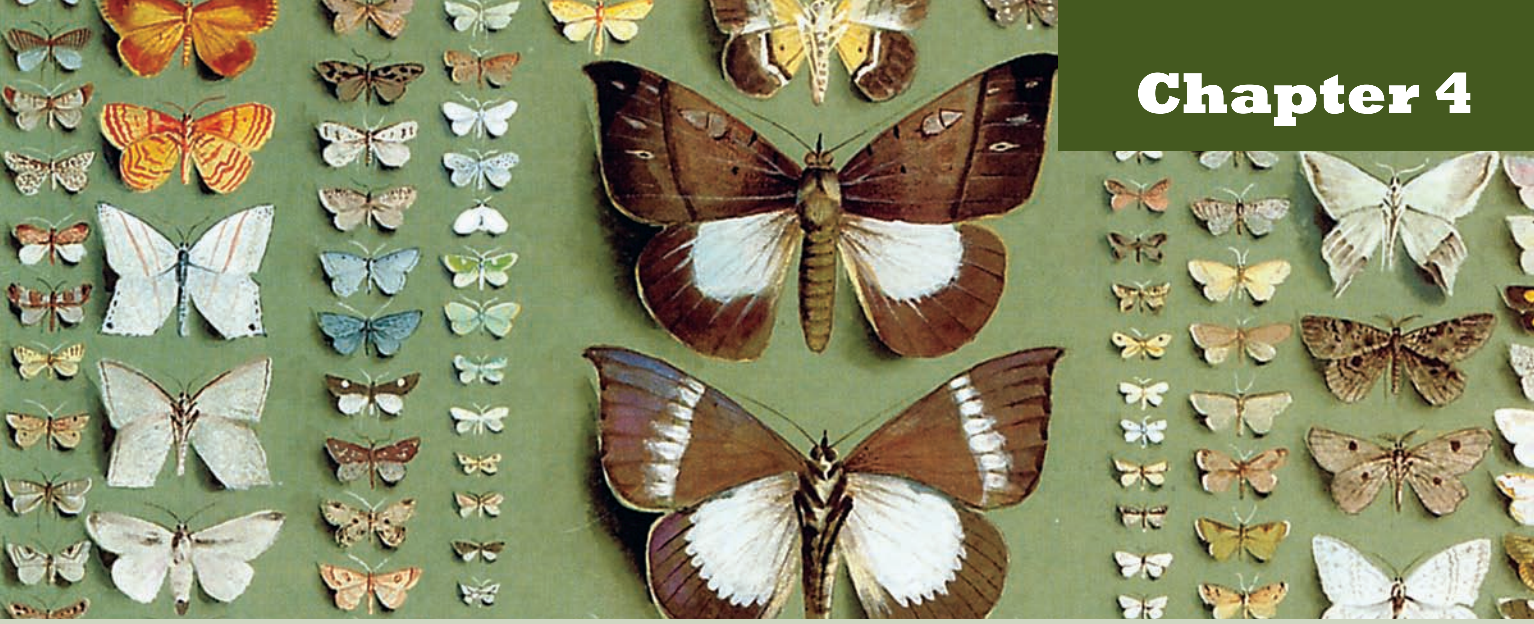

Chapter 4

Ecological research in Papua New Guinean rainforests: insects, plants and people

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Ecological research: why in Papua New Guinea?

New Guinea, one of the largest tropical islands, remains covered by the third largest rainforest in the world (after the Amazon and the Congo Basin). Papua New Guinea (PNG) is therefore suitable for the study of biological variability within large, continuously forested areas, across a range of soil, hydrological and climatic conditions. PNG biologists can still build research stations in forests with largely intact vegetation and vertebrate fauna (Figure 50). In contrast, researchers at some of the most active research stations in the tropics, including the Barro Colorado Island in Panama, La Selva in Costa Rica, or Lambir Hills in Malaysia, have access limited to forest fragments or defaunated forests (e.g., Harrison *et al*. 2013).

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Figure 50. **Field research infrastructure in PNG: (A) the Swire Research Station in the centre of the Wanang Conservation Area, with a 50-ha lowland forest dynamics plot that is following the individual fate of 288,204 plants (details at www.entu.cas.cz/png/wanang); (B) Wanang paraecologists Ruma Umari (front) and Jonah Filip (back) rearing insects from rainforest fruits at the station. Photo M. Leponce (A) and V. Novotny (B).**

PNG is one of the few countries in the Old World tropics in possession of complete rainforest altitudinal gradients, where continuous forest spans from the lowlands to its natural limits at about 3,700 m. There are several such gradients along the Central Cordillera, including Mt. Wilhelm, as well as in the Finisterre Mts., another, geologically younger range. The altitudinal gradients at both Mt. Wilhelm and the Finisterre Mts. have been recently opened for research (e.g, Sam *et al.* 2014, Freeman *et al.* 2013), coordinated by the New Guinea Binatang Research Center and the Tree Kangaroo Conservation Project respectively. Both transects rely on access agreements with local landowners, and so far comprise only temporary field camps. They have the potential, if developed further, to become internationally important research facilities, particularly for the study of the effects of climate change on biodiversity.

Long altitudinal gradients in humid tropics also represent globally important maxima of species diversity, generated by rapid change in species composition with altitude. Mt. Wilhelm is ranked among the seven most species-rich areas in the world for plants, with >5,000 species per 10,000 km2 (Barthlott *et al.* 2007). Our studies show that almost a third of butterfly and half of bird species from PNG fauna live on the slopes of Mt. Wilhelm (Table 5), mostly in unprotected forests outside of the Mt. Wilhelm National Park.

Table 5. Diversity of plants, insects and vertebrates along a complete rainforest altitudinal gradient (200 – 3700 m asl.) at Mt. Wilhelm. S_{tra} – total number of species recorded at eight study sites along the transect, S_{max} – maximum species diversity per site, A_{max} – altitude (in m) where local diversity reaches its maximum, S_{tot}/S_{max} – ratio of transect to maximum diversity, S_{tot} – the number of species in PNG or New Guinea (*Ficus* spp.: NG from Weiblen 2006, butterflies: PNG from Tennent 2006, ants: NG from Antweb 2015, frogs: PNG from AmphibiaWeb 2015, birds: PNG mainland from Sam & Koane 2014), S_{tra}/S_{tot} – the proportion of regional fauna found along the Mt. Wilhelm transect.

Taxon	S_{tra}	S_{max}	A_{max}	S_{tra}/S_{max}	S_{tot}	S_{tra}/S_{tot}	Reference
Ficus spp.	70	49	700	1.4	151	0.46	L. Sam unpubl.
butterflies	247	140	200	1.8	924	0.27	Sam 2011
geometrids	892	327	1200	2.7	?	?	Toko 2011
leafhoppers	450	138	200	3.3	?	?	Dem 2011
ants	232	104	700	2.2	782	0.30	Moses 2014
frogs	54	17	1700	3.2	367	0.15	Dahl 2011
birds	238	113	200	2.1	465	0.51	Sam & Koane 2014

PNG provides biologists with ample supply of islands of various sizes and degrees of isolation from the main island, allowing researchers to study the effects of habitat fragmentation on forest ecosystems. Islands, as nature's replicated experiments in the evolution and ecology of natural ecosystems, have inspired many researchers, including the founders of evolutionary theory C. Darwin and A. R. Wallace. The islands in PNG played a smaller, yet significant role in the history of science. Their ants inspired E. O. Wilson's theory of the taxon cycle, describing sequential phases of expansion and contraction of species ranges (Wilson 1961). J. Diamond developed the concept of the "checkerboard distribution" of species when he found that certain combinations of potentially competing bird species never occurred together on the same island (Diamond 1975). We can reasonably expect more discoveries awaiting ecologists upon the hundreds of New Guinea islands.

