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森林樹冠層
生態保育國際研討會

指導單位 內政部營建署

主辦單位 雪霸國家公園管理處

協辦單位 行政院農業委員會林業試驗所

國立臺灣大學生物資源暨農學院實驗林管理處

承辦單位 國立臺灣大學森林環境暨資源學系

『2014 森林樹冠層生態保育國際研討會』議程

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林業試驗所所長　黃裕星
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2014 International Symposium of Canopy Ecology Conservation Program

Schedule	Panels		
08:30－09:00	Registration		
09:00－09:30	Opening Chair Dr. Biing-T. Guan	Director of Shei-Pa National Park	Chiu-Fang Lee
		Director of Taiwan Forestry Research Institute	Yue-Hsing Huang
		Director of NTU Experimental Forest	Ya-Nan Wang
		Director General of Construction and Planning Agency	Yu-Qun Ding
09:30－09:35	Group Photo		
09:35－10:30	Chair Andy Lee	Speaker	Keynote Speech
		Dr. Margaret Lowman	Life in the Treetops – Exploration of the World's Canopies.
10:30－11:00	Break		
11:00－12:00	Chair Andy Lee	Speaker	Speech
		Dr. David Shaw	Canopy Biodiversity in Douglas-fir Forests of the Pacific Northwest of North America.
		Dr. Rebecca Hsu	Regional and Altitudinal Patterns in Vascular Epiphyte Richness in Taiwan.
12:00－13:00	Lunch		
13:00－14:50	Chair Andy Lee	Speaker	Speech
		Dr. Maklarin Lakim	Forest Canopy of Tawau Hills Park in Sabah Parks.
		Dr. Wen-Bin Yeh	The Comparison of Insects from Canopy, Understory, and Shrub Layers by Different Sampling Methods in Mid-montane Xuejian Reserved Forest.
		Wesley Hunting (PhD Candidate)/ Dr. Man-Miao Yang	Fogging a Subtropical Forest of Central Taiwan: a Study of Arboreal Beetle Assemblages and Insect Recolonization.
14:50－15:10	Break		
15:10－16:30	Chair Andy Lee	Speaker	Speech
		Dr. Philip Wittman	Construction of Canopy Walkways.
		Mr. Alim Biun/ Mr. Fred Tuh	Poring Canopy Walkway, is a Recreational and Educational Facility that is Attracting Many Visitors.
16:30－17:00	Chair Dr. Biing-T. Guan	Comprehensive Group Discussion	
17:00		Closing Remarks	

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Life in the Treetops – Exploration of the World's Canopies

爬樹的女人：探索世界樹冠層

Dr. "CanopyMeg" Lowman

Chief of Science and Sustainability, California Academy of Sciences, USA

www.canopymeg.com www.treefoundation.org www.calacademy.org

Our ancestors were tree dwellers. Throughout human history, people have taken to the trees as safe havens, sites of special spiritual connection, and a cornucopia for food, medicines, materials, and productivity. With their billions of green leaves that produce sugars from sunlight, tree canopies are epicenters of life and food chains throughout the planet. In an evolutionary sense, humans descended from ancestors in the treetops. Anyone who pauses at the zoo to watch a monkey cavorting in the branches is amused, inspired, and subconsciously reminded of some aerial sensation that tugs on our evolutionary memory banks.

In Papua New Guinea, a tribe called the Korowai still lives in the treetops, erecting amazing aerial houses accessible by twig ladders. It is speculated that their unusual habit of community tree houses evolved as a mechanism to escape enemies on the forest floor, and provide a healthy environment above the dank, dark understory. Tree houses remain a recreational vestige of children and adults alike that inspire links between humans and the natural world. Many famous people have escaped to childhood tree houses – John Lennon (of the Beatles), Winston Churchill, the Roman Emperor Caligula, and Queen Victoria when she was a young princess. Recent medical findings indicate that children who play outdoors and learn about nature have better health and well-being.

Why do the treetops hold such a spiritual, as well as scientific, importance for cultures throughout the world? And why have scientists only recently explored these heights for scientific discovery? Relatively few unknown frontiers of exploration remain in the twenty-first century, but the treetops are considered the "eighth continent," since they are so unexplored. Similar to astronauts, scientists who explore the canopy are called "arbornauts!"

The treetops reputably house almost 50% of the land-based biodiversity of Planet Earth. The combination of sun, fruits, flowers, and year-round productivity of the foliage in tropical rainforests provide ideal conditions for an enormous diversity of inhabitants. Thousands of species of trees and vines produce a veritable salad bar for millions of insects that are in turn eaten by myriad reptiles, amphibians, and mammals; and in turn those primary consumers are eaten by secondary consumers such as harpy eagles, jaguars, and other carnivores. Finally, the cycle of life is completed when soil decomposers break down and recycle all matter back into the canopy.

In addition to classic food chains circling from sunlight to leaves to herbivores to carnivores/omnivores to decomposers, forest canopies house extra niches for other unique forms of life. Bromeliad tanks, tree crotches, leaf surfaces, and epiphyte communities host extra layers of miniature life in forest canopies. For example, bromeliad tanks house virtual swimming pools in the sky that are home to an entire microcosm of tiny organisms. Mosquito larvae, nematodes, tarantulas, katydids, shovel-tailed lizards, and monkeys live in and/or drink from these aerial watering holes. Some poison dart frogs trek all the way from the forest floor into emergent trees to deposit their eggs in phytotelms (canopy pools of water). Other unique canopy niches include the crotches of trees which provide germination sites for strangler figs, and soil repositories that house millipedes, nematodes and other critters usually associated with the forest floor. Strangler figs are the only tree known to start life "at the top" and send their aerial roots extending downward, eventually penetrating the soil below to expand and strangle their unwitting host plants. Air plants, technically called epiphytes, add an extra layer of biodiversity in the moist, sun-flecked branches about two thirds of the way toward the treetops. Even more amazing, the surfaces of canopy leaves provide homes for "epiphlly," another extra layer of miniature plants including lichens, mosses, and fungi, many of which grow exclusively on leaf surfaces. Within the "canopies" of these epiphylls live an entire microcosm of tiny invertebrates and other undiscovered critters visible only with a microscope. Nothing rivals the forest canopy in terms of biodiversity – layers of life upon life, all nurtured by sunlight, moisture, and warmth in a unique combination that fosters an extraordinary diversity of species.

This world of canopy plants, insects, birds, mammals, and their interactions remained relatively unknown and out-of-reach to scientists until as recently as thirty years ago. Field ecologists first used slingshots to propel ropes into the treetops in the late 1970s, but even then no one fully understood that this green umbrella overhead was a critical component of global health. Exploration of both undersea and outer space was relatively commonplace prior to the exploration of forest canopies. But with the recent escalation of climate change and landscape degradation, canopies have become a proverbial "canary in the coal mine" since their declining health is a harbinger of environmental changes on a global scale. Currently, forest canopy scientists – along with reef ecologists, ice physicists, soil biologists, water chemists, and others– are taking on the role of planetary physicians, working against a near-impossible timeline in hopes of unraveling the critical mysteries of how our planet functions. With access into forest canopies, our knowledge of the machinery of forest ecosystems has greatly expanded. And perhaps less appreciated in a technical sense, forest canopies enhance our sense of wonder and appreciation of the natural world, leading to more ambitious conservation agendas.

Biologists in the nineteenth and twentieth centuries traditionally based their ideas about forests on observations made at ground level. These ground-based perceptions are summarized in a comment by Alfred R. Wallace in 1878:

> *Overhead, at a height, perhaps of a hundred feet, is an almost unbroken canopy of foliage formed by the meeting together of these great trees and their interlacing branches; and this canopy is usually so dense that but an indistinct glimmer of the sky is to be seen, and even the intense tropical sunlight only penetrates to the ground subdued and broken up into scattered fragments…it is a world in which man seems an intruder, and where he feels overwhelmed*.

Binoculars and telescopes were probably the first tools for canopy exploration. Charles Darwin, in the nineteenth century, looked into the tropical rainforest foliage with his scope, but did not sample except for those canopy denizens that fell to the ground. He was nonetheless enthusiastic about the diversity of tropical forests. Ideas about forest canopies changed very little for almost a hundred years from Darwin's day until the 1950s, when a steel tower was constructed in Mpanga Forest Reserve in Uganda to study gradients from the forest floor to the canopy. Towers provided access to monitor insect vectors of human diseases, representing one of the first applied biological studies conducted in the forest canopy.

The 1970s represented the golden age of canopy access with development of SRT (single rope techniques) for long-term canopy research, not just occasional collections **(Figure 1)**. Whereas SCUBA equipment heralded the age of exploration for coral reefs, ropes and harnesses inspired the "race to the top" (of trees). This versatile method enabled scientists to reach the mid-canopy with ease, and dangle from a rope to observe pollinators, epiphytes, herbivores, birds, monkeys, and even sloths. Portable and relatively inexpensive, SRT allowed even graduate students with a modest budget to survey life in the treetops. This method was developed by Lowman in Australia in 1979, and at almost the same time independently by Don Perry in Costa Rica. Ropes were ineffective, however, to reach the leafy perimeters of tree crowns, since the ropes had to be looped over sturdy branches usually close to the tree trunk. To access the leafy outer foliage of canopy trees, new devices were invented to overcome this limitation. For example, botanists in Indonesia devised the canopy boom, a horizontal bar with a bosun's chair at one end, which could be swung around the leafy canopy away from the woody trunks. In Pasoh, Malaysia, a combination of ladders, ropes, and booms launched research that solved the mystery of the pollination of dipterocarp flowers.

Creative engineers and canopy biologists partnered to construct the first canopy bridges and platforms for public access in the 1980s. The first two such canopy walkways were constructed simultaneously: one in Malaysia anchored in tree crowns, and another in Queensland, Australia supported by telephone poles. North America's first canopy walkway was built as recently as 1992, suspended between oak trees in Massachusetts; but America's first public canopy walkway was opened among oak-palm hammocks in Myakka River State Park in Florida in 2000 **(Figure 2)**. Canopy walkways were replicated throughout the world in the 1990s, using a modular construction design developed by Canopy Construction Associates (www.canopyaccess.com) and others. Since then, canopy walkways and ladders used in conjunction with climbing ropes, zip lines, and other tools have become popular for ecotouris as well as for research. Subsequently, canopy walkways provide sustainable economy to local people in tropical forests (e.g., www.treefoundation.org). The world's longest walkway, supported by trees, exists in the Peruvian Amazon and provides income for over 100 local families **(Figure 3.**). The world's newest canopy walkway is opening in 2014 in Taiwan in She-ih National Park.

Perhaps one of the most creative canopy access tools is the French-designed hot-air balloon, called *Radeau des Cimes* (translation: raft on the rooftop of the world). It flies independently, but also operates in conjunction with an inflatable raft (27 meters in diameter) that serves as a base camp or platform atop the uppermost branches of tall trees. In 1991, the Radeau des Cimes expedition team pioneered a new technique called the *sled*, or skimmer. This small (5 meter across) equilateral, triangular mini-raft was towed across the canopy by the dirigible, similar to a boat with a trawling apparatus in the water column. The sled allowed rapid exploration between trees to compare pollinators, photosynthesis, herbivores, and relative diversity and abundance of canopy life.

Construction cranes represent the most recent tool for safe access into the forest canopy. In 1990, the Smithsonian Tropical Research Institute erected a 40-m-long crane in a Panamanian seasonally dry forest; since then, ten other crane operations have commenced operation in countries such as Australia, Switzerland, Germany, Japan, Indonesia, the United States, and Venezuela. Cranes are expensive to install and operate (usually ranging from US $1 to $5 million), but offer unparalleled, repeated access to the uppermost canopy as well as to any section of the understory within reach of the crane arm.

In the 1800s, naturalist Charles Darwin estimated that approximately eight hundred thousand species inhabited the Earth. (One can only imagine that the Queen of England was most impressed by his scientific prowess in calculating this apparently enormous number!) Access to forest canopies has led to the discoveries of millions of species inhabiting this above-ground world. One hundred years after Darwin, Dr. Terry Erwin of the Smithsonian Institution first quantified the abundance of life in the treetops. Erwin sprayed several tree canopies in the tropics with a mild insecticide, and all of the arthropod residents fell to the ground in a heap, enabling him to count and catalogue them. From his initial harvest of insects in Panamanian rainforest trees in 1982, Erwin extrapolated that there may be 30 million species on our planet, not 1-2 million as previously estimated. Since then, studies by other canopy biologists confirmed Erwin's predictions that millions of insects inhabit forest canopies. My own work in Australia, using the same fogging techniques, provided similar data to Erwin, with millions of species (mostly insects) in the canopy. Professor Edward O. Wilson, eminent biologist at Harvard University, speculated that as many as 100 million species may inhabit our Earth based upon initial surveys of the canopy, soil, and oceanic biodiversity combined. The jury is still out as to exactly how many species inhabit Earth; however, estimates range from as low as 10 million to as high as 100 million!

Field biologists who focus on biodiversity seek to catalog, identify, and understand the role of all creatures on Earth. This is not simply a naming game: its ultimate purpose is to understand the structure and function of an ecosystem, almost the same way that we seek to know how the components of a car engine operate together to create an efficient machine. The challenge to discover and identify species throughout the world is not easy. Finding a new beetle in the treetops is akin to locating the proverbial needle in the haystack –ninety percent perspiration and ten percent luck. All organisms collectively – orchids, beetles, birds, vines, frogs, and many others – constitute biodiversity, otherwise known as the variety of species on Earth. The word "biodiversity" has become politically and scientifically important over the past two decades, as human activities have accelerated ecosystem degradation and subsequent loss of species throughout the world.

