on seed eaters (Janzen, 1969; Ramírez & Traveset, 2010; Sam et al., 2017). Overall, we conclude that the composition and guild structure of insect assemblages feeding on seeds/fruits in tropical rain forests are partly shaped by seed predation syndromes, both at the local and regional scale, but that the factors shaping these assemblages are hard to identify.

Further, assemblages of insects feeding on seeds/fruits were richer at BCI, than at other sites, when we considered rarefaction of either the number of species sorted or the number of BINs sequenced. This observation is not an artefact of different sample size. Different studies targeting weevils and Lepidoptera indicated, despite larger sample sizes in both the number of plant species surveyed and the number of insect individuals reared, much less species-rich insect assemblage feeding on fruits/seeds in Papua New Guinea or Kenya than at BCI (Copeland et al., 2009; Ctvrtecka et al., 2014, 2016). This high insect species richness at BCI is at odd when considering other insect assemblages that have been studied at our study sites. Butterflies are more diverse at KHC or WAN than at BCI (Basset et al., 2013), and Geometridae and litter ants are also more species-rich at KHC than at BCI (Y. Basset et al., unpubl. data). We hypothesize that the high species richness of insect feeding on seeds/fruits at BCI may result from a conjunction of low plant species richness and high seed availability of dry fruits (see below; it may also be partly related to the high proportion and productivity of shrubs and liana) per plant species, which may favour such rich insect assemblages.

4.3 | Insect assemblages attacking the seeds of rare and common trees

At BCI, more insects and seed eaters were reared from rare tree species than from common tree species, whereas these patterns did not exist at KHC and WAN. This appears to invalidate the resource concentration hypothesis (Root, 1973) and the higher likelihood of community convergence when abundant resources are available (Agrawal, 2017), in relation with question (2). If we assume that seed eaters are very host-specific (Janzen, 1980) and that few hosts can escape them, then we would expect a concentration of damage (and reared seed eaters) on rare tree species and a dilution of damage over common tree species. This mechanism would require a very high insect host specificity and ability to locate hosts, as well as a large resource base easily traceable over which seed eaters may be satiated (Wright, 1990). During the period of our study, these conditions were more like to exist at BCI than at KHC or WAN.

4.4 | Seed attack

Contrary to our predictions related to question (3), the number of confamilial plant species appeared to be unimportant in explaining the apparent rate of seed attack per plant species. Species-rich plant family did not sustain higher seed attack than less diverse plant families. Our logistic regressions indicated that at BCI the probability of seeds of a plant species being attacked depended more on seed availability than on the measured seed traits of that plant species. This issue was less clear at KHC (possible effect of sample size) or WAN (low variance explained). Other traits, such as seed chemistry, nutritional quality, fruiting frequency and host phylogeny may be substantial in this regard (Janzen, 1969; Nakagawa et al., 2003; Ramírez & Traveset, 2010). Resource availability may nevertheless represent a relatively important predictor of the probability of seed attack.

5 | CONCLUSIONS

Studies of insect herbivores in tropical rain forests are few, and often focus on leaf-feeding insects (Lewinsohn et al., 2005). The assemblages of seed-eating insects studied here did not conform to two out of three general predictions (see Introduction) that were coined more specifically for leaf-feeding insect herbivores. As such, seed-eating insects may represent a rather distinct guild from insect herbivores that may be difficult to study but may have great potential to lower the fitness of their hosts (Lewis & Gripenberg, 2008). As a further example, we note that in the tropics, increased damage or pathogens are often associated with increased rainfall (Coley & Barone, 1996). Our study suggests that seed eaters may be better reared from dry fruits and perhaps at relatively dry tropical sites where fleshy fruits may be less prevalent (Kissling, Böhning-Gaese, & Jetz, 2009). However, biogeographical and host phylogenetical factors may complicate this pattern.

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ORCID

Yves Basset http://orcid.org/0000-0002-1942-5717

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BIOSKETCH

Yves Basset is interested in the community ecology of tropical arthropods.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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