New Guinea: an island with a complicated history

The island of New Guinea is important biogeographically, as it comprises the majority of all tropical rainforests within the Australian biogeographic region, and an even larger majority in the newly recognized Oceanian zoogeographic region (Holt *et al.* 2013). It has a highly complicated geological history (Toussaint *et al.* 2014, Ufford & Cloos 2005), to the delight of some and despair of other biologists. The southern part of the island is a part of the old and stable Australian craton, floating slowly northwards on the Australian tectonic plate. Southern New Guinea is therefore technically a part of Australia, or, if we choose to focus on biodiversity rather than land area, we may prefer to see Australia as a southern province of New Guinea. New Guinea and Australia form a single land mass, also called Sahul or Meganesia, at the time of low sea levels, such as during the last ice age 18,000 years ago. The northern part of New Guinea existed originally as a collection of islands, pushed towards the Australian craton by the movement of the Pacific tectonic plate. The islands floated towards, and finally crashed into the craton, assembling what is now northern New Guinea as a jigsaw puzzle of terranes of various ages. The crashes also lead to the uplift of the Central Cordillera, as well as a number of smaller, and younger, montane ranges in the northern part of the island. The latest such collision, 3.0-3.7 million years ago, uplifted the Finisterre Mts., which is therefore PNG's youngest montane range, still growing at the geologically rather impressive rate of 0.8-2.1 mm per year (Abbott 1995, Abbott *et al.* 1997). This complicated history is likely to have contributed to increased speciation, since both islands and high mountains are well known generators of species. The importance of geological history was difficult to test using the contemporary distribution of species (Polhemus & Polhemus 1998, De Boer & Duffels 1996), but recent phylogenetic analyses of speciation history point to the importance of the past in explaining the high present-day diversity of insects, and likely also other taxa (Toussaint *et al.* 2014).

While only one in every 1,000 people in the world is Papua New Guinean, as many as one in every 20 species of the world's plants and animals live in PNG (Sekhran & Miller 1995). The country's 5%, largely endemic, share of biological diversity (including, for instance, 924 butterfly species from the global total of approximately 18,000 species; Table 1), and its 12% share of language diversity (Lewis 2009, Novotny & Drozd 2000), makes Papua New Guinea more important in the world for its diversity than its economic impact, based mostly on the production of 3% of the world's gold, 2% of its copper, 3% of its coffee and 1% of its palm oil. The key question remains whether Papua New Guineans will be able to look after the wealth of biodiversity in their own country, particularly as it is coming under increasing threat.

Given the biological potential of the country, could we envisage PNG becoming prominent in ecological research? Before dismissing this notion as over-optimistic, if not plainly unrealistic, let us consider two events in PNG history. In 2013, cargo transported throughout PNG by air represented an utterly negligible share of the global total (0.003%). It may therefore come as a surprise that less than a century ago, in the 1930s, Guinea Airways carried more freight by air, from Lae to Bulolo goldfields, than the rest of the world's airlines put together. The Bulolo – Wau area experienced another unusual operation thirty years later, in 1961, when J. L. Gressitt, an entomologist from the Bishop Museum in Honolulu, founded the New Guinea Field Station, later known as the Wau Ecology Institute. In the 1960s and 1970s, Wau became the home of one of the largest entomological research projects in the Pacific, if not the world, creating the world's largest collection of PNG insects. It is housed at the J. L. Gressitt Center for Research in Entomology, established by the Bishop Museum shortly after Gressitt died in a plane crash in China in 1982.

Discovering and naming Papua New Guinea's species

Papua New Guineans have, in their 850 local languages, hundreds of names for each of their Cassowary species, as well as for other birds. At the same time, local names for insects are scarce, despite the forests teeming with insect life. Modern taxonomists show similar bias towards cassowaries, all of which were properly named as early as 1860, over insects. Even today, an afternoon walk in any New Guinean forest will bring encounters with many insect species that are unknown to science. Even expert biologists cannot answer simple questions about insects, the questions any curious child might ask, such as how many insects species are living in the forest around us, and in Papua New Guinea overall, or what would happen to the forests if all the insects suddenly vanished.

The Queen Alexandra's Birdwing, *Ornithoptera alexandriae*, the largest butterfly in the world, living only in parts of the Oro Province and increasingly endangered by encroaching oil palm plantations (Parsons 1992), is the PNG's most famous insect species. The type specimen (used to describe the species, and to resolve any future questions about the species' identity) was collected by Albert Meek, an English naturalist (Meek 1913). He used a shotgun to get a high flying female; the bullet holes are still visible in the wings of the type specimen, described in 1907 by a renowned collector Walter Rothschild and later donated to the Natural History Museum in London, together with almost a million of other Rothschild's butterflies (Ackery 1997).

Until recently, types and other museum specimens, inspected in person by taxonomists, often provided the only safe means of identification for new material. For instance, in our study of 272 species of large moths (Macrolepidoptera), 60% of species were identified and taxonomically well known, but only half of this number was sufficiently well described in the literature so that a museum visit to see specimens was not necessary (S. E. Miller, pers. comm.). This situation is particularly inconvenient for tropical countries, where insect collections are difficult to maintain, and the type material for their fauna is often kept overseas, as is the case for *O. alexandriae*. The largest collection of PNG insects is almost 7,000 km away, at the Bishop Museum in Honolulu.

Fortunately, the taxonomy of tropical insects is entering a revolution fuelled by molecular techniques, particularly DNA barcoding (Miller 2007, 2015), combined with the availability of images of species and interactive keys via internet. The DNA barcode is a sequence of 648 bases in the mitochondrial cytochrome c oxidase 1 (COI) gene that has the right mutation rate – neither too low nor too high - that can be used for the identification of individual insect species, each of them typically characterized by a unique COI sequence. Barcoded individuals can be grouped into putative species, each given a stable numerical identifier (BIN, or barcode index number), used for preliminary classification of species (Ratnasingham & Hebert 2013). A complete library of COI sequences for insect species in PNG would allow quick identification of newly sampled specimens. Comprehensive barcode databases are now being built, particularly in the species-poor temperate zone countries with well known fauna, but also in Australia (Hebert *et al*. 2013). Barcode of Life (www.boldsystems.org), an on-line database, comprises 2.5 million barcodes from 200,000 insect species, sent there from all over the world. PNG, with almost 31,000 insect barcodes, ranks amongst the leading 15 countries (BOLD 2015), mostly due to the joint activity of the New Guinea Binatang Research Center and the Smithsonian Institution (Figure 51).