Many canopy species provide essential ecosystem services that human beings depend upon for survival. In the Amazon, plants produce chemical defenses against insect attack; and these chemicals, in turn, are used by indigenous cultures for medicinal purposes. The shaman (or medicine man) is a highly respected community leader who has inherited generations of knowledge about the practice of using plants for medicinal purposes. Canopy leaves, barks, and fruits provide a veritable apothecary in the sky, all of which have evolved over time due to the unique interactions of plants with their herbivores (mostly insects!).

As a result of this tumultuous history of developing creative methods for exploration and asking questions in a three-dimensional and complex habitat, the role of canopy biologists has changed. No longer can scientists dangle leisurely from the trees and simply contemplate the beauty of harpy eagles and katydids; instead, they are caught up in an urgent race against time whereby answers are needed before the chainsaws win. In short, canopy scientists cannot afford to sleep! To date, only 1.8 million of an estimated 10-30 (or perhaps 100?) million species have been identified. At their current rate, taxonomists classify approximately 7,000 new species per year, so the pace is agonizingly slow as compared to the carnage of deforestation. The notion of sorting, counting, and naming as many as one hundred million species is daunting. The ecological task of determining which ones are most important to forest health is even more challenging. As Stewart Udall, former U.S. Secretary of the Interior once said: “Over the long haul of life on this planet, it is the ecologists, and not the bookkeepers of business, who are the ultimate accountants.”

How *many* is one hundred million species? Is there a way to make that enormous number more meaningful for those of us who are not mathematicians? If 200 scientists discovered and identified one new species every day for the rest of their lives, they would need almost 1,500 years including weekends and holidays to complete their task of identifying the estimated biodiversity on Earth. That is a lot of time and effort! What a lot of species! But even more urgent than names alone, biologists need to determine benchmarks for forest canopy health. Is biodiversity important? And do we care if some species become extinct? How much forest and which tree species are critical to maintain this global machinery that we call a forest ecosystem? Can forests function in fragments, and will they remain healthy if replanted in single-species plantations? Unfortunately, no one has answers to these important questions. Biologists have not studied forest canopies long enough to understand the processes that are critical to their health. In the wisdom of *Sand County Almanac* (Oxford University Press, 1949), renowned ecologist Aldo Leopold said: “To save every cog and wheel is the first precaution of intelligent tinkering.” Another famous scientist, Paul Ehrlich, considered biodiversity analogous to the mechanical parts of an airplane. He speculated that if an airplane mechanic continued to remove nuts and bolts from a plane, the machine will eventually cease to fly. Similarly, as species disappear, we may find that our ecosystems can no longer “fly”, i.e., support life. The critical question asked most often still remains: Will such extinctions reach a critical threshold beyond which humans cannot survive?

Sixty years later, Leopold’s words hold true today. We need to preserve all the pieces of ecosystems (i.e., species) until we identify which ones are essential to the operation of their machinery. Forest canopies represent “home” to a disproportionately large number of species. Because forests are such efficient machines producing energy, medicines, materials, fibers, foods, nutrient cycling, and atmospheric gases critical to all life on Earth, the continued health of forests is directly intertwined with human health.

Since the construction of the first canopy walkway over 25 years ago, millions of hectares of tropical rainforest have disappeared, along with thousands of as-yet-unnamed new species. Losses of forest canopies, as well as other ecosystems, are critical issues for our children and their children, as they grow up to inherit the stewardship of our planet. Earth is full of exciting discoveries relating to forest canopies –new medicines, exotic perfumes, ecosystem services such as cleaning the air and storing carbon dioxide, keystone predators, and other food chain dynamics, and important economic products such as chocolate, corn, oranges, coffee, and rubber, to name but a few. The next decade is critical. Forest canopies are essential to healthy ecosystems that translate into sound economic policies. As my children summarized in our recent book, *It's a Jungle Up There* (Yale University Press, 2006), "Conservation over conversation is critical to the next generation." Simply changing the order of the letters "s" and "v" creates action that will likely determine the fate of forest canopies. The world's forests are in the hands of the next generation of scientists; forest canopies may inspire them to seek sustainable solutions **(Figure 4)**.

[譯文] 爬樹的女人：探索世界樹冠層

瑪格麗特·羅曼 博士

www.canopymeg.com　www.treefoundation.org　www.calacademy.org

人類的祖先是樹居者。綜觀人類歷史，人類利用樹木連結靈性、採集食物藥物並製作各種木製品。無數的葉子將陽光轉換成醣類，樹冠層可以視為整個地球食物鏈的中心。就演化的觀點來看，人類從樹上的祖先演化而來。任何人都曾在動物園看到猴子跳躍在樹梢而羨慕，潛意識地回想起滯留空中的演化記憶。

在巴布亞紐幾內亞有一個名為 Korowai 的部落，至今仍然住在樹上，利用樹梯建造了令人嘆為觀止的樹屋。據推測這種生活習慣可能源於躲避森林底層的敵人，並且逃離潮濕陰暗的地面。樹屋在小孩和成人之間保留了一點痕跡，如同人們和自然的精神連結。許多著名的人曾逃避至小時候的樹屋：披頭四的約翰藍儂、英國首相邱吉爾、羅馬皇帝卡利古拉，以及還是年輕公主時的維多利亞女王。最近的醫學研究也指出常在戶外活動學習的孩童會有比較健康的身體和個性。

為什麼樹冠層在人類的精神、科學及文化內涵上有這麼多重要的影響？為什麼科學家直到最近才能探索樹冠層？二十世紀有極少數的樹冠層先驅，但樹冠層仍然被認為是地球的第八塊大陸，因為它鮮少有人探訪。

樹冠層是性能卓越的房屋，約涵括了整個地球 50%的地面生物多樣性。熱帶雨林中陽光、果實、花以及葉子年復一年的生長，提供了各種生物的理想棲地。數以千計的樹種及藤蔓給提供了昆蟲名副其實的沙拉吧，而昆蟲又是一級消費者如爬蟲、兩棲及哺乳類的食物，一級消費者則為二級消費者如老鷹、美洲豹及各種食肉動物獵食。最終，土壤中的分解者分解並讓所有物質循環回樹冠層。

除了傳統食物鏈上的貢獻之外，樹冠層有額外的生態棲位給特殊的生命體。鳳梨科植物的貯水杯、樹枝的分岔、葉子的表面，以及附生植物提供了額外的樹冠層微型分層。例如鳳梨科植物的貯水杯可以承接雨水，以致於裡面會出現微小生物。蚊子幼蟲、線蟲、狼蛛、蠡斯、蜥蜴以及猴子會居住或飲用這些空中的小水池，有些箭毒蛙甚至會千里迢迢從森林底層爬到樹上的小水池中下蛋。其他特別的樹冠生態棲位包括了樹枝的分岔提供了纏勒性無花果樹的發芽場所，堆積土壤提供馬陸、 線蟲這些原本生活在森林底層的生物生存的環境。纏勒性無花果樹是唯一已知會在樹上發芽生長的物種，同時將氣根延伸到地面，最後滲透到土壤層以拓展自身並且纏勒住宿主植物。附生植物生長在潮濕且有光斑的枝條上，額外增加一層生物多樣性的空

間。甚至更令人驚奇的是，葉片表面還能提供一層空間給地衣、苔蘚、真菌生長。而在這些苔蘚植物的「樹冠層」裡，還能生長微小的無脊椎動物以及一些只有在顯微鏡下才能看到的微生物。一層層的生命結構，全都滋養於陽光、濕氣和溫暖，森林以一種特殊的形式提供令人嘆為觀止的生物多樣性。

直到三十年前，樹冠層的植物、昆蟲、鳥類、哺乳類以及他們之間的交互作用還鮮為人知。1970 年代後期，野外生態學家首先使用彈弓將繩索架設到樹冠層，但仍然不太明白這片綠色的大傘其實是地球健康的重要關鍵。海平面之下以及外太空之外的探索都比森林樹冠層的探索更加優先。但隨著近年來全球氣候的上升以及地景的退化，樹冠層變成一個重要的指標，因其衰退可以作為全球環境變遷的預兆。最近，森林樹冠層科學家和珊瑚礁生態學家、冰層物理學家、土壤生物學家以及水化學家共同合作，試圖發現地球功能之最神祕處。透過進入森林樹冠層，森林生態系統功能的知識大幅躍進。森林樹冠層也能增進我們對這自然世界的好奇和感激，引導那些更宏觀的保育進程。

望遠鏡也許是被用來探索樹冠層的第一個工具。十九世紀時達爾文就使用望遠鏡探索樹冠層，但除了掉到地面的生物之外，並沒有取得任何樹上的生命體。但是他仍然對熱帶雨林樹冠層的多樣性很感興趣。在達爾文之後探索冠層的想法進展得很緩慢，直到 1950 年代，在烏干達的 Mpanga 保護區裡建造了一個高塔。高塔提供了監測引起人類疾病昆蟲的方法，樹冠層第一次展現了在生物研究上的應用。

1970 年代是樹冠層探索的黃金時期，開始使用 SRT(單索攀樹技術)(圖一)技術做長期的樹冠層研究，而非偶爾一次的採集。這種靈活的技術讓科學家能容易到達冠層的中間，並且可以懸掛在繩索上觀察生物。裝備容易攜帶，價格也不昂貴，SRT 甚至可以讓預算不多的研究生探索樹冠層。1979 年羅曼(Lowman)博士在澳洲發展 SRT 技術，同時唐・培利(Don Perry)也在哥斯大黎加發展。然而繩索無法抵達冠層邊緣的枝葉，因為它必須固定在靠近主幹的地方。科學家試圖克服這種無法抵達邊緣的困境，例如印尼的生物學家發展出樹冠層帆布，水平的平臺有許多水手椅繫在一端，就可以從主幹擺盪到樹冠層外圍。在馬來西亞的 Pasoh，則結合了梯子、繩索以及帆布船而研究龍腦香科的授粉作用。

1980 年代有創意的工程師以及樹冠層生物學家聯手建造第一條給大眾使用的冠層橋樑和平臺。一開始的兩條冠層走道幾乎同時建造：一條是在馬來西亞的樹枝上，另一條在澳洲昆士蘭的電線杆間。北美洲的第一條樹冠走道建於 1992 年的麻塞諸塞州的橡樹上。但第一條給民眾使用的冠層走道則於 2000 啟用於佛羅里達的邁阿卡河州立公園(Myakka River State Park)(圖二)。1990 年代開始，世界各地陸續建造樹冠層走道，由樹冠層走道建造協會(Canopy

Construction Associates, www.canopyaccess.com)及其他組織設計建造。也因此樹冠層走道、梯子、攀樹繩索及其他工具的結合，受到研究者和生態旅遊業的歡迎。此外，樹冠層走道提供了當地居民一項穩定持續的經濟收入 (www.treefoundation.org)。世界上最長的樹冠層走道，是由樹木支撐，位於祕魯境內的亞馬遜雨林區，並且提供當地超過 100 個家庭的經濟收入(圖三)。世界上最新的一條冠層走道則將於 2014 年於臺灣的雪霸國家公園啟用。

也許最有創意的樹冠層探索工具是法國設計的熱氣球 *Radeau des Cimes* 。它由平坦的木筏組成，可以自主飛行，可以在高樹的最頂端提供基地或平臺 (直徑 27 公尺)。1991 年，*Radeau des Cimes* 的設計團隊發展了新技術，由邊長五公尺的正三角形迷你木筏組成的飛船，可以在樹梢快速地探索花粉、光合作用、食植行為以及冠層生態的多樣性及組成。

起重機則代表了近年來能安全進入森林冠層的工具。1990 年，史密森熱帶研究所(Smithsonian Tropical Research Institute)在巴拿馬季節性乾旱森林裡建造了一座 40 公尺高的起重機。之後，十座起重設備分別在澳洲、瑞士、德國、日本、印尼、美國和委內瑞拉設立。起重機的建造及操作非常昂貴，通常在美金 1 百萬到 5 百萬之間，但提供了前所未有的、重複性進入上部冠層的機會。

在 1880 年代，自然學家達爾文估算地球上大約有 80 萬種生物。進入樹冠層之後則發現了起碼百萬種以上的生物生活在這「地面上」的世界。達爾文之後的 100 年，史密森熱帶研究所的厄文博士(Terry Erwin)首先計數了樹冠層的生命數量。使用噴霧法採集幾棵樹的樹冠層，收集全部的節肢動物後計數並分類。根據他於 1982 年巴拿馬雨林裡的研究指出，地球上可能有三千萬的物種，而不是如之前估算的 1 百萬至 2 百萬。之後，其他的樹冠層生物學家證實了厄文博士的推測。羅曼博士在澳洲使用同樣的噴霧技術，也得出了相似的結果，估計約有 100 萬的物種生活在冠層中(絕大部分是昆蟲)。哈佛大學生物學家威爾遜(Edward O. Wilson)特別指出，地球上大約有一億種生物。世界上究竟有多少種生物其實還有爭議， 從目前的推估來看最少有 1 千萬，最多則可能有 1 億。