The COI sequences combined with morphological descriptions and high-resolution digital images, published on-line, can simplify formal descriptions of large numbers of new species, providing at last a feasible method for the description of insect diversity in PNG in the foreseeable future. This concept of "turbo-taxonomy" is being explored by research team with PNG participation (K. Sagata) and using PNG insects (Tanzler *et al*. 2012, Riedel *et al*. 2013). PNG does not need molecular laboratories to implement it, since DNA barcoding is being done mostly by a few specialized laboratories, whose services are used by many countries. What PNG needs is in-country expertise in the analysis and taxonomic use of barcode information so that it could be combined with internet databases and collections into tools for identification of PNG insects. Examples of online resources for PNG insects include the BOLD database, key to the forest insect pests (Schneider 1999), Ants of New Guinea (Janda 2015), Caterpillars feeding on New Guinea plants (Miller *et al*. 2015), a key to ambrosia beetles (Hulcr 2015), and a web site on New Guinea insects (http://www.papua-insects.nl/).

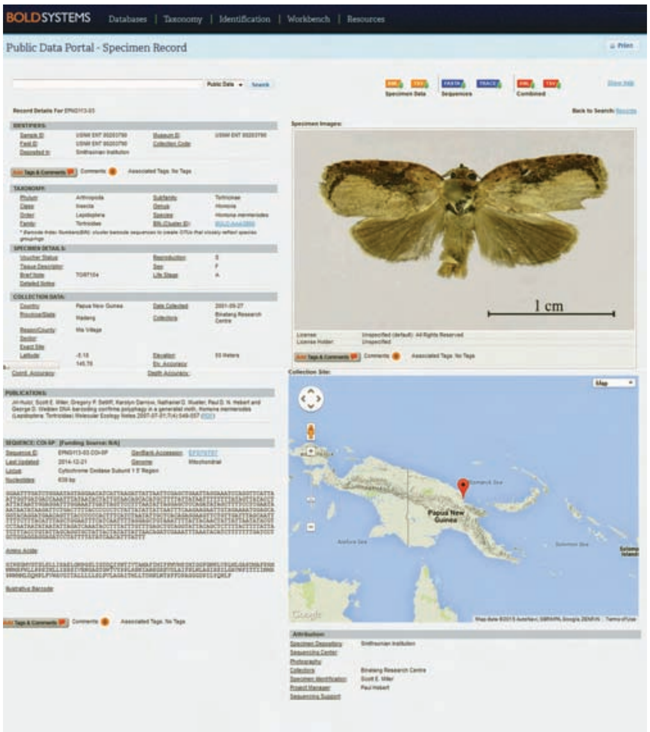

Figure 51. Molecular and morphological resources for the taxonomy of PNG insects available on-line: a specimen page for Homona mermerodes (Tortricidae) in the Barcoding of Life database, providing public access to DNA sequences, images and geographic location of the specimen (http://barcodinglife.org/index.php/Public_RecordView?processid=EPNG113-03).

Insect diversity: travelling from local to global estimates

Butterflies (Papilionoidea) are perhaps the only insect group rich in species and well known taxonomically, in PNG (Parsons 1999) and elsewhere in the tropics. The fastest growth of knowledge of PNG butterfly species took place early, from 1850 to 1900, the time of numerous expeditions to New Guinea by mostly European naturalists, including A. R. Wallace (1858), L. M. D'Albertis (1872), A. B. Meyer (1873), F. H. H. Guillemard (1883), H. Fruhstorfer (1891), W. Doherty (1892) or H. C. Webster (1894), all of them interested in butterflies. This intense interest led to almost half of all PNG butterfly species being known as early as in 1900 (Figure 52). The pace of discovery slowed after 1920 to a steady rate of 2.5 – 3.0 new species per year that has been maintained for 90 years, until the present day. Discovering a species new for PNG is rather more difficult than in other insect taxa. This is good news since it qualifies butterflies as a suitable model group for ecological studies. The study of ants, in comparison, started later than butterflies, experienced a similar boom at the turn of the 20th century and a slow-down in more recent years. Rather surprisingly, the species accumulation curve gives no hint of the fact that the PNG diversity that remains to be described is far greater in ants than in butterflies.

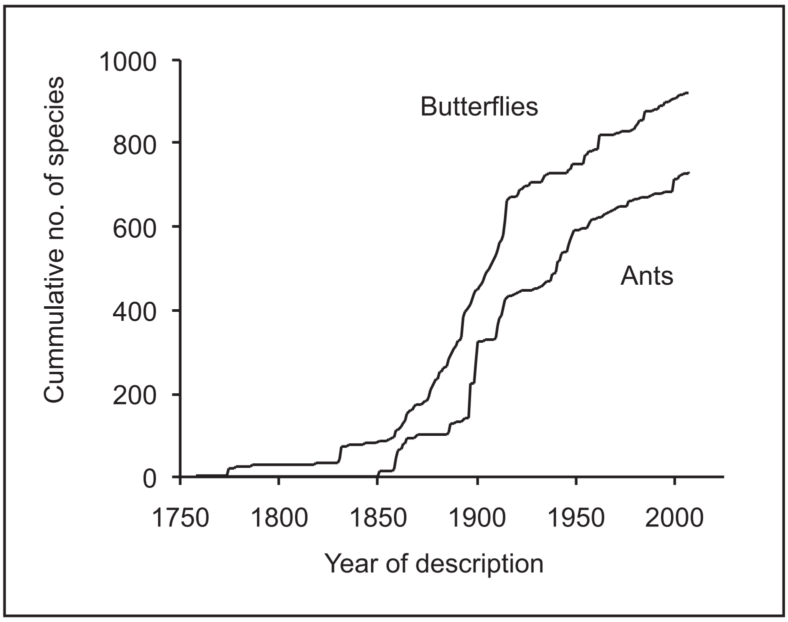

Figure 52. Cumulative total of presently recognized species of butterflies from Papua New Guinea (data from Tennent 2006) and ants from New Guinea.
(data from Antweb 2015).

Butterflies are a good model group also because they are interesting to the general public. The monitoring scheme in Great Britain, for instance, includes the country's 59 species (note that it would be difficult to find a single site in PNG that would be as poor in butterflies as to only match the entire fauna of Great Britain), runs since 1976, covers over 1,500 sites and counted more than 16 million butterflies (http://www.ukbms.org/). Such detailed monitoring of a few species may seem boring and unnecessary, but the scheme has provided invaluable information on the population decline of endangered species, as well as changes in species distribution ranges and seasonality in response to climate change and habitat disturbance (e.g., Dennis 1993). In contrast to Great Britain, PNG butterflies are monitored at only a single site, at the Swire Research Station in Wanang (Basset el al. 2013). Unlike the British, obsessed with butterflies, Papua New Guineans do not have a similar tradition of amateur biologists who could volunteer for broader surveys. There is at least one village, Swagup on the banks of the Sepik river, that has another insect, the praying mantis, as a totem animal, so hope remains that Papua New Guineas might yet convert to butterfly worship as the British have done. Failing that, many schools located in remote rainforest areas could become, with appropriate training, centres for simple butterfly surveys that could become an interesting teaching tool for biological education. PNG used to be one of the leading countries in insect farming and trade, which provided income to village-based collectors, selling mostly butterflies and beetles through the Insect Farming and Trading Agency. Regrettably, this small-scale, conservation-friendly business (Slone *et al*. 1977, Orsak 1993) has collapsed in the past decade.

Unfortunately, butterflies are an aberration in the taxonomic knowledge of PNG insects. Many insect taxa remain almost completely unknown to science. L. Baje, a University of PNG student, decided to study leafhoppers from Typhlocybinae subfamily, a group of small, plain looking insects sucking on plant leaves that are difficult to identify and thus ignored by just about everybody. She sampled 65 tree species in Madang and discovered 47 typhlocybine species, most of them specialized to a single tree species (Baje *et al*. 2014). She estimated their "effective specialization" at 0.3 for PNG, which means that each plant species should have, on average, 0.3 unique typhlocybine species feeding on it. There are at least 10,662 plant species in PNG (listed by Hoft 1992, and excluding orchids that have virtually no herbivores). This number, multiplied by effective specialization, gives us the estimate of 3,554 typhlocybine species feeding on PNG vegetation. However, only 40 species, i.e. less than 1.5%, have been taxonomically described from PNG, and only 4,508 species are known globally. Typhlocybines thus exemplify a taxonomically almost completely unknown group of herbivores. Many other taxa in PNG remain unknown, mostly those with small body size. For instance, only seven from 119 species of parasitoid wasps, reared from caterpillars, were already known taxonomically (Hrcek *et al*. 2013 and pers. comm.). We can still study communities of these species, using arbitrary names or numerical codes instead of species names, but such data sets cannot be combined into a country-wide database. This is why insect ecology in the tropics is heavily biased towards the study of communities, rather than broader geographic patterns.

L. Baje was not the first biologist to use plant-based extrapolation to estimate the diversity of insects. Westwood (1833) multiplied 100,000 vascular plant species, believed at that time to grow on the entire planet, by 4 - 6 unique insect species per plant, from his studies in Britain, to estimate the global diversity of insects at 400,000 – 600,000 species. Erwin (1982) applied the same approach 150 years later to his data on 682 beetle species sampled by applying insecticide to the canopies of 10 *Luehea seemannii* trees in Panama and calculated, after corrections for host specificity, arthropod taxa other than beetles, and non-canopy species, that there were 30 million insect species on the global flora of 50,000 tree species. We have used data on the number of insect herbivores feeding on almost 100 tree species in PNG and recalculated the global insect estimate again, suggesting that there are 6.1 million species (with a 90% confidence interval of 3.6 – 11.4 million species) of insects on Earth (Novotny *et al*. 2002; Hamilton *et al*. 2010, 2011). This estimate, supported by other studies (Odegaard *et al*. 2000, Miller *et al*. 2002), has been widely accepted. Our best estimate of global diversity of insects thus relies on the insect data collected in three PNG villages near Madang town: Ohu, Baitabag and Mis.

Rainforest food webs: insect herbivores, their host plants and their enemies

Ohu, Baitabag and Mis villages have hosted 15 years of insect studies, the former two in their community-based forest conservation areas. This research sampled insects feeding on tree species representing all main plant lineages: *Gnetum gnemon* from the gymnosperms, species representing the basal angiosperms, monocots including palms and gingers, and the two main lineages of eudicots: rosids and asterids. It also included herbivorous insects living many different lifestyles; the so called guilds are groups of species feeding on the same plant part in the same manner. And so we set off to study one guild after another: insects feeding as adults or larvae on leaves, semi-concealed larvae in rolled leaves, mining larvae chewing tunnels inside leaves, gallers chemically manipulating plants to produce galls, sap-sucking insects piercing individual leaf cells, or phloem, or xylem vascular elements, larvae boring in the phloem or xylem part of wood, or using wood to grow fungi as food, as well as larvae feeding on roots, and on fruits – either fruit pulp or seeds. Some of these guilds have been rarely studied before. For instance, adult chrysomelid beetles feeding on leaves are well known, while their larvae, feeding on roots, are not since nobody likes digging in the mud. R. Pokon, a PNG University of Technology student, avoided that necessity by setting up traps catching adult beetles freshly emerging from the soil, and traced them back to the roots they fed upon as larvae. He discovered that the larvae were mostly generalists, feeding on many different tree species, and showed how important these soil-dwelling chrysomelids were: there were about 200,000 of them emerging from each hectare of the forest every year (Pokon *et al.* 2005).

The three villages near Madang presently have 31 research papers listed in Google Scholar (2015) to their credit, and have become the world's most comprehensively studied sites for a wide range of insect herbivore guilds (Novotny *et al.* 2010, 2012). This research allowed us to study rainforest plant-insect food webs. They map the abundance of each plant and herbivore species and the frequency of their trophic interactions, i.e. which insect species feeds on which plant species, and how often (Figure 53). Over the years, we sampled 1,500 herbivore species and traced nearly 7,000 feeding interactions with their host plant species. However, even these seemingly impressive figures represent only 15% of the total herbivore species and trophic interactions in a lowland forest. We estimated that the entire rainforest plant – insect herbivore food web comprised ~50,000 distinct trophic interactions between ~200 plant and ~9,600 herbivore species (Novotny *et al.* 2010). The food web in Figure 53 may look complicated, but it shows only 251 trophic interactions, i.e. 0.5% of the total that may be found in a single rainforest.

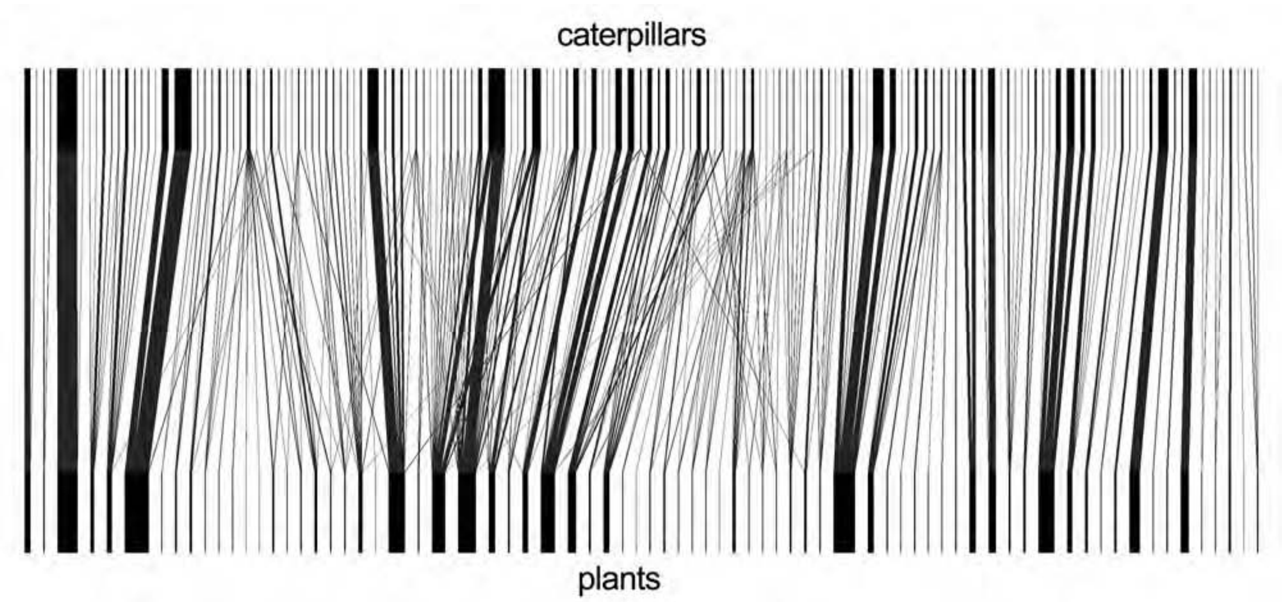

Figure 53. **Plant-herbivore food web for 151 species of leaf-rolling and leaf-tying caterpillars feeding on 88 plant species in a lowland New Guinea rainforest. The lower bars represent the frequency with which each host plant is consumed by herbivores and the upper bars represent herbivore species in proportion of their abundance. The widths of the links are proportional to the frequency of each interaction. Data from Novotny *et al.* (2010).**