田野生物學家著重在生物多樣性的分類、物種鑑定以及了解各種生物在地球上的地位。這並不僅僅是簡單的命名活動，主要的目的是為了了解一個生態系統的結構和功能，如同我們希望知道汽車引擎的組成以創造更有效率的引擎。發現並且界定世界上所有的物種並不容易，在樹冠層裡發現一個新的甲蟲物種就跟大海撈針一樣難，更遑論要界定所有的物種包含蘭花、甲蟲、鳥類、藤蔓、青蛙以及其他不勝枚舉的種種生物。在過去 20 年來，因為人類活動加速了地景的退化以及許多物種的消失，「生物多樣性」在政治上及科學上都益顯重要。

許多樹冠層物種提供了人類生存必需的生態系統。在亞馬遜地區，植物製造化學物質抵抗昆蟲的攻擊，而這些化學物質會被當地居民作為藥用。薩滿是當地極受尊重的領袖，擁有許多使用藥用植物的知識和經驗。由於植物和食植動物(大部分是昆蟲)間特殊的交互作用，樹冠層的葉子、樹皮和果實提供了名副其實的藥材。

經過這一段樹冠層技術發展的歷史以及對樹冠層 3D 結構和棲地的研究，樹冠層生物學家的地位開始轉變。已經沒有科學家可以單純悠閒地欣賞老鷹和蠡斯的美麗，相反地，他們必須和伐木業者比賽。簡單來說，樹冠層科學家們沒有時間休息；至今為止被發現命名的物種遠不及所預估的數量。分類學家鑑定並分類新物種的速度，遠不及伐木業者的開發。

世界上究竟有多少物種？如果 200 個科學家每人每天都發現一個新物種，至少需要 1500 年才能完成整個地球上的物種鑑定。由此可知世界上的物種有多少！但比起命名更為重要的是生物學家需要設定森林樹冠層健康的基準點。生物多樣性重要嗎？物種滅絕會影響人類嗎？需要多少森林和樹種才能維持整個地球功能的運作？如果樹種單一而且棲地破碎，森林還能維持同樣的功能嗎？這些問題很重要，但沒有人可以回答。生物學家對樹冠層的瞭解還不足以回答這些重要的問題。在李奧帕德(Aldo Leopold)的沙郡年紀中說道，「保護每根螺絲就是維修的首要步驟」。而另一個很有名的科學家保羅・埃爾利希(Paul Ehrlich)則說生物多樣性的趨同化很類似飛機的維修：如果維修人員不斷地移除飛機上的基本要素，最終這架飛機就無法飛行。同樣地，如果物種一直不停地消失，總有一天生態系統會失去功能。而最關鍵的問題是，消失多少物種之後人類將無法生存？

六十年後的今天，李奧帕德的話仍然是正確的。我們需要保護所有生態系統中的物種，直到完全界定他們在生態系統中的功能為止。森林樹冠層是無數物種的「家」，而森林在地球上製造能量、藥材、原物料、食物，並進行養分循環及氣體交換，森林的健康就攸關著人類的健康。

從 25 年前第一條樹冠層走道建造之後，數百萬公頃的熱帶雨林已經消失，連帶上千種尚未被發現及命名的新物種。失去森林樹冠層及其生態系統，對未來的子孫而言將是個嚴重的問題。世界上令人驚奇的發現都和樹冠層相關：新藥物、香水、提供乾淨空氣並儲存二氧化碳的生態系統、高階掠食者和食物鏈動態，以及各種經濟產物如巧克力、玉米、棉花、咖啡、橡膠等等。未來的十年將至關重要。森林樹冠層是維持健康生態系統的重點，應制定於重要的經濟政策裡。這個世界的森林掌握在未來的科學家手裡，而森林樹冠層可以激勵他們去尋找永續生存的解決之道(圖四)。

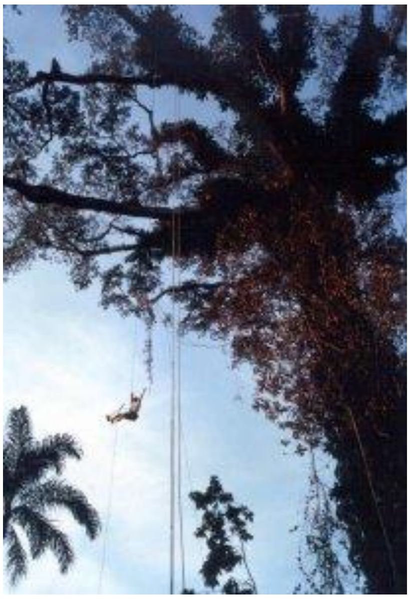


Figure 1 (left). Single rope techniques in a Ceiba pentandra tree

Figure 2 (right). Canopy walkway with poles at Myakka State Park, Florida


Figure 3 (left). Canopy walkway with tree support in Amazonian Peru

Figure 4 (right). Children using canopy walkway in Florida

Canopy Biodiversity in *Pseudotsuga menziesii* (Douglas-fir) Forests of the Pacific Northwest of North America

北美太平洋西北區花旗松樹冠層之生物多樣性

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The conifer dominated forests of the Pacific Northwest of North America span a range of environmental conditions across primarily north-south trending mountain systems. The vegetation is influenced by Pacific Ocean weather systems moving into the region from the west and the interplay with the drier continental climate of the interior from the east, which is colder in winter, and hotter in summer (Franklin and Dyrness 1973). In Oregon and Washington USA, the Cascade Mountain Range is the primary mountain system which defines the environment of the region with the Oregon Coast Range, Willapa Hills, and Olympic Mountains characterizing the near-coast area. Hypermaritime coastal rain forests occur as a narrow band along the coast dominated by *Picea sitchensis* and *Tsuga heterophylla* which shifts to *Sequoia sempervirons* to the south in California. Seasonally dry forests dominated by *Pseudotsuga menziesii*, with *T. heterophylla*, *Thuja plicata* dominate northwestern Oregon and western Washington, which is known as the 'Douglas-fir' region by forest industry. Montane forests are dominated by *T. heterophylla*, *T. plicata*, *P. menziesii* with *Abies procera*, *A. amabilis*, and *T. mertensiana* occurring on the wetter western Cascades. Along the eastern Cascade Mountains a shift occurs as the environment is drier and within a rain shadow. Here, *Abies grandis*, *Larix occidentalis*, *Pinus contorta*, and the interior form of *P. menziesii*, occur in the higher elevations. *Pinus ponderosa* dominates much of the lower elevation forests, but will occur in the mixed conifer of higher elevations.

Douglas-fir forests considered in this discussion refer to the region of north-western Oregon and western Washington, USA where forest canopy research has focused on regional old-growth forests (> 200 yr old) that occur on lands managed for timber, wildlife and people by the U.S. Government (US Forest Service, Dept. of Agriculture) and preserved in National Parks (US Dept. of Interior) such as Olympic, Rainier, and North Cascades National Parks. This is because complex and interesting crowns and canopies develop in old coniferous forests of the Pacific Northwest where trees can be long-lived; *P. menziesii* ~ 700 yrs, *T. heterophylla* ~350 yrs, *T. plicata* ~1,000 years, *P. ponderosa* ~ 500 yrs. In additions, these trees can reach heights of > 60 meters and an individual crown may have over 40 m of vertical foliage. In some coastal sites, western Cascade valleys and in the Olympic rainforests, *P. menziesii* can attain heights of 80 m or more, and diameter at breast height (DBH) of 2.5 m in 450 yrs. The public appreciates old-growth forests and wants them preserved. In addition, old-growth forests have been shown by a considerable body of research, to be important for biodiversity preservation, maintenance of ecosystem function, and wildlife habitat (Franklin et al. 1981).

Perhaps the beginning of what is considered modern forest canopy biodiversity research in the Pacific Northwest began with the U.S. International Biological Program, and the link to the United Nations International Biological Program in the 1960's and 1970's (Edmonds 1982). Researchers investigated Douglas-fir whole-forest ecosystems in several age classes. Old-growth Douglas-fir forests of the H.J. Andrews Experimental Forest, in the western Cascade Mts. near Eugene, Oregon (Willamette National Forest) were particularly interesting from a forest biology point of view. Here researchers used drills and bolts to insert metal clips into the tree so a climber could ascend like an ice climber. They described canopy trophic N cycles based on epiphytic microfungi that were capturing N from through-flow originating in nitrogen fixing lichens and tree foliage. The microfungi are grazed by mites, micro-litter was grazed by Collembola, Diptera larvae, and mites, litter accumulated in bryophytes and lichens, on large branches, and a within-canopy food web develops (Denison 1973, Carroll 1979). Canopy microfungi are an important component of these Douglas-fir forest canopies (Stone et al. 1996), with a standing-crop biomass of foliar fungal epiphytes alone estimated at 30 kg/ha, and with the combined tree epiphytic fungi annual production estimated at 450kg/ha (Carroll et al. 1980).

The lichen and bryophyte biodiversity and ecology in Douglas-fir forests has been a major research area topic in the region (Sillett and Antoine 2004). At the Wind River Canopy Crane Research Facility for example, a 2.3 ha patch of a 450 yr-old forest canopy had 97 lichen species and 14 bryophyte species (McCune et al. 2000). The nitrogen fixing lichen, *Lobaria oregana*, was estimated to contribute 3-4 kg/ha/yr in fixed nitrogen in the H.J. Andrews Experimental Forest (Denison 1973). Lichens and bryophyte species are very sensitive to microenvironment and sort out along clearly defined patterns. In these old-growth forests, bryophytes (*Antitrichia*, *Dicranum*, *Isothecieum*) dominate the lower canopy and large old branches in the interior crowns of old trees. Cyanolichens (*Lobaria*, *Nephroma*), dominated by *L. oregana* occur in the mid canopy environment, and Alectoriod (*Alectoria*, *Bryoria*, *Usnea*) and non-nitrogen fixing foliose (*Platismatia*, *Hypogymnia*) lichens occur in the upper and outer crowns (McCune 1993, McCune et al. 1997).

Research on forest canopy epiphytes such as *Lobaria oregana* led to the development of the similar gradient hypothesis (McCune 1993). For example, as one moved west into the hypermaritime forests the lichen is found higher and higher in the canopy, while as one moves to the east in drier forests, the lichen is found lower and lower in the canopy until it becomes too dry. While the lichen is absent from young stands. McCune put this together into the similar gradient hypothesis which I have paraphrased and enhanced here (Shaw 2004):

1. Epiphytic lichens are sorted along a vertical gradient within any stand of trees.
2. The optimum height of an epiphyte in a forest canopy, given forests of the same age and tree composition, changes along a landscape-scale axis of wet to dry.
3. The density or openness of a canopy, given the same age and species of trees, will influence the optimum height of an epiphyte.
4. Within a given stand, there is a gradient of time, where the biodiversity of the community increases, and the optimum height of an epiphyte also increasing with time.

Wildlife biologists have also been active in studying the vertebrates of northwest forest canopies. Carey (1996) developed a 12 point "arboreality" index for non-bat mammals. A zero indicates a mammal that does not occur in the canopy at all, while a 12 indicates a mammal that spends almost its entire life in the canopy. In the Douglas-fir region, only the red tree vole (*Phenacomys longicaudus*) scored a 12, with the western gray squirrel (*Sciurus griseus*) scoring an eight, and the northern flying squirrel (*Glaucomys sabrinus*), red squirrel (*Tamiasciurus hudsonicus*) and dusky-footed woodrat (*Neotoma fuscipes*) scoring a seven. Eleven of the 15 species of bats (for example, *Myotis* species) that are native to Oregon and Washington make regular use of the forest canopy for roosting, foraging and reproduction (Wunder and Carey 1996).

Two birds, the spotted owl (*Strix occidentalis*) and the marbled murrelet (*Brachyramphus marmoratus*), have been identified as endangered and dependent on old-growth forest canopies in the Northwest USA. Although the marbled murrelet is a seabird which eats fish, it nests in tall, old conifer trees within about 50 k of the ocean and with loss of this habitat is declining in number (Miller et al. 2012). The spotted owl (Bart and Forsman 1992) preys on the flying squirrel, red tree vole and bushy tailed woodrat from mid and low canopy perches and requires old-growth snags and broken topped trees for nesting. In the NW, USA, congressional legislation call the Endangered Species Act requires that the federal government protect endangered species from extinction. Although logging of these forests at 4-5 billion board feet (a board foot is one inch thick, and 12 inches on each side)/year was active, most old-growth logging was stopped by 1990, and logging in these federal lands is under 1 billion board feet today. However, an interesting food web involving leaves, fungi, flying squirrels and the owl was discovered. Carbohydrates produced in the canopy are translocated to the roots and shared with mycorrhizal fungi that produce truffles. Flying squirrels are fungivores that eat lichens, but also descend to the ground to dig these truffles (Maser and Maser 1988). This behavior by the squirrel makes it vulnerable as prey to the spotted owl.

In the early 1990's the Wind River Canopy Research Facility was established by the University of Washington and the US Forest Service, PNW Research Station at the Wind River Experimental Forest on the Gifford Pinchot National Forest, Washington State (Shaw et al. 2004a). The canopy crane allowed access to the three dimensions of an old-growth Douglas-fir forest canopy from 1995 until 2007. Both forest biology and ecosystems studies focused on the crane site, but included other age classes of Douglas-fir forests in the region. A major initiative concerning the carbon dynamics of an old-growth forest was successful (Suchanek et al. 2007), while a suite of biodiversity studies included insects (Showalter and Ganio 1998, Shaw 1998, Braun et al. 2002), birds (Shaw et al. 2002a), mammals (Shaw 2002b) dwarf mistletoes (Shaw et al. 2004b), and lichens and bryophytes (McCune et al. 1997, Clement and Shaw 1999, McCune et al. 2000, Lyons et al. 2000).