Such complexity is not good news for tropical ecology. Ecologists should be able to explain how all these species coexist in the same forest, and predict how they will respond to disturbance, such as removal or addition of certain species. At present, we are unable to make these predictions from the knowledge we have. However, we can play with the food webs experimentally, change them in various ways and see what happens, hoping that we could understand the mechanisms of observed changes. PNG is a perfect place for manipulative rainforest experiments. Large forest areas are felled every year for subsistence agriculture. Most landowners are happy to try ecological experiments instead of gardening, as long as the discovery of fundamental ecological principles pays better than growing sweet potatoes for the nearest market. One of such experiments is described later in this chapter (Klimes *et al.* 2011).

How can so many species coexist in a tropical rainforest? This is one of the fundamental questions of ecology that keeps ecologists awake at night. The fascination of ecologists with high diversity in the tropics is partly due to the fact that many of them grew up in species-poor countries of the northern temperate zone. From such vantage point, rainforests may seem particularly diverse and exotic, while this perspective is not necessarily shared by PNG ecologists. However, the coexistence of almost 10,000 herbivore species in the same forest does require an explanation, even for an unprejudiced Papua New Guinean mind. A large number of herbivore species can be supported either by equally diverse plant resources (bottom-up effects), or by natural enemies that keep all herbivore species at low population densities, reducing thus their mutual competition for resources (top-down effects) (Denno *et al.* 2005). The number of distinct resources available to herbivores depends on plant diversity and host specialization of herbivores. It is well known that plant diversity is highest in the tropics (e.g. there are 5–10 times more plant species per 10,000 km^2, and six times more woody species per hectare in tropical than temperate areas; Novotny *et al.* 2006; Barthlott *et al.* 2007), but it remains unclear whether plant diversity is the only factor driving insect herbivore diversity.

Secondary forests, in PNG and elsewhere, have greatly reduced diversity of plants. Since the number of herbivore species per plant species remains the same between primary and secondary forests (Leps *et al.* 2001), this impoverishment of vegetation is driving the diversity of herbivorous insects. Further, secondary forests appear to support greater abundance of caterpillars (Whitfeld *et al* 2012). Given the extent of forest conversion that is taking place in New Guinea, the possibility of increased abundance of caterpillars poses a challenge for forest management, especially where pest outbreaks may threaten forest regeneration after logging.

Herbivores species are feeding on fewer plant species in tropical than temperate forests (Forrister *et al.* 2015), and higher specialization may thus facilitate their coexistence in tropical forests. However, we found no difference in host specificity between leaf-chewing insects in PNG and European forests, as long as it was measured on sets of plants with the same phylogenetic diversity in each forest (Novotny *et al.* 2006). It is thus possible that narrow host ranges in the tropics are driven by the composition of tropical vegetation, particularly by its many rare species of plants. The diversity of herbivores can be also maintained by top-down control, by their natural enemies. This is particularly likely when an increase in population density of herbivore species leads to higher mortality from their natural enemies, for instance because it is easier for them to focus on a more abundant resource.

Mosquitoes and malaria: a density dependent regulation of human populations in New Guinea?

Positive density-dependent mortality might have also been important in regulating human populations in PNG. Lowland populations are more resistant to malaria than the Highlanders, partly because they carry several red blood cell mutations. These are mildly harmful for the ability of blood to carry oxygen, but also protect against malaria (Clark & Kelly 1993, Kwiatkowski 2005). A high frequency of these mutations in the lowlands suggests that malaria protection afforded by the mutations is more important than their negative health effects, which points to malaria as an important mortality factor. In malaria-free areas the mutations disappear quickly, as they have done in the Highlands. Malaria probably controlled human populations in a density-dependent manner, since its transmission by Anopheles mosquitoes becomes more efficient in dense human populations. Higher transmission causes higher mortality from malaria, reducing the population density, and thus also returning malaria transmission to low levels. This mechanism may explain, together with differences in soil fertility, why the population density in PNG peaks in malaria-free montane valleys at 1700 m asl, while the lowlands remain sparsely populated (Muller *et al.*, 2003). Differences in population density shape other aspects of human societies, explaining perhaps why are the highlands societies more competitive and readier to fight for scarce resources that are those from the lowlands (Wiessner & Pupu, 2012). Differences in the competitiveness of lowland and highland populations are manifested in many ways; for instance, all taxi drivers in the lowland capital city, Port Moresby, are from the Highlands, as they have out-competed everybody else. For a biologist, the connection between the *Plasmodium malaria* parasite, frequent tribal wars in the Highlands and the predominance of Mt. Hagen taxi drivers in the capital city is rather straightforward indeed. Malaria research, including work on the malaria vaccine, is also an active area of PNG research, based at the PNG Institute of Medical Research (e.g., Muller *et al.* 2003, Genton *et al.* 2003).

The top-down impact of predators on insect herbivores is difficult to study since the acts of predation are hard to observe in the field. However, any defenceless insect exposed on rainforest vegetation – such as a termite worker glued to a leaf – is quickly discovered and attacked by ants; how quickly can be measured, as an index of predators' activity. For instance, 15% of such tasty baits were discovered and attacked within 30 minutes (Novotny *et al.* 1999). Another experiment pinned hundreds of artificial caterpillars, made of children's modelling clay, on leaves and monitored attacks by ants and birds, leaving recognizable marks on the clay caterpillars from their attacks. We found that caterpillars were increasingly safe at higher elevations, and that while ants were the most dangerous enemies of plasticine caterpillars in the lowlands, birds become more important at elevations above 1,500 m (Sam *et al.* 2014).

The importance of ants in lowland forests, where they seem to be literally everywhere, leads to an intriguing and seemingly naive question: how would a lowland rainforest look and function if all of a sudden, its ants disappeared? We tried to answer this question by an experiment in a 25 x 25 m forest plot. We isolated the plot from the surrounding forest by felling a narrow strip of vegetation along the perimeter and cutting lianas overlapping into the plot, then fenced the plot using plastic sheet coated with insect glue, and hung 135 traps, accessible only to ants and containing tuna laced with insecticide, in the canopy of all larger trees. We managed to reduce the number of ants in the forest by 80% (Klimes *et al.* 2011). After 10 months of the experiment, we sampled insect herbivores and measured the damage they had done to the plants. Rather surprisingly, the ant exclusion did not lead to any increase in herbivore abundance or damage. The missing ants could have been compensated by higher predation by birds, or ants may not be such important predators as previously thought. Although they quickly attack any available baits, they may be less successful attacking real insects. Ants also obtain energy from plants, directly from extrafloral nectaries or indirectly from honeydew produced by sap-sucking hemipteran insects. A pioneering study using isotope analysis of ant biomass that can distinguish between plant and animal origin of carbon and nitrogen discovered that rainforest ants obtain a large share of energy from plants (Davidson *et al.* 2003). Our ant exclusion demonstrates the importance of experiments in the study of complicated food webs in tropical forests, where seemingly logical theoretical expectations are not always confirmed by real plants and insects.

Plant diversity may very well sustain herbivorous insect diversity, but the opposite relationship, where insect herbivores (or other plant enemies, such as fungal pathogens) control plant diversity, is also possible and intensely discussed by ecologists. Explaining high rainforest diversity is even more difficult for plants than insects, since plants all have very similar essential requirements: water, sunlight, and soil nutrients. With 536 plant species growing within a 50-ha forest plot in PNG (Vincent *et al.* 2014), it is quite difficult to envisage 536 distinct niches, determined by unique combinations of environmental conditions, needed for coexistence of all plant species. Top-down control by natural enemies is thus more likely in plants than insects, and insect herbivores could be one of the density-dependent mortality factors providing such control. This mechanism was proposed independently by D. Janzen and J. Connell almost half a century ago (Janzen 1970, Connell 1971). It can be inferred indirectly from spatial patterns of plants in forest plots (Bagchi *et al.* 2011), or tested by excluding plant enemies by insecticides and fungicides (Bagchi *et al.* 2014). We have reared insects, including beetles, moths, and fruit flies, from 3,500 kg of fruits sampled from 531 rainforest plant species (Figure 50a) and found that insect attacks on fruits are too rare in most of the plant species to cause the seed mortality needed for the density-dependent mortality effects hypothesized by Janzen (Ctvrtecka *et al.* 2014). We can thus cross off seed-eating herbivores from the list of likely suspects for top-down control of plant diversity in PNG forests.

Rainforest research of insect herbivores, and their enemies, has obvious forestry and agricultural applications. In particular, many cash crop trees, including coffee or cocoa, are alien species in PNG that has become targets for insect herbivores from local rainforests. For instance, we have reared cocoa pod borer (*Conopomorpha cramerella*), a major pest of cocoa (Yen *et al.* 2010), also from several rainforest tree species (unpubl. data). The colonization of introduced tree species by herbivores can be observed on two alien species spreading in PNG on their own: *Piper aduncum* from South America, and *Spathodea campanulata* from Africa (Figure 54, Figure 55). They remain limited to disturbed and secondary forest vegetation, as predicted by ecological theory (Leps *et al.* 2002). Both alien species were quickly colonized by local herbivore communities that reached diversity comparable with the herbivore diversity on native plant species, but composed predominately from generalists (Bito 2007, Novotny *et al.* 2003). We can expect similar process for tree crops.

Figure 54. ***Piper aduncum*** **(light green) invading secondary forest in the Bulolo region.**

Figure 55. **The invasive species** ***Piper aduncum*** **(light green) invading grassland and scrub in the Bulolo region.**

Coffee and betel nut in New Guinea: benefactors or parasites?

Seeds, as packages of valuable nutrients ready to support a germinating embryo, tend to be well protected against predators, mechanically by hard shells or chemically by a variety of poisons. In some cases, this protection can be hijacked by seed predators for their own benefits. The PNG economy relies on such "misuse" of two poisons: caffeine, an alkaloid originally used by Coffee shrubs in Africa to protect their seeds against predators, and arecoline, used together with a mix of other alkaloids to protect seeds of *Areca catechu* palm (Wink 1993, West 2012). In both cases, these chemicals became unexpectedly attractive to one seed predator species, namely humans. This relationship may be seen as an example of mutualism, where both humans and plants benefit. In particular, coffee and betel palm reached population sizes and geographic distributions that would have been impossible without human assistance. An alternative interpretation of human relationship with the two plants suggests that the plants are the only beneficiaries here so that both coffee and betel palm are parasitizing on humans, chemically manipulating millions of human brains to ensure that people would spare no expense and effort for the benefit of these two plants, planting them on huge areas of land, and protecting them from pests and competition by other plant species. A look at the streets of European cities, almost entirely given to coffee shops, or streets in PNG, lined with betel nut stalls, lends some credibility to the parasitism hypothesis.

Rainforest adventures of alpha, beta and gamma diversity

The 924 butterfly species in PNG represent the pool of available species, produced by in situ evolution or immigration, from which local communities can be drawn. Alternately, we can see the PNG fauna as an aggregate of all local butterfly communities. Its size, or gamma diversity, depends on the species richness of individual communities (alpha diversity) and change in species composition among communities (beta diversity). PNG butterflies may form either locally species-rich communities that do not change too much from one site to another (high alpha and low beta diversity scenario), or species-poor communities unique in composition at each site.

Beta diversity in insect communities is a composite result of dispersal limitation, depending on the geographic distance, and differences in environment between sites. There is little surprise that herbivore species change with changes in the composition of vegetation. That is why we focused on a more interesting case of herbivore communities feeding on the same plant species, and explored the effect of dispersal limitation in ecologically uniform lowland forests. Our team of six researchers descended on eight study sites forming a regular grid within a 500 x 150 km area in the floodplains of the Sepik and Ramu rivers and, together with local villages, completed three months of insect sampling at each site. We found low beta diversity of insects feeding on the same plant species, even for sites 500 km apart that still shared 70% of their caterpillar species (Novotny *et al*. 2007). Lowland herbivore communities may be locally very diverse, but they do not change much from one area to another. In other words, they have high alpha but low beta diversity.

We also caught 5,903 live butterflies at one of the study sites, marked each with a personal number written on its wings, and released them again. Then we managed to catch 1,803 of them again and see how far they had moved since their previous capture. The butterfly species moved 184 m on average, but in six of the 14 species studied, >1% of individuals moved 1 km or more (Vlasanek *et al*. 2013). In view of this mobility, travelling 500 km through continuous rainforest should not be a problem, certainly not during 18,000 years available for travel since the end of the last ice age.

Beta diversity should be much higher in the forests along steep environmental gradients, such as elevational gradients. At Mt. Wilhelm, the mean annual temperature drops 0.54 °C with each 100 m gain in elevation so that the rainforests there are experiencing mean temperatures from 27.3 °C (200 m asl) to 8.6 °C (3,700 m asl), across less than 50 km distance. Six students went to Mt. Wilhelm to study altitudinal biodiversity trends in their favourite animal groups: Legi Sam surveyed butterflies (Papilionoidea) flying along transects, Pagi Toko sampled geometrid moths (Geometridae) attracted to light, Francesca Dem used sweep net to sample leafhoppers (Auchenorrhyncha) from the vegetation, Jimmy Moses sampled ants (Formicidae) by various methods using baits and pitfalls, Chris Dahl conducted night surveys of frogs, and Katerina Sam studied birds by point counts and mist netting. Together they found 2,113 species (Table 1). While most taxa reached their maximum alpha diversity in the lowlands, geometrids and frogs were most diverse at mid-elevations. The ratio of total diversity along the entire transect to the local maximum ranged from

1.8 to 3.3, suggesting that environmental variability generated by changes in altitude enriched Mt Wilhelm species pool by 80 – 230% compared to even the most diverse community at a single altitude. Mt. Wilhelm represents a nationally important biodiversity hotspot, with 15 – 51% of all PNG species present in the taxa where such analysis could be performed. Although important, the species counts do not tell the whole story. For instance, butterflies are most diverse at 200 m and decrease steadily with elevation to 2 species at 3,700 m, but the species with the smallest geographic ranges, and thus of highest conservation concern, prefer higher elevations (Sam 2011).