An important disturbance agent is western hemlock dwarf mistletoe (*Arceuthobium tsugense*, Viscaceae) an arboreal parasitic plant with diminutive aerial shoots < 12 cm tall. However, they cause deformation of the branches, and profoundly influence canopy structure of *T. heterophylla* as the population of plants intensifies (Shaw et al. 2005). The species is dioecious and after pollination the berry takes 15 months to mature. The seed is explosively discharged which creates aggregated infection centers within the forest. There are 13 taxa of *Arceuthobium* in Oregon and Washington states with *A. douglasii* being very important on Douglas-fir in SW Oregon and eastern Oregon and Washington. However it does not occur in the Douglas-fir forests of the northwestern Oregon and western Washington and *A. tsugense* is the only dwarf mistletoe present.

Some general observations on the unique features of old-growth Douglas-fir forests include a low level of conifer herbivory (< 1%), the importance of year-round resident insectivorous birds such as golden-crowned kinglet (*Regulus satrapa*) chestnut-backed chickadee (*Poecile rufescens*) and red-breasted nuthatch (*Sitta canadensis*), and winter wren (*Troglodytes troglodytes*), and the interplay of seasonal weather and the deep vertical structure. The upper forest canopy is deep and provides winter thermal attributes important to biodiversity because these forests are cold and wet. Ants, which are normally abundant in most global forests, are represented by very few species in generally low abundance in comparison. Arthropod herbivores are primarily Coleoptera and Lepdioptera, with Orthoptera rare. Spiders are very important insect predators. High biodiversity in the canopy is expressed in the lichen and bryophyte epiphytes, which show a strong vertical pattern related to microenvironment. Vascular plant epiphytes are rare.

Applied Canopy Biology

Applied canopy biology is increasingly important to Douglas-fir forest management. For example, the northwest native Ascomycete foliage fungus, *Phaeocryptopus gaeumannii*, causes a disease syndrome known as Swiss needle cast in Douglas-fir plantations (Shaw et al. 2011). Since the mid- 1980's the disease has intensified to the point where a zone of ~2,000,000 ha along coastal Oregon and Washington in impacted by the disease. Although mortality is rare, growth losses to Douglas-fir average about 20% in this zone. Epidemiological studies link both warm-mild winter and spring temperatures and occurrence of late spring and summer precipitation and fog to areas of high disease severity (Hansen et al. 2000, Manter et al. 2005). Leaf wetness is required during May-August during the spore dispersal period, and warm winters apparently allow rapid development of this normally benign leaf endophyte. In the zone of the epidemic, reproductive structures called pseudothecia (no asexual stage is known) mature on one- and two-year old needles. These pseudothecia emerge from the stomates, and cause plugging, which interferes with gas exchange and photosynthesis. Trees with disease symptoms have low needle retention, chlorotic foliage, and slowed tree growth. A research cooperative known as the Swiss Needle Cast Cooperative, now leads research, monitoring, and forest management research and application programs.

Native canopy and crown forest pathogens and insect pests are particularly important to plantation management, but perhaps it is the invasive non-native ones we are most concerned about, especially the *Phytophthora* species (Hansen 2008). For example the crown, foliage, branch, and bole fungal pathogen *Phytophthora ramorum*, cause of "sudden oak death" is now present in SW Oregon and the redwood region of California. In Oregon, attempted eradication and an active program of slow-the-spread are being directed by applied research on the canopy biology and ecology of this disease agent. *Phytophthora ramorum* has two asexual spore types, a resting spore (chlamydospore) and mobile flagellated zoospores that emerge from dehiscent sporangia. The resting spore can persist in infected plant material for long time periods, while the sporangia are important for dispersal in wet weather. Seasonal patterns of spread are directly linked to weather patterns, and the within crown dynamics of the pathogen are driven by stand composition and microclimate. Therefore, this is yet another example where canopy biology is central to a full understanding of both natural and planted forests.

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[譯文] 北美太平洋西北區花旗松樹冠層之生物多樣性

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北美洲太平洋西岸的針葉林需要克服許多環境上的限制。其植群受到西邊太平洋氣候系統及東邊大陸型氣候的影響，冬冷夏熱。在美國奧勒岡州及華盛頓州，卡斯克德山脈(Cascade Mountain Range)是主要山脈系統，與奧勒岡海岸山脈(Oregon Coast Range)、維萊巴丘陵(Willapa Hills)以及奧林匹克山脈(Olympic Mountains)同屬於海岸地區。海岸型雨林沿著海岸線分布於南北狹長的區域，主要樹種為錫德卡雲杉(*Picea sitchensi*) 及西部鐵杉(*Tsuga heterophylla*)，在南加州地區則主要為長葉世界爺(*Sequoia sempervirons*)。而季節性乾旱森林的主要物種是花旗松(*Pseudotsuga menziesii*)和西部鐵杉。美西側柏(*Thuja plicata*)主要生長在奧勒岡西北部及華盛頓西部的花旗松區域。山區森林的主要樹種是西部鐵杉、美西側柏、花旗松，在潮濕的卡斯克德山脈西邊則有壯麗紅冷杉(*Abies procera*)、美國冷杉(*A. amabilis*)和高山鐵杉(*T. mertensiana*)。卡斯克德山脈的東邊氣候較為乾燥，北美冷杉(*Abies grandis*)、西部落葉松(*Larix occidentalis*)、美國黑松(*Pinus contorta*)以及花旗松會生長在較高的海拔；西部黃松(*Pinus ponderosa*)則主要分布於低海拔森林及高海拔混生林。

在這篇文章裡，「花旗松森林」特指奧勒岡西北部及華盛頓西部地區的森林。美國的森林樹冠層研究主要針對 200 年以上的老熟林，由美國政府農業部以及國家公園管理包括木材、野生動物以及人類活動在內的土地經營。西北太平洋老熟針葉林的樹冠層結構複雜而有趣，且樹齡通常非常老，例如花旗松約 700 年，西部鐵杉約 350 年，美西側柏約 1000 年，西部黃松約 500 年。除此之外，這些樹高通常高於 60 公尺，而且單一樹木可以擁有超過 40 公尺的冠幅。在一些海岸地區，如卡斯克德山谷西邊以及奧林匹克雨林裡，花旗松可以在 450 年以內生長到 80 公尺以上，且胸高直徑(DBH)可以大於 2.5 公尺。一般民眾都很喜歡這些老熟林並且希望能保存它們。此外，在許多研究中都顯示老熟林在保存生物多樣性、維持生態系統功能以及提供野生動物棲地上佔有非常重要的地位。

近代西北太平洋森林樹冠層多樣性的研究開始於美國國際生物計畫，並且在 1960 及 1970 年代和聯邦國際生物計畫結合。研究人員調查數個不同齡級的花旗松森林生態系統。其中，在 HJ 安德魯實驗林(H.J. Andrews Experimental Forest)的花旗松老熟林裡，樹冠層中氮元素的循環，

是基於附生微真菌能捕捉供氣中的氮並且固定於地衣及葉片上。這些微真菌是花旗松冠層裡重要的組成部分，存在於一些雙翅目的幼蟲及地衣苔蘚之中。

在花旗松森林中，地衣和苔蘚的生物多樣性及生態學是主要的研究對象。舉例而言，在風河樹冠層吊塔(Wind River Canopy Crane Research Facility)，一塊 2.3 公頃 450 年樹齡的樹冠層裡會有 97 種地衣及 14 種苔蘚。能夠固氮的地衣估計可以在 HJ 安德魯實驗林裡製造每年每公頃 3 到 4 公斤重的固氮量。地衣及苔蘚是對微環境非常敏感的物種。在老熟林中，苔蘚主要分布在較低的樹冠層位置以及較大且靠近主幹的枝條上。貓耳衣屬地衣(Cyanolichens)主要分布在樹冠層較中間的位置，而那些沒有固氮共生菌的地衣則主要分布在樹頂以及外側的位置。

樹冠層附生植物的研究引導了相似梯度假說(similar gradient hypothesis)的發展。舉例來說，漸往西行，進到海岸型雨林後會發現地衣位在較高的樹冠層；但往東進入較乾燥的森林時會發現地衣位在較低的位置。而在年輕的森林裡則沒有地衣存在。麥克昆恩(McCune)統整了相似梯度假說內容如下：

1. 可依據垂直梯度分類附生的地衣。
2. 在樹木年齡相同的森林結構條件下，附生植物最理想的生存高度會由濕到乾有地景尺度的漂移。
3. 在樹木年齡相同的森林結構條件下，樹冠層的開闊程度會影響附生植物的理想生存高度。
4. 在同一塊林地上，附生植物的分布會有時間梯度；當族群的生物多樣性增加時，附生植物的最適生存高度也會隨時間而增加。

野生動物學家也在西北森林樹冠層中研究脊椎動物。1996 年 Carey 針對蝙蝠以外的哺乳動物提出樹棲評量法：0 表示完全不會在樹冠層出現的哺乳動物，12 則表示幾乎終其一生都在樹冠層生活的哺乳動物。在花旗松森林區，只有紅樹鼠(*Phenacomys longicaudus*)是 12 分，其他如西方灰松鼠(*Sciurus griseus*)是 8 分，北方飛鼠(*Glaucomys sabrinus*)、紅松鼠(*Tamiasciurus hudsonicus*)、黑腳木鼠(*Neotoma fuscipes*)則都是 7 分。而 15 種蝙蝠之中有 11 種是奧勒岡和華盛頓特有種，會季節性使用森林樹冠層作為棲地、儲藏食物和繁殖。

目前已被確定為瀕危物種的兩種鳥類，斑點鴞(*Strix occidentalis*)和斑海雀(*Brachyramphus marmoratus*)，都生存於美國西北部的老熟森林樹冠層中。雖然斑海雀是一種捕食魚類的海鳥，但會將巢築在離海 50 公里、高大而年長的針葉樹樹冠層裡；因此，失去森林棲地會造成斑海雀的數量驟減。斑點鴞會在樹冠層的中低部位捕食飛鼠和紅樹鼠和木鼠，並以老熟的斷枝或裂

開的樹頂為巢。在美國西北部，議會已立法保護這些瀕危物種。雖然目前仍然有伐木行為，但基本上自 1990 年後就禁止老熟林的砍伐。樹冠層中有一條由樹葉、真菌、飛鼠和貓頭鷹組成的食物鏈：樹冠層製造碳水化合物，然後轉移至根部和共生真菌共用，生成松露；飛鼠雖然是以地衣為食的動物，但也會下到地面挖食松露，斑點鴞因此而有機會獵取它為食。

在 1990 年代早期，華盛頓大學及美國林業部建立了風河樹冠層吊塔。1995 到 2007 年間，這座樹冠層起重機在花旗松老熟林內進行 3D 空間的探索。森林生物學和生態系統的研究都會集中在這塊起重機區域，同時也包含了此區域其他不同齡級的花旗松森林。完整的生物多樣性研究，包括昆蟲、鳥類、哺乳動物、侏儒槲寄生、地衣及苔蘚等各種生物，能成功解釋老熟林的碳循環概念。

西部鐵杉侏儒槲寄生(*Arceuthobium tsugense*, Viscaceae) 是森林樹冠層中一個重要的擾動因子。這種樹棲的寄生植物有著微小的氣根且植株矮於 12 公分，然而卻能引起枝條枯死並嚴重影響西部鐵杉的樹冠層結構。這種侏儒槲寄生雌雄異株，授粉後 15 個月果實才能成熟，種子會大量四散於整片森林。奧勒岡和華盛頓有 13 種侏儒槲寄生，其中花旗松侏儒槲寄生(*A. douglasii*)主要影響奧勒岡西南以及東邊至華盛頓地區的花旗松，而西部鐵杉侏儒槲寄生則是奧勒岡西北以及華盛頓西方的花旗松森林中唯一出現的侏儒槲寄生。

花旗松老熟林中也包含了食植昆蟲、食蟲留鳥、以及季節性氣候跟樹冠層垂直結構之間的交互作用。在濕冷的森林中，高大的樹木會有較長的冠幅，冬季時比較溫暖，能營造較為豐富的生物多樣性。在全球的森林中，通常有一定數量的螞蟻，但有些種類在花旗松森林中的數量卻相對較低。以植物為食的節肢動物主要是鞘翅目和鱗翅目，幾乎沒有直翅目的昆蟲。蜘蛛則是重要的昆蟲掠食者。樹冠層中的豐富生物多樣性也表現在地衣和苔蘚等附生植物上，通常和微環境相關並且有非常明顯的垂直分布。至於維管束的附生植物則非常少見。

應用樹冠層生物學

在花旗松森林的經營管理上，應用冠層生物學愈來愈重要。舉例而言，一種美國西北物當地的種子囊菌類(*Phaeocryptopus gaeumannii*)會在花旗松人工林中引起一種名為瑞士落葉病(Swiss needle cast)的疾病。自 1980 年代起這種疾病迅速感染了奧勒岡沿海及華盛頓約 200 萬公頃的花旗松。雖然死亡率很低，但平均而言會減少花旗松 20%的生長量。根據流行病學的研究，較高的春冬溫度以及晚春、夏季的降水起霧，容易導致花旗松的感染。5 到 8 月孢子散播季節影響了葉面的潮濕度，且溫暖的冬天明顯促進了內生菌的生長。被感染之後，假囊殼(pseudothecia)會在一到兩年生的針葉上逐漸成熟。這些假囊殼會突出氣孔，造成栓塞，干擾氣

體交換和光合作用。感染疾病的樹木會出現大量落葉、葉色枯黃以及生長減緩等等症狀。瑞士落葉病聯合機構(Swiss Needle Cast Cooperative)專為此設立，並研究、偵測此一疾病以及森林經營管理的研究和應用。

當地的樹冠層和病原體以及昆蟲都是造林地管理很重要的部分，但也許外來種更是要注意的對象，特別是疫黴屬(*Phytophthora*)的物種。舉例來說，橡樹猝死菌(*Phytophthora ramorum*)是一種會感染樹冠層、葉片和枝幹，繼而造成橡樹意外死亡的病菌，現在出現在奧勒岡西南部和加州的紅杉林地區。在奧勒岡，一項試圖減緩橡樹猝死菌散播的計畫直接應用在樹冠層生物學及生態學上。橡樹猝死菌有兩種無性繁殖孢子型態：休眠狀態的衣型芽孢和自開裂包子囊長出的鞭狀遊走芽孢。當孢子囊在潮濕季節大量擴散的時候，衣型芽孢能在被感染的植物體內潛伏很長的時間。孢子囊擴散的季節性變化可能直接和天氣的變化相關，而在樹冠層內病原體的季節動態則受到林地組成和微氣候的影響。由此可知樹冠層生物學是了解天然林和人工林的重要核心。

Figure 1 (left). Western Cascade Mts looking to the east, HJA Exp For, note the young plantation among old growth Photo Al Levno

Figure 2 (right). *Lobaria oregana* (Foliose) and *Alectoria sarmentosa* (fruiticose)

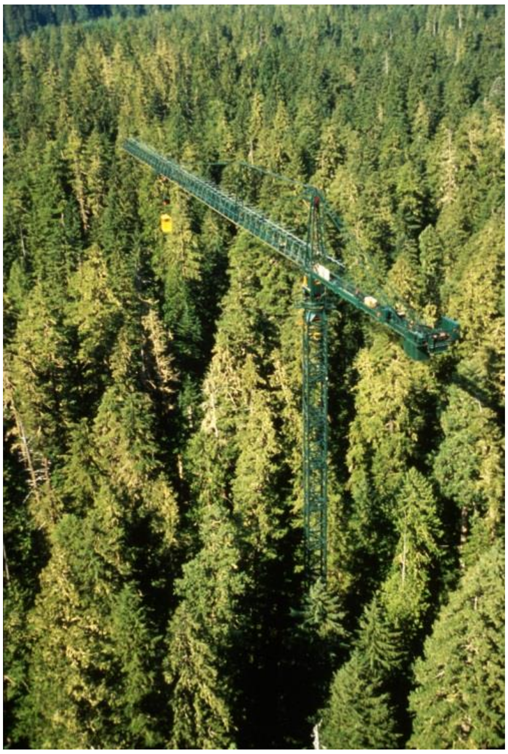


Figure 3 (left). Wind River Canopy Crane, in a 60 m tall forest photo Jerry Franklin

Figure 4(right). Golden-crowned kinglet *Regulus satrapa* a resident insectivore of old-growth


Figure 5 (left) Complex upper canopy of old growth Douglas fir forest

Figure 6 (right) Douglas-fir infected by *Phaeocryptopus gaeumannii* showing yellowing and loss of needs. Note the green trees with are *Tsuga heterophylla* which is not a host

Regional and Altitudinal Patterns in Vascular Epiphyte Richness in Taiwan

臺灣維管束附生植物的垂直與區域分布型式

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摘要

藉由收集標本館藏及訪談植物學家，筆者編製了附生植物資料庫共包含 39084 筆採集紀錄。分析將近 300 個物種的採集紀錄，顯示物種最豐富的區間位於 500-1500 公尺的中海拔，然而此中海拔物種特別豐富的現象，經統計檢測後無法以中域效應(Mid domain effect)解釋，顯示附生植物的豐富度與環境因子較為相關。此外，筆者使用物種分布模式工具 MaxEnt 及相關的環境因子來模擬臺灣附生植物的分布，模式結果與前述利用採集紀錄分析的結果相同，也顯示附生植物的多樣性在中海拔到達峰值，且模式結果同時也指出，有 2 個位於臺灣北部及中部的中海拔地理區，擁有較高的附生植物多樣性，推測這 2 個附生植物熱點的形成原因，可能與盛行風向相關。序列分析(Ordination analysis)結果顯示，年雨量以及與海拔相關的年均溫是影響附生植物分布最主要的因子，不過不同的分類群對溫度的偏好也有差異，例如半附生植物多生長在低海拔的溪谷，而附生蕨類則喜愛涼爽的山地氣候。序列分析結果也指出，臺灣的附生植物對溫度敏感(Thermal specialisation)的程度，隨海拔上升而增加，此趨勢顯然與 Rapoport 法則的假設相反，而在全球暖化的趨勢下，臺灣高海拔物種可能將遭受比較大的威脅。

Abstract

The distribution of species on mountains has been related to various predictor variables, especially temperature. Thermal specialization, which is presumed to be more pronounced on tropical mountains than on temperate mountains, accounts for the elevational pattern of species richness and varies between organisms and geographic areas. In this study, the elevational and regional distribution patterns of 331 epiphyte species in Taiwan were explored using 39,084 unique botanic collections, mostly from herbaria. Species richness showed a peak in elevation between 500 and 1500 m. This peak could not be explained by a null model, the mid-domain effect, suggesting that environmental variables accounted mostly for the distribution of species on the mountains. Next, species distributions were modelled (with 30 predictor variables) to assess epiphyte regional and altitudinal distribution patterns. The model results not only corroborated the position of the

mid-elevation peak in richness, they also identified two mountain areas on the island with exceptionally high species richness. These areas of high epiphyte diversity coincide with areas of high rainfall in relation to the direction of the prevailing winds. Moreover, a subsequent exploratory ordination analysis showed a varied thermal preference between epiphyte subcategories (hemiepiphytes, dicotyledons, orchids and ferns). In contrast to predictions by the elevational Rapoport's rule, ordination analysis also showed that the degree of thermal specialization increased with elevation, suggesting that highland species may be especially vulnerable to global warming.
Key words: hemiepiphytes; MaxEnt; mid-domain effect; Rapoport's rule; species distribution model; Taiwan; thermal specialization

Introduction

The distribution of species on tropical mountains has received renewed interest since high-elevation thermal specialists in the tropics could be among the most imperiled species on earth due to global warming (Laurance *et al.*, 2011). Compared with species in temperate areas, species in the tropics experience limited annual thermal variability and presumed resulting thermal specialization may explain the generally relatively low elevation-range of species on tropical mountains (Janzen 1967). The degree of thermal specialization is nevertheless not universal, varying among taxa, elevations and geographic locations. Hence, studies with various species and from different areas are required to attain a complete picture. Moreover, the assessment of thermal specialization is obscured because, in addition to thermal factors, hydrological, biotic and other unknown factors may determine the distribution of species on mountains (Bruijnzeel *et al.*, 2010). Another arguably characteristic of species in tropical areas is that mountain species have less thermal specialization than lowland species as an extension of Rapoport's latitudinal rule (Stevens 1992). Accordingly, on small continental islands such as Taiwan, overall thermal specialists are relatively rare, largely due to a paucity of upper-zone specialists (Laurance *et al.*, 2011).

Species distribution patterns on mountains account for the variability in species richness with elevation. Many organisms show a peak in species richness at mid-elevation (Laurance *et al.*, 2011), and this is also true for epiphytes (Wolf and Flamenco-S 2003, McCain 2004, Cardelus *et al.*, 2006). In addition to environmental factors, such as temperature, rainfall and fogs, and historical factors (Gentry and Dodson 1987a, Küper *et al.*, 2004), the mid-elevation peak in species richness has been explained solely by applying a distribution null model (*i.e.* the mid-domain effect). The mid-domain effect arises from geographic constraints on species range within a bounded domain (Colwell and Lees 2000). Within a landmass boundary (e.g. from coasts to mountain tops), the null model predicts a peak in species richness at mid-elevation, simply based on overlapping species' ranges. For epiphytic bryophytes in Colombia, the mid-elevation maximum in species richness was indeed explained by a mid-domain effect (Wolf 1993, Ah-Peng *et al.*, 2012). In contrast, the richness of ferns on mountains was best accounted for by climatic factors (Kessler *et al.*, 2011).

Here, we present for the first time data on the elevational distribution of epiphytes in Taiwan, an island in the western Pacific on the transition from tropical to subtropical latitudes. The aim of this study is to explore regional and altitudinal patterns in the distribution of Taiwanese vascular epiphytes. We used over 39,000 herbarium records to evaluate the altitudinal species richness pattern, which we compared with the pattern generated by a distribution null model. Moreover, using the same records, we compiled a grid-based database to model species distributions that was further analysed using multivariate ordination techniques. In particular, we were interested in the detection of epiphyte richness hotspots and in the incidence of thermal specialisation.

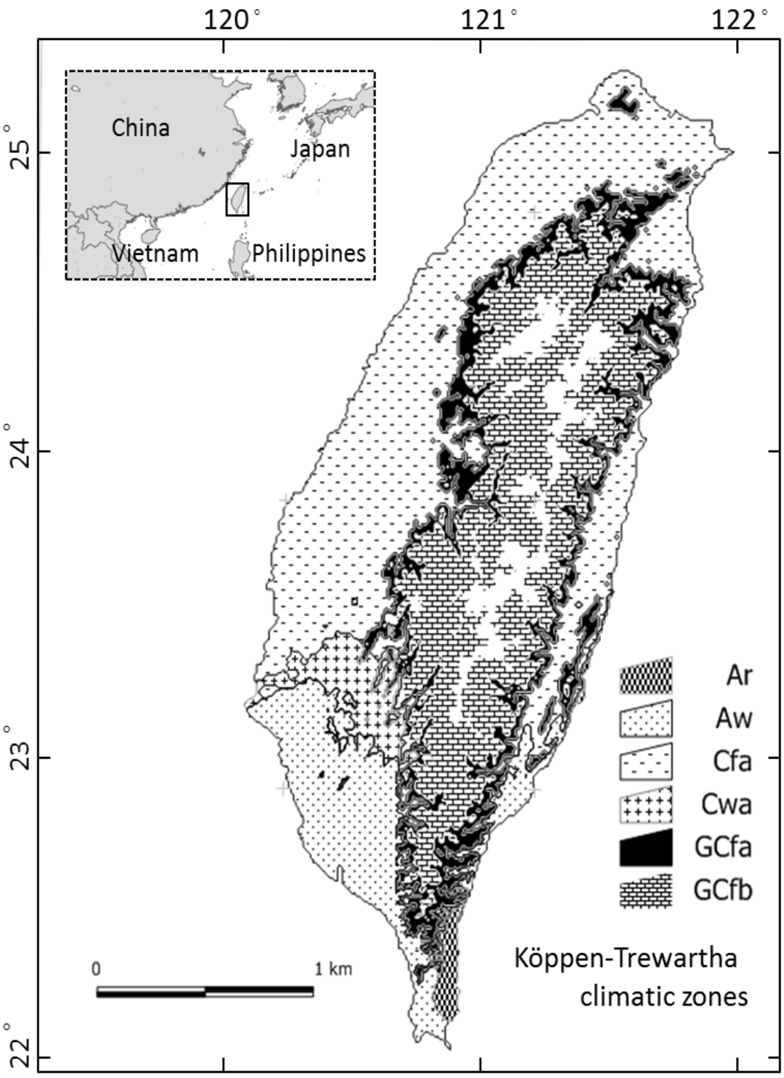

Fig. 1 The geographical location of Taiwan and climatic zones in the island according to the Köppen-Trewartha climate system. Ar = tropical wet climate (coolest month > 18℃), south-eastern peninsula (< 500 m); Aw = tropical savannah climate (winter dry > two dry months), southern lowlands (< 500 m); Cfa = wet subtropical climate (warmest month > 22℃, no distinct dry season), island-wide (< 500 m); Cwa = wet subtropical -winter dry climate (warmest month > 22℃), south-western inland hills (500–1000 m); GCfa = mountain climate (warmest month > 22℃, no distinct dry season), island-wide (500–1500 m); GCfb = mountain climate (warmest month < 22℃, no distinct dry season), island-wide (1500–3000m). The central range, with an altitude > 3000 m is unshaded.

Methods

Study site

Taiwan is a 36,000 km2 tropical-subtropical transition island (21°45'–25°56'N and 119°18'E–124°34'E, Fig. 1). About 30 percent of the island is covered by mountains (> 1,000 m above sea level [asl]; Fig. 1), including more than 50 peaks > 3000 m in altitude. Active orogenesis has created an extensive mountain system with diverse vegetation types, ranging from alpine tundra to tropical rainforests. Habitating approximately 4000 species of vascular plants (including *ca.* 600 Pteridophytes), the floristic diversity of Taiwan is exceptionally high compared with other (sub-) tropical islands (Dawson 1963, Reyes-Betancort *et al.*, 2008, Creese *et al.*, 2011). Taiwan is also one of the botanically best explored regions in Southeast Asia, and digitized herbarium collections contain over 200,000 records. Annual rainfall ranges from 1000 mm to > 6000 mm, and falls mainly during the north-east (NE) monsoon (October–January) and during typhoon-induced heavy rain events (July–September). The NE monsoon accounts for 45 percent of the total annual rainfall in north-eastern Taiwan (Kao et al. 2004).