Ecological research and the conservation crisis in Papua New Guinea

The permanent forest dynamics plot in Wanang does not look it, but it is probably the most expensive infrastructure for ecological research ever built in PNG. It is the only member of the Center for Tropical Forest Science, an international consortium of plant plots (www.ctfs.si.edu), from the Australian biogeographic region. The 1.0 x 0.5 km plot is situated in the centre of the Wanang Conservation Area, a 10,000 ha rainforest on the Ramu River floodplains owned and managed by eight clans from the Wanang village. The plot comprises 288,204 plant stems with diameter >1 cm, all of them individually tagged, measured, mapped and identified to 536 species (Vincent *et al*. 2014) so that the precise distribution of each species can be studied (Figure 56). The plant data are also linked to regular surveys of selected insect taxa, including butterflies, ants, termites, and fruit flies in the plot.

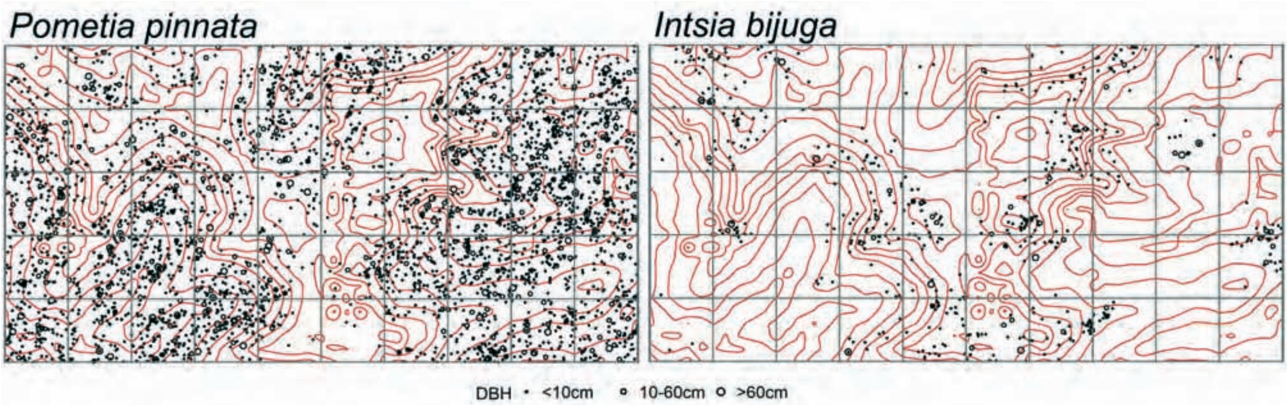

Figure 56. Spatial distribution for two important tree species in the 50 ha Wanang forest dynamics plot: (A) *Pometia pinnata* (Sapindaceae), species with edible fruits, known as taun, and (B) *Intsia bijuga* (Fabaceae), commercially valuable species, known as kwila. The map shows that *P. pinnata* prefers lower slopes while *I. bijuga* prefers ridges (Vincent *et al.* 2014).

The tagging of the trees took a team of six researchers three years of steady work, and used over 500 kg of aluminium tags, nailed or tied to each plant stems in the forest by over 50 km of copper wires. The list of all tagged trees would fill ten books 500 pages each, although this would not be a particularly exciting read. The plot will be re-surveyed every five years so that we can study changes in the forest growth and composition. Which trees grow faster, which suffer high mortality, how does the terrain, or the tree neighbours, affect growth and survival, is overall forest biomass or carbon stock increasing, how does it respond to El Niño? There are many interesting question to ask with such a large data set.

Wanang Conservation Area: a recipe for conservation success?

Adjacent to the 50 ha forest dynamics plot is the Swire Research Station: three permanent buildings with laboratory and accommodation space, and autonomous water and solar electricity systems, built from 15 tons of material dropped by a helicopter in the middle of the forest (Figure 50). The station is accessible from Madang by a three hour drive followed by a three hour walk. The plot, research station and conservation area are a result of collaboration between Wanang village, the New Guinea Binatang Research Center, the PNG Forestry Research Institute, the University of PNG, the Department of Environment and Conservation, Swire and Sons, and the Steamships Trading Company, with links to overseas academic partners in USA (University of Minnesota, Smithsonian Institution) and Europe (Czech Academy of Sciences, University of South Bohemia). The collaboration achieved a synergy between rainforest conservation, research and training. In particular, research activities provide steady employment for Wanang villagers and pay conservation royalties, therefore financially supporting the landowners' decision to conserve, rather than log, their forests. This rainforest conservation is also attracting private funds for community development projects, including a village school.

Not all PNG conservation can be supported by income from research, but a funding mechanism that rewards landowners for conservation, similarly as they are rewarded for the use of their lands for timber or mineral extraction, is crucial for the future of conservation in PNG (Novotny 2010). Conservation looks deceptively inexpensive since, when successful, it means that not much happens to the protected forest. In fact, the real cost of conservation equals the potential profits that could be generated by alternative uses of the forest: conservation's opportunity cost. The cash-generating schemes proposed for conservation include ecotourism, sustainable harvest of rainforest products, or agriculture, such as coffee or vanilla farming. These have proved economically unviable, and/or required full time work by the landowners, making them unattractive in comparison to logging royalties. The PNG government should recognize that landowners conserving the country's biodiversity play equally important role as those allowing the extraction of the country's mineral and timber resources, and reward both land use with appropriate royalties.

PNG is entering a critical phase in its development that will determine, probably within a single generation, the fate of the country's environmental wealth. The dynamics of land use in neighbouring countries provides examples of possible trajectories for PNG. In particular, while selectively logged forests after the first cut remain biologically valuable, they are often subject to degradation through premature repeated cuts and finally conversion to plantations, as illustrated by rapid deterioration of the majority of lowland forests in Borneo (Reynolds *et al*. 2011). In contrast, Australia demonstrates that there is a point in economic development when tropical forests become valued by the society to the extent that their conservation is widely supported. The key issue for PNG is whether there will be enough forests left when the country reaches this point of economic and political development. There is no global correlation between the country's wealth and the proportion of its land under forest cover (Gapminder 2015), suggesting that logging is not a secure path to economic development. Unlike many other developing countries, PNG has an alternative to large scale logging and forest conversion in its highly profitable mining industry that generates several orders of magnitude higher revenue per hectare of impacted land than is the case for logging and plantation industries.

PNG is one of the few countries in the world where customary ownership of the land, originating in a tribal past, is recognized by the country's legislation and an enforceable reality on the ground. This land tenure makes conservation areas difficult to negotiate, as they may include numerous landowner groups with different priorities and expectations. However, the same is true for logging projects, and these have been negotiated much more successfully than conservation areas. As a result, PNG has an impressive network of logging concessions, while the network of protected areas to conserve the country's biodiversity is rudimental (Shearman & Bryan 2010).