Data collection

We compiled occurrences of epiphytic species in herbarium records, published plant inventories and our own botanical observations as a georeferenced epiphyte database that finally comprised 39,084 records in 331 species (24 families, 105 genera). Pteridophytes contributed most species (171), followed by orchids (120). The epiphyte species in the database were divided into four subcategories based on life form and taxonomy: hemiepiphytes, (abbreviation Hemis, e.g. Moraceae, Araceae), ferns and fern allies (Ferns), orchids (Orchids) and dicotyledons (abbreviation Dicots). For more detailed information on the species in the database, see Hsu and Wolf (2009).

To assess species richness patterns along the altitudinal gradient, we used the entire epiphyte collection database. We computed species accumulation curves (sample-based rarefaction) and associated richness estimators (Chao 2005), using the freeware program EstimateS 8.2 (Colwell 2011). The species range sizes were tested against the mid-domain effect hypothesis using Mid-Domain Null, a Monte Carlo based simulation programme, applying 1000 permutations without replacement (McCain 2004). As recommended, in the model we used empirical range sizes sampled without replacement and randomly chosen range midpoints of species (Colwell et al. 2004).

We subsequently assembled the plotless herbarium collection localities as records in grid cells with a spatial resolution of 1 km^2. Multiple occurrences of the same species in a single cell were considered a ‘unique’ record. The final database comprised 29,087 species records, including species with a single occurrence to the most widespread species that occurred in 1613 cells (Fig 4B). It is well known that systematic botanists have a bias for certain accessible localities and taxonomic groups, and the absence of species in cells is likely due to insufficient sampling. Therefore, we endeavoured to fill in the distribution gaps by using species distribution models (SDMs). The SDM results were used to evaluate regional species richness and species thermal niches.

Epiphyte species distribution models

In our SDM, we used a maximum entropy method, MaxEnt (version 3.3.3k) (Phillips et al. 2006). In MaxEnt, species' occurrences (i.e. presence-only data) are related to predictor variables across a series of observation sites to recognize the realized niche of each species (Guisan & Thuiller 2005). Statistically speaking, the MaxEnt model minimizes the relative entropy between probability densities of species presence data and the background landscape (Elith et al. 2011). Since MaxEnt puts no weight on the absence of a species, it is particularly suited for high-canopy epiphytes, which are often difficult to detect from the ground (Flores-Palacios & García-Franco 2001). To ensure model reliability, we excluded species with fewer than 10 records in the 1 km2 grid cells (79 species), leaving 252 species (28,693 records in total) of which the distribution was modelled by MaxEnt.

Based on the ecological understanding of epiphytes, 30 environmental predictor variables were selected for building SDMs (Table 1). The predictor values were estimated for each cell in the same 1-km^2 coordinate system as used for the species (35,928 grid cells in total). There was a correlation between some of our predictors (e.g. annual precipitation and precipitation of the driest quarter). We preselected the variables to avoid model over-parameterizing. Using Pearson's correlation test and a cut-off level of 0.75, generally wide-ranging variables were chosen over specific ones (eg. mean temperature over the temperature in the coldest month) (Table 1).For more details on variable selection, see Hsu et al. (2012).

In MaxEnt, a finite collection of points with associated covariates (environmental predictors) from the geographic area (landscape) of interest is called a background sample (VanDerWal et al. 2009). The choice of background samples reflects prior assumptions for the species' distributions (Merow et al. 2013). Conceptually, the landscape used for the background sample should include the full environmental range required by the species, and exclude the areas where species are unlikely to disperse (Elith et al. 2011). In this study, we used the MaxEnt program's default setting, randomly sampled 10,000 background locations from the given 35,928 grids of covariates covering the island for the common species (≥ 80 records). Alternatively, in order to emphasize the preferred habitat of rarer species (< 80 records), we restricted backgrounds samples to the full set of epiphyte occurrences (5,476 unique grid cells), and a reduced set of 5,000 backgrounds.

MaxEnt uses the term ‘feature’to describe the transformation of predictors. Currently, MaxEnt has six feature classes: linear, product, quadratic, hinge, threshold and categorical. The programme by default (i.e. using Auto features) restricts models to simple features if few samples were introduced. We ran preliminary models using 10-fold cross-validation to estimate predictive performance via held-out data (Phillips 2008). For species with ≥ 80 records, the test statistic (the area under the receiver operating characteristic curve [AUC]) was significantly higher when using all features than when using only the hinge feature as suggested by Elith et al. (2011). However, for species with few (< 80) records, using auto features provided a significantly lower 10-fold cross-validated AUC than the linear and hinge features (the last two features had statistically equal AUC values). Nevertheless, the hinge feature exhibited many more violations of AIC (Akaike’s Information Criterion) values than the linear feature for species with few samples. Therefore, the final models were fitted on the full data sets (i.e. all samples for model training) using all feature types for species with ≥ 80 samples and using the linear feature for species with < 80 samples.

Model validation

We used two measures to validate the resulting SDMs. First, we calculated AIC values using ENMtools 1.3 to determine whether the models had more parameters than samples, which would have violated the assumptions of AIC (Warren & Seifert 2010). Three SDMs (containing < 80 samples) were excluded from later analyses at this stage. Next, we used a null method to test the model significance (Raes & ter Steege 2007). Models with randomly chosen samples were fitted with the same settings as described above, and to identify which SDM had a significantly higher AUC value than expected by chance alone ($p < 0.05$). See Hsu et al. (2012) for the details of null model validation. There were 94 SDMs (< 80 samples) excluded from later analyses at this stage. We did not apply the null test to species with ≥ 80 samples because it had been found previously that models based on more than 80 samples were rarely insignificant.

Creating an epiphyte richness map

We obtained 156 validated SDMs, comprising 68 relatively rare (< 80 samples) and 88 common (≥ 80 samples) species. To create an epiphyte richness map, we applied a threshold of sensitivity-specificity sum maximization (Liu et al. 2005) to convert the MaxEnt probability distribution to a predicted presence map for each species. We then overlaid every single-species map to produce a species richness map for epiphytes in Taiwan.

Ordination analysis

We used a direct gradient ordination analysis, canonical correspondence analysis (CCA) to assess the influence of climatic factors (including typhoons) on epiphyte distribution, and the thermal specialization of species (Braak & Smilauer 2002). For predictor variables, we used the same 30 environmental variables that we used in MaxEnt (Table 1). For species, we used the resulting presence-absence data from the 156 epiphyte SDMs that we used to create the species richness map. To avoid multicollinearity, we performed a principal component analysis (PCA) on all variables. The first extracted PCA component was highly correlated with temperature, and the second PCA component was highly correlated with rainfall. The first and second component together explained 52 percent of the variation. Both components were retained in the CCA, as opposed to a third component that had little additional explanatory value (9%). Next, the species and environmental variables (PCA component-1 and -2) were subjected to CCA. We tested the significance of the first extracted CCA axis using a Monte Carlo test (999 permutations). CCA not only generates the species scores on the axes, but also their standard deviations (called tolerances in CCA), which may be seen as a measure of niche width (Lepš & Smilauer 2003). Hence, on the first generated axis that is highly correlated with elevation, the species tolerance is a measure of thermal specialization. The ordination analyses were performed in R with vegan, a community ecology package (Oksanen et al. 2012, R Core Team 2012).

Results

A map of the observed epiphyte species shows that the collections were not evenly distributed over the island (Fig. 2A). For example, relatively many collections were made along the both roads that transverse the central range. Nevertheless, the species accumulation curves per altitudinal interval generally flattened out, indicating adequate sampling (Fig. 3). The 500-1000m and 1000-1500m curves were positioned above the other curves when more than 3000 collections were considered, indicating a species richness maximum at these altitudes. The species richness estimator, Schao, also showed a peak in epiphyte richness between 500 and 1000 m (Table 2). Although the difference between the species richness at < 500 m and richness at 500–1000 m was small, it was significant ($M = 306.03$, $SD = 8.53$ and $M = 308.33$, $SD = 9.47$, respectively; paired $t(24740) = 20.1$, $p < 0.05$). The elevation-species richness curve fell outside the 95% CI curves of the mid-domain null model curve (Fig. 4); hence the mid-elevation peak in richness could not be explained by a mid-domain effect.

Table 1. Predictors that were used for modelling species distribution, including four temperature-related (1–4), 12 precipitation-related (5–16), nine topographic variables (17–25), and five land-cover/vegetation indices (16–30).

* Predictors only used in model building.

Predictor		Description	Unit
1	Tmean*	Annual mean temperature	
2	TcoldM	Mean temperature of coldest month	℃
3	TdryQ	Mean temperature of driest quarter	
4	Tsd*	The standard deviation of the monthly mean temperatures	No dimension
5	Pannual*	Annual precipitation	
6	PdryM	Precipitation of driest month	
7	PdryQ	Precipitation of driest quarter	Millimetre
8	PcoldQ	Precipitation of coldest quarter	
9-14	P.1, P.4, P.5, P.6 P.7*, P.10*	Monthly rainfall: January, April, May, June, July, October	
15	Pdef	Water deficiency: monthly precipitation minus doubled monthly mean temperature	Millimetre minus ℃
16	Pcv*	The coefficient of variation of the monthly mean precipitation	No dimension
17-18	Eastness* Northness*	Aspect transformed by sin(aspect rad) and cos(aspect rad)	Ordinal: 0–8
19	Soilcode	Soil category	Cardinal: 0–9
20	SoilPH	Soil alkalinity	Ordinal: 0–9
21	Estd	The standard deviation of elevation within 1-km^2	No dimension
22	Elevation	Altitude above sea level	
23	Dto3000*	The distance to the nearest location above 3000 m [asl]	Metre
24	DtoSea	The distance to the nearest coast	
25	DtoRiver	The distance to the nearest river	
26	Landcover*	Land-cover classification	Cardinal: 0–27
27-30	EVI.1–4	Monthly enhanced vegetation index, EVI.1: spring (April to May), EVI.2: summer (June to September), EVI.3: NE monsoon initiation (October to November), EVI.4: slow growth season (December to March)	No dimension

Table 2. Number of epiphyte species per altitudinal interval in Taiwan; n = number of records, Sobs = the number of observed species, singletons = number of species that were only recorded once and Schao = estimated number of species for 95% CI and standard deviations (SD).

Altitudinal interval	n	S_{obs}	Singletons	S_{chao}	S_{chao} 95% CI	SD
< 500m	12944	286	39	306.03	(294.99, 330.59)	8.53
500–1000m	11798	289	29	308.33	(296.79, 336.98)	9.47
1000–1500m	7198	281	28	293.6	(285.91, 313.32)	6.42
1500–2000m	4024	235	39	276.17	(253.47, 326.76)	17.56
2000–2500m	2197	205	39	232.44	(217.43, 265.590	11.56
> 2500m	923	165	37	185.81	(174.2, 212.08)	9.06

The mid-elevation peak in species richness was also shown by the epiphyte SDMs: most epiphyte species being found in the mild mountain climate of the GCfa Köppen-Trewartha climate zone between 500 and 1500 m (Fig. 1). The SDMs also projected two regions with high diversity on the western slope of the central range at mid-elevations: HsuehShan in northern Taiwan and AliShan in central Taiwan (Fig. 4B). Both areas are sheltered from east-coast landing typhoons and receive high amounts of annual rainfall under the influence of NE monsoons and SW flows, respectively. SDMs also showed considerable variation in distribution patterns between epiphyte subcategories. The most south-eastern tip of Taiwan (Fig. 1, HenChun peninsula) is characterized by a tropical wet lowland climate (Ar), and contained the highest percentage (11%) of hemiepiphytes (Hemis) of all the climatic zones. Epiphytic ferns were most often found in the cool mountain climate of the Köppen-Trewartha GCfb climate zone (67%), at an altitude of 1500–2500 m.

The thermal preference of the subcategories was also indicated by the CCA analysis. The distribution of the species on a significant first axis (explained variance 15.0%, Monte Carlo, $p = 0.001$) constrained by elevation, PCA component-1, indicated that hemiepiphytes (e.g. *Ficus spp.*) were predominately found at lower elevations, whilst epiphytic ferns (e.g. *Crypsinus quasidivaricatus*, *Lepisorus clathratus* and *L. suboligolepidus*) were the most prominent low temperature specialists (Fig. 5). Epiphytic orchids were found from low elevations (e.g. *Liparis grossa* and *Appendicula reflexa)* to upper mountains (Gastrochilus hoii). The thermal specialization (inverse niche-width) of the 156 analysed species was higher with increasing elevation, particularly for some epiphytic ferns and orchids (Pearson´s $R = -0.39$, $p < 0.001$, Fig. 6). Moreover, the half of the species (78 species) possessing relatively high thermal specialization (low tolerance values) exhibited an obvious mid-elevational pattern (Fig. 2C) in comparison to the indistinct distribution of the other half of species with a higher tolerance value (Fig. 2D).