Conservation is driven primarily by biologists who are concerned that conservation areas are situated in biodiversity hotspots. Starting with the PNG Country Study on Biological Diversity (Sekhran & Miller 1995) and the PNG Conservation Needs Assessment (Beehler 1993), we have seen 20 years of prioritizing different regions of the country for some hypothetical future conservation that would be, one day, miraculously delivered to its biodiversity hotspots. There has been many failed conservation projects in the PNG history, all due to inadequate popular, political or financial support for conservation and ensuing conflicts about the use of land (West 2006, Mack 2014, Novotny 2009, 2010). There are hardly any conservation projects that have failed because they lacked adequate biodiversity information and were therefore erroneously protecting a species poor forest. This experience tells us that conservation areas should be located primarily where conservation enjoys strong support from the landowners. The Wanang Conservation Area, for instance, exists because it has been spearheaded by an effective community leader, Filip Damen, later recognized for his leadership qualities also internationally, as a recipient of the Seacology Prize (www.seacology.org/about/seacology-prize/). We should embark on a broad search for the communities supporting conservation, places where we can find leaders of similar calibre as Mr. Damen, and ensure fair economic compensation of landowners for conservation efforts. In the longer-term perspective, training more PNG biologists and developing more education- and a more research-oriented society in general may be the most efficient path to better conservation (Mack 2014). Conservation measures need to be formulated, explained to, and promoted in the general population for them to succeed politically. These tasks are there for both present and future PNG biologists.

Ecological research in Papua New Guinea: how to make it better?

The progress in the enormous task of mapping and understanding biodiversity of PNG has been rather slow, even considering that PNG has a small population and is not a particularly wealthy country. For instance, "Papua New Guinea" featured in the title of 397 papers in non-medicinal biological research published in 10 years from 2003 to 2012 (and listed in Web of Science, an international database for research papers), compared to 1023 papers on Costa Rica, another developing tropical country with a small population. Even more importantly, only 95 papers on PNG, i.e. one quarter of the total, had at least one PNG author, while almost a half of papers from Costa Rica had a local author. The minority role of PNG researchers in the study of their own country's biodiversity is also a concern for conservation, which needs a vibrant local academic community to support it politically. PNG has the potential to produce a strong cohort of research biologists in the next generation since its population is predominately young (a consequence of rapid population growth, 2.7% annually; Laurance at el. 2012), English-speaking, and continues to be knowledgeable about the natural environment, typically as a result of a rural, village-based adolescence.

Declining language skills and ecological knowledge in New Guinea: a case for concern?

The rainforest dwelling societies, in PNG and elsewhere, are well known for detailed knowledge of the natural environment, including classification and ecological knowledge of their plants, birds and mammals (e.g., Majnep *et al.* 1978, Majnep & Bulmer 2007). High cultural diversity in PNG is a product of the past tribal isolation and as such can become impractical in modern life.. While PNG languages still thrive in the village environment, only 52% of respondents were fluent in their local language among urban internet users, compared to 95% of their parents (Baro 2015). Baro (2015) also documented that ethno-biological knowledge is linked to fluency in local language, and as such also in decline, even in many remote villages.

There is probably no other country in the world with a young generation as comfortable in the rainforest environment as PNG. This extensive rainforest experience has presented an opportunity to develop paraecologist training programmes in PNG, combining the experience from rainforest living with science-oriented education in research techniques. Over the past 20 years, PNG has become one of the two leading countries in paraecologist training and research, together with Costa Rica (Basset el al. 2000, 2004, Janzen 2004, Simons 2011). This programme is lead by the New Guinea Binatang Research Center and contributed to the majority of recent entomological research in PNG, including almost all studies discussed in this chapter. Paraecologists are trained in general science, collecting methods, specimen preparation, microscopy, photography, computing, logistics of biodiversity surveys, and principles of resource conservation. Further, they can became experts on local flora and fauna, and constitute efficient teams for biodiversity surveys. The paraecologist programmes have potential to build a large and qualified workforce that, in collaboration with researchers and students, can significantly advance the study of PNG biodiversity.

Postgraduate students are the driving force of biodiversity research in developed countries, providing enthusiastic and inexpensive workforce as well as fresh ideas. In PNG, postgraduate education opportunities are extremely limited and expensive. It is striking how few Honours and MSc gowns can be spotted in the student crowd at the annual University of PNG, as well as other universities, graduations. The scarcity of postgraduate students remains the principal weakness holding back biodiversity research in PNG (Mack 2014). Many papers cited in this chapter were lead by postgraduate students from PNG (L. Sam, N. Baro, F. Dem, L. Baje, R. Pokon, P. Toko, C. Dahl) and overseas (K. Sam, P. Vlasanek, P. Klimes), illustrating the potential of students in research.

PNG research also suffers from the unfortunate split between universities, where excessive teaching loads leave the staff with little opportunities to engage in research, and research institutes, where researchers lack daily contact with postgraduate students. This institutional split could be bridged by having postgraduate students in residence at the research institutes, and researchers from these institutes as guest lecturers at universities. This approach to student training has been already tested by some NGOs as well as the PNG Institute of Medical Research. An International Cooperative Biodiversity Group project based at the University of PNG (Barrows *et al*. 2009) represents an example to follow in combining student training, biodiversity research and commercial applications.

PNG is in an excellent position to capitalize on its advantages for tropical ecology field work by providing suitable research facilities for ecological research, attracting both local and international researchers and students to biodiversity research. This role has been played over the past 50 years by a series of mostly non-governmental organizations, including the Wau Ecology Institute, the King Leopold III Biological Station, the Christensen Research Institute, the Sera Field Station of the Wildlife Conservation Society, the Swire Research Station of the New Guinea Binatang Research Center, the Kamiali Biological Field Station and the Motupore Island Research Station of the University of PNG. Most of these stations are no longer active, highlighting the instability of NGO driven facilities in PNG, dependent on overseas donors with ever changing priorities. A more stable field research facility could bring more overseas research to PNG with potential benefits, including opportunities for international collaborations, access to overseas facilities and student training.

Further, PNG is lacking a mechanism for funding biodiversity, and other, research that would be open to applicants from all universities, research institutes and NGOs, and award funds according to the merit of submitted research proposals, judged by an independent panel of researchers. Australia, UK and USA, among other countries, spent a lot of time testing the optimum methods for research funding and, rather remarkably, all converged on a more or less identical model, exemplified by their respective grant agencies: ARC, NERC, and NSF. Researchers in PNG would be well served by adopting this model. Finally, while there are research institutes focused on agriculture and forestry, the country is lacking a PNG Biodiversity Research Institute.

The PNG Government has recently begun to address the pressing issues of research funding, management and training through the PNG Research, Science and Technology Council, founded in 2013. These efforts have been noted and applauded in a "Papua New Guinea: Pacific Positivity" feature in Nature (Campbell & Grayson 2014).

In conclusion

Papua New Guinea remains a country "at the edge of the world", or, more precisely, the Pacific, where many global trends, both positive and negative, arrive with some delay. This is largely a good thing, allowing the country to learn from the successes and mistakes of others. The tsunami of rainforest exploitation that destroyed most of the forests of the continental Asia, then the Philippines, followed recently by Borneo, has now arrived to the shores of New Guinea. It is the present generation that will make decisions about the future of PNG biodiversity that will influence the country's trajectory for many years to come. Biological research in PNG has great, yet so far mostly unfulfilled, potential to expand, and help to steer the country towards informed decisions about its future. It is time for PNG biologists to go to work, to study and protect the country's biodiversity "from the mountains to seas".

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