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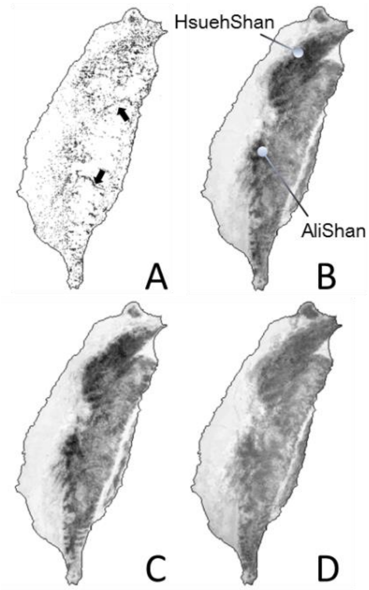

Fig.2 (A) The distribution of epiphyte collection. The two arrows indicate collections along the roads transecting the central range. (B) Modelled richness of pooled epiphytes (156 spp.) and two regions with exceptional high epiphyte diversity, namely HsuehShan and AliShan, both located at mid-elevation (800–2000 m asl). (C) Richness pattern for the half of the modelled species (78 spp.) that had lower thermal tolerance values (i.e. the species with the highest thermal specialization). (D) Richness pattern for the other half of the modelled species that possessed higher thermal tolerance values.

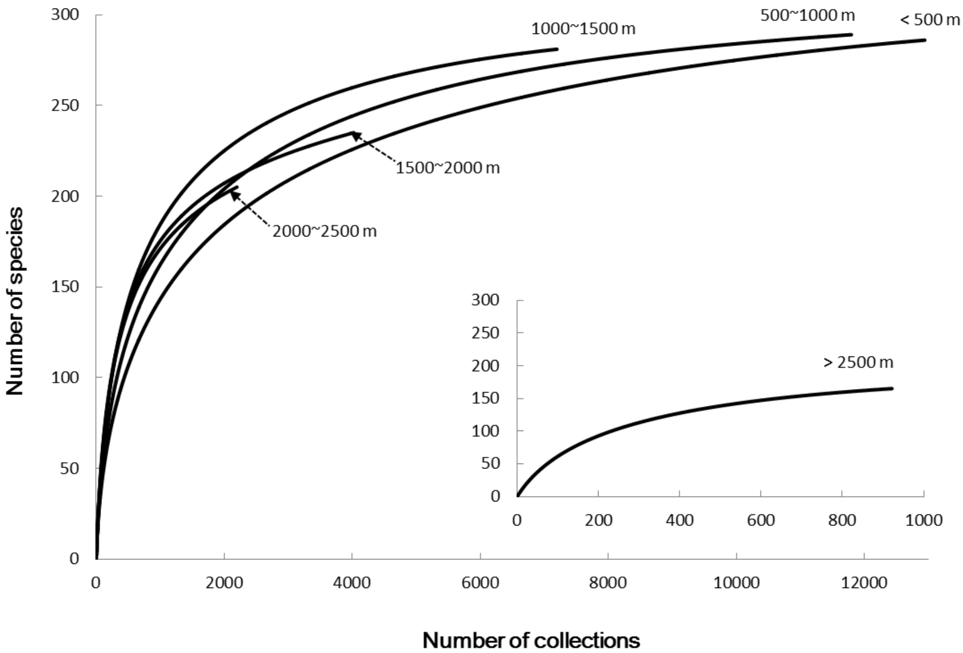

Fig. 3 Epiphyte species accumulation curves based on sample-based rarefaction (software program EstimateS 8.2). Records per altitudinal interval: 12,944 (< 500 m), 11,798 (500–1000 m), 7,198 (1000–1500 m), 4,024 (1500–2000 m), 2,197 (2000–2500 m) and 923 (> 2500 m).

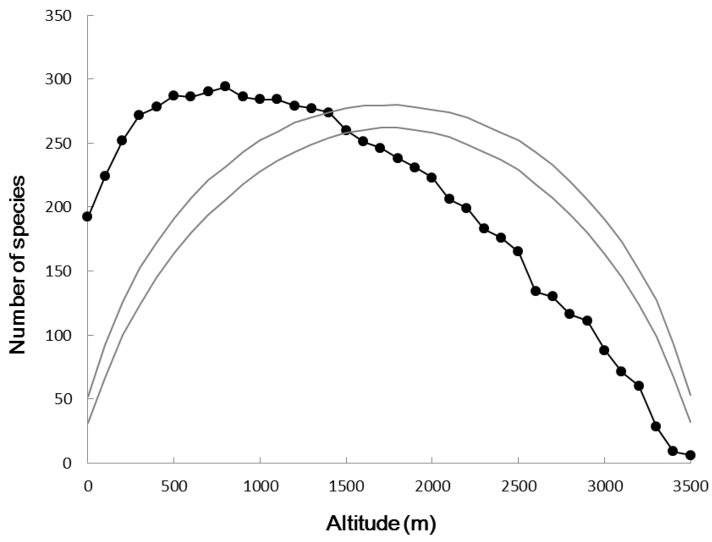

Fig. 4 The species richness curve (with data points), based on the range sizes of 39,084 collections (331 species), and the 95% CI null model prediction curves, using empirical range sizes sampled without replacement (McCain 2004, software program Mid-Domain Null, 1000 simulations).

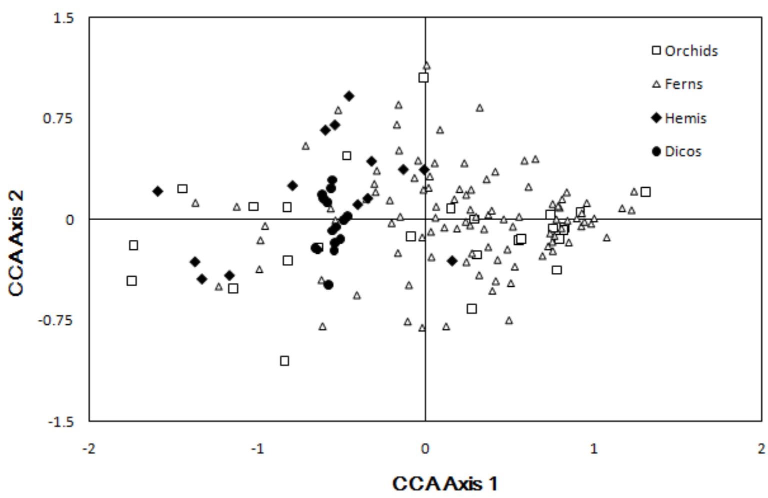

Fig. 5 CCA ordination diagram of the species scores (156 spp.) on the first two axes with epiphyte species arranged by subcategory: orchids (open squares), ferns (open triangles), hemiepiphytes (black diamonds) and dicotyledons (black circles). The first axis (eigenvalue 0.4534, explaining 15% of total variance; Monte Carlo $p < 0.001$), is highly correlated with temperature (PCA:Tmean (Loading [L]: –0.27), TcoldM (L: –0.26), TwarmM (L: –0.26), TdryQ (L: –0.27) and Elevation (L: 0.26), with higher elevation shown towards the right. The second axis (eigenvalue 0.1173, explaining 4% of variance) is related to water availability (PCA: Pcv (L: –0.30), PdryM (L: 0.29), PdryQ (L: 0.28), PcoldQ (L: 0.29), P01 (L: 0.29), PTY (L: –0.27), and P06 (L: –0.26)), with reduced water availability shown towards the top. See TABLE 1 for variable abbreviations.

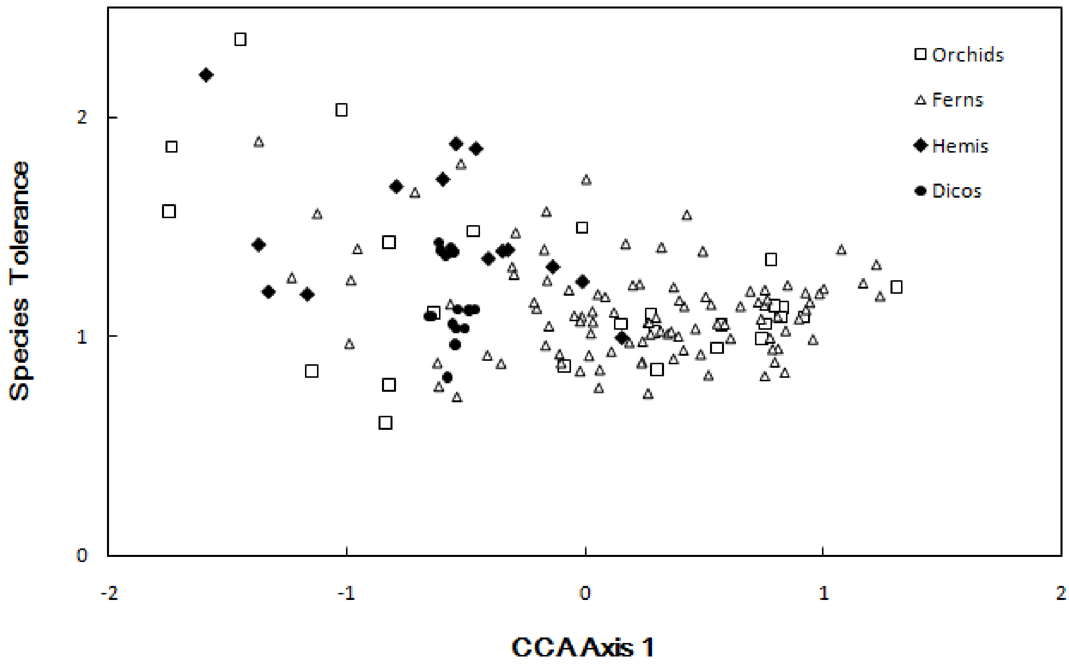

Fig. 6 Species scores (156 spp.) on the first constrained canonical axis generated by CCA and standard deviations. The first axis is highly correlated with temperature (elevation), and thus its standard deviation (i.e. tolerance) may be interpreted as a measure of niche-width. The thermal tolerance of the species is lower (i.e. higher thermal specialization) with increasing elevation towards the right (Pearson´s R = –0.39, p < 0.001). Epiphyte species are arranged by subcategory: orchids (open squares), ferns (open triangles), hemiepiphytes (black diamonds), and dicotyledons (black circles).

Discussion

In agreement with many tropical epiphyte studies from the American continent (Gentry & Dodson 1987, Wolf 1993, Wolf & Flamenco-S. 2003, Krömer et al. 2005, but see Ibisch et al. 1996), our analyses, which used both empirical collections and SDMs, showed that vascular epiphytes had a peak in species richness at a mid-elevation on mountains. Recognizing that the used botanic collections were essentially non-random, we nevertheless presume that for our data a meaningful assessment of the observed distribution and diversity patterns is possible because of the extremely high number of unique records in the database (39,084).

The position of the mid-elevational peak in species richness could not be explained by a null model. The analysis indicated a richness peak at lower elevations than expected by the null test. A similar pattern has also been described for an Indian Ocean island (Ah-Peng et al. 2012). Such a pattern may be explained by the Massenerhebung effect (i.e. mountain mass elevation effect;

Schroeter 1908, Bruijnzeel et al. 1993). This phenomenon occurs on isolated, small coastal mountains, where floristically-similar vegetation types tend to distribute at lower altitudes than on large mountain masses due to climatic compression. Environmental factors may thus account for the observed epiphyte distribution and, with this in mind, our approach using SDMs to complement grid cells with absent species is not unreasonable.

The SDMs projected two centres of epiphyte diversity, one in the north (HsuehShan) and another in central Taiwan (AliShan). The two hotspots of epiphyte diversity, situated at a mid-elevation (500–2500 m asl), did not particularly coincide with areas with relatively many epiphyte collection sites. Apparently, the SDMs did correct the sampling bias in the botanical data, such as for road side collections. Both hotspot areas are subject to significant precipitation, being under the influence of the NE monsoon in the winter or the SW rains that follow typhoons in the summer, respectively. Prevailing winds probably import diaspores to these two regions, since the majority of epiphytes in Taiwan (89%) are wind dispersed (Hsu & Wolf 2009); the ferns *Asplenium hondoense* and *A. pekinense,* which have an affinity with temperate East Asia and Japan, are only found in small regions under the influence of the NE monsoon (Moore 2000). Humid conditions and accessibility probably both contribute to the presence of areas of high epiphyte richness and endemism. Accordingly, the HsuehShan and AliShan regions merit special attention from conservationists.

The SDMs also showed that whilst epiphytic ferns were relatively common in northern Taiwan, central Taiwan has a relatively high number of epiphytic orchids. Central Taiwan receives little influence from the NE monsoon and is therefore relatively dry and warm in winter. Thus, in agreement with many other epiphyte studies (Gentry & Dodson 1987, Benzing 1990, Wolf 1994), elevation and water availability, of all environmental predictors that were used in the models, accounted to a great extent for the distribution of epiphytes in Taiwan.

The relative importance of temperature (elevation) and water availability was also demonstrated by the exploratory multivariate ordination analysis, where temperature was identified as the most important variable. In agreement with patterns in the neotropics (Wolf & Flamenco-S. 2003, Benavides et al. 2010), hemiepiphytes such as aroids and Ficus species dominated moist stream valleys in the lowlands (< 1000 m asl), especially in the south-eastern peninsula where monthly mean temperature was > 18 ˚C. As in the Andes, epiphytic ferns were particularly adapted to mountain climates (Kessler 2011); the epiphytic fern Crypsinus quasidivaricatus (Hayata) Copel was recorded near the timberline (3500 m asl).

Interestingly, our results showed that thermal specialization or inverse thermal niche-width was not uniform along the elevational gradient, but increased with altitude. Epiphytic ferns in Bolivia show a similar pattern (Kessler 2011). This is important because high altitude thermal specialists may be especially vulnerable to global warming (Laurance et al. 2011). However, this pattern contrasts with the Rapoport's rule, which suggests that the elevational ranges of species are greatest at higher altitudes, and consequently thermal-specialist species are more likely to colonize lower altitudes than higher altitudes (Stevens 1992, Laurance et al. 2011). Studies on thermal specialization in tropical mountains are clearly not conclusive and Rapoport's rule may not apply universally for mountain species (McCain & Knight, 2013). In reality, a spurious Rapoport effect could be caused simply by biased sampling procedures (Colwell & Hurtt, 1994). Our study also identified several montane cloud forests at mid-elevations with many epiphytic thermal specialists. In mid-elevational cloud forests, the frequently occurring fog events lead to little diurnal (and seasonal) thermal variation, which promotes thermal specialization (Foster 2001, Mulligan 2010, Ah-Peng et al. 2012).

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Forest Canopy of Tawau Hills Park, Sabah, Malaysia

沙巴斗湖國家公園的森林樹冠生態

Dr. Maklarin Lakim

Sabah Parks

www.sabahparks.org.my/eng/public/08c-asst.asp

Abstract

Borneo is well known for its biological richness due to its geographical location sitting right on the equator. Tawau Hills Park is an example of pristine rain forest of Borneo preserved more than three decades ago. The richness of flora, fauna and physical attributes are priceless natural resources. It has been the sites of many scientific researches since 1970s. Several scientific expeditions were conducted over the last 35 years of its protection. The park provides ample foods for the animals of various species and specialty such as primates and birds. The rich flora and fauna contained in a huge tropical rain forest canopy is a superb field laboratory for further ecological researches especially concerning the forest canopy. The tallest tropical tree of the world, the Seraya Kuning Siput (*Shorea faguetiana*) measured at 88.35 meter is located in Tawau Hills Park. In order to diversify the traditional tourist attractions in Tawau Hills Park, a canopy walkway was built aimed to bring the tall forest canopy to the park visitor. The premium forest canopy of Tawau Hills Park is simply priceless and is our gift to the world.

Introduction to Forest Canopy

Sabah is located in the northern part of Borneo island. The area well known for its biological richness due to its geographical location sits right on the equator. The presence of highland area in the central part of the island, provided climatic variation that combined with minerals and soil types, that dictated the presence and distribution of various natural resources on the island. Sabah is also blessed with the existence of Mount Kinabalu in its territory. Mountainous area diversified resources and to some extend limit the physical development. It helps preservation of nature. These are arguably the main reason behind the existence of state parks covering the highlands of Sabah namely, Kinabalu Park, Tawau Hills Park and Crocker Range Park. Originality of rain forest of Sabah is showcased here.

Generally speaking highland areas are located in a remote site and spared from human activity and conserved as a protected areas. We have preserved such special areas since the last fifty years when the Kinabalu Park was gazetted as a park. Other parks followed suit; namely Tawau Hills Park in 1979 and Crocker Range Park in 1984. The natural preservation continues for the protected areas over the fifty years, however, unprotected forests were subjected to forest conversion for various human development. With human population steadily growing, this has put many of the rain forest sites on the edge of townships and relatively accessible to human. As such many forested area were degraded at least in terms of its original canopy formation. The presence of high quality rain forest with the presence of good canopy cover is limited to these fully protected areas.

This paper aims to deliberate on the forest canopy of Tawau Hills Park in Sabah. While the park is preserved and played its roles in our ecosystem services, prospects and opportunities for further exploration is discussed in a sustainable conservation perspective.

Tawau Hills Park

Tawau Hills Park is one of the three terrestrial parks in Sabah. It is situated on the Southeast corner of the State and was gazette in 1979 for the preservation of the lowland tropical rain forest and the protection of watershed or water catchment for the area on the Southeast corner of Sabah. Covering an area approximately half the size of Singapore, the park has preserved pristine rain forest since more than three decades ago. The richness of flora, fauna and physical attributes are priceless natural resources contained within the park. It rendered vital ecosystem services for the people of Sabah locally, and to the mankind globally. Most prominently the park is the main water catchment area that supplied water for nearby towns namely Tawau, Semporna and Kunak.

Location (site selection)

Tawau Hills Park is located on the Southeast corner of Sabah, with its headquartes situated at latitude N 04° 23.873’ and longitude E 117° 53.274’. This site has been designated as a long term ecological research site by the Sabah Parks aimed at providing research facilities. The site is characterized by the presence of research trail system, botanical plots, weather station and accommodation. The existence of trail system in particular has enabled researchers to explore a wide area for their own research interests. This has paved the way for other research activities to be carried out here.

THP is bordered by Kalumpang Forest Reserve on the northern part and vast oil palm and cocoa plantations on the west, south and east (Figure 1). THP is part of the last remaining forested area in the southeast corner of Sabah. The area lies on volcanic soils (Phillipps, 1988) and consists of a mixture of both primary and disturbed lowland and hill dipterocarp forest. Part of the park area was selectively logged in 1970s.

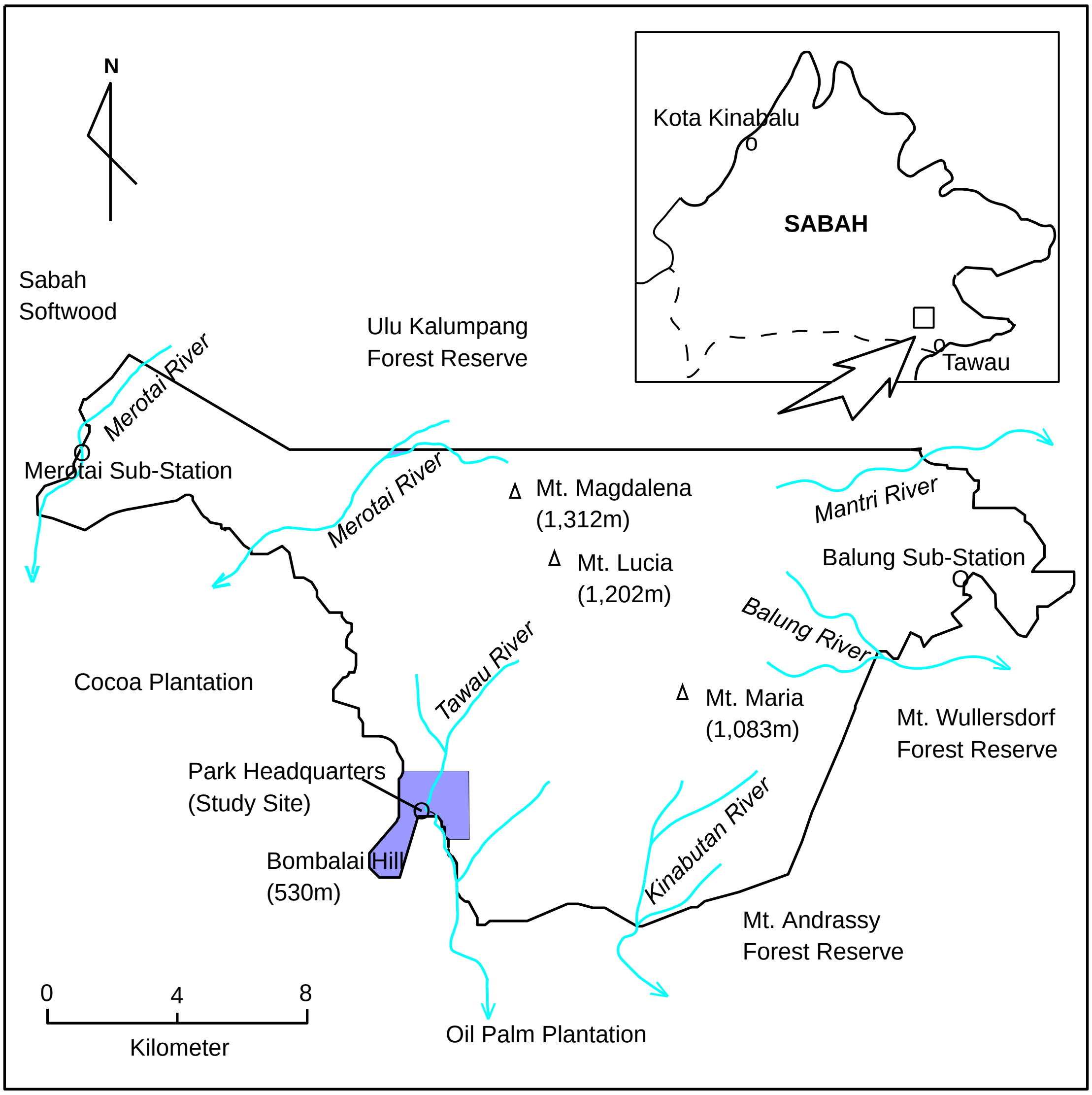

Figure 1. Location and area of Tawau Hills Park in Sabah.

Long Term Ecological Research

Scientific research is an integral part of protected area management and ecotourism. Tawau Hills Park has been the sites of many scientific researches since 1970s, prior to its gazettement as a park. Since the last 35 years of its protection, several scientific expeditions were organized in Tawau Hills Park, usually ended with findings of many unanswered questions. It prompted further researches aimed to address specific questions of particular researcher interest. Apart from basic resources inventory in the form of flora and fauna specimens collection, ecological researches were also conducted here.

Rain forest of Tawau Hills Park is unique and special because of its big sized trees. Dominated by dipterocarps, the forest canopy here is relatively huge. Big trees above 70 meters tall are rampant, creating a tall canopy layer with various niches for animals and plants to thrive. Forest structure is exceptionally outstanding. In several instances, we were confused with the classification of forest canopy due to differences in tree measurements. Presence of big and old trees elevated the height of forest canopy from above the ground. Exceptionally huge crown of trees are also created a thick cover for the forest floor that differentiated this area from other nearby forest sites.

Primate studies

Forest canopy researches conducted here included on primates and birds as subjects. I focus my presentation on primate researches where 3 projects were carried out on niche separation among sympatric primates, feeding ecology of Bornean gibbon and comparative ecology of macaques and leaf monkeys. The park provides ample foods for the animals of various species and specialty. Similarly, it provides ample spaces for the animals to take shelter and protection from predation. The rich flora and fauna contained in a huge tropical rain forest canopy provides a magnificient field laboratory for further interesting ecological researches especially concerning canopy researches.

Scientific data is needed for an effective management of the park. Research activities are also the basis of sustainable ecotourism development. Tawau Hills Park has benefitted from intensified research activities especially on primates since the last 20 years. Systematic exploration in trekking and following the monkeys over an extended period of time have successfully identified and habituated the animals surrounding the park headquarters. Tame wild animals like monkeys are asset of ecotourism, since park visitors are appealed to this kind of animals. Knowledge of their ranges and habits could be an asset for the development of ecotourism programme at Tawau Hills Park.

It is interesting to note that orang-utan (*Pongo* pygmaeus) is also present at the park. It presence has been noted since 1978 (Davies & Payne, 1982) in the northern part of the park. Moreover the proboscis monkey, *Nasalis larvatus* has also been observed in the west part of the park since 1996 (Lakim, 1998). It is also interesting to note that white leaf monkey occur within the park. Individuals white leaf monkey are quite frequently observed within *Presbytis rubicunda* and *Presbytis hosei* groups since 1980s. Although such white monkey is not common, 2-4 white individuals could opportunistically be encountered in several wild groups of *Presbytis rubicunda* and *Presbytis hosei* (Lakim, 2000) in forested area about 1 km from the park headquarters. The white individuals comprised adult and young individuals. Further study has been conducted to investigate this issue. It is assumed as a semi-albinism phenomenon and not associated with speciation (Md-Zain *et al.* (2005), Md-Zain *et al*. (2006)).

Bird studies

Birds are the most conspicuous wild animals in Tawau Hills park. No wonder, the unofficial logo of this park is the Rhinoceros Hornbill. The selection was owed mostly to the daily presence of this big flight birds in the surrounding of the park headquartes. It is refuted that all eight species of hornbills occur in this park. Since hornbills are depending on old and big trees for nesting, foraging and mating, a pristine tropical rain forest of Tawau Hills Park are safe home for their survival. A population study of this charismatic bird was carried out in Tawau Hills Park (Lakim & Biun, 2001). It was projected that its population is considered common at this site. Continuous preservation of the forest habitat, is an assurance of its healthy and growing population at this particular site.

Latest study on birds at Tawau Hills Park was conducted by a group of researcher from the University of Cornell, United States, headed by Professor Dr. David Winkler. This time around this study was focused on breeding biology of selected species of canopy birds. It was a challenging tasks, as most birds opted to place their nests high in the canopy where access to their eggs for necessary measurements were extremely difficult. Nevertheless, frequent findings of many species of forest canopy birds are always invaluable assets for such study. Such findings as these are indication of birds survival strategy in a pristine rain forest habitat. Ample forest canopy spaces provides habitat to many types of birds to coexist, share and divide the resources here.

World's Tallest Tropical tree

Exceptionally 'inaccurate' measurements of trees within the existing botanical plots of Tawau Hills Park is well documented in previous studies conducted at this particular area. Real forest with higher roof of tree crowns is the beauty of this park. Ecologically, it provides ample space between forest floor and forest canopy. In 2006, a group of rope climbers headed by Dr. Roman Dial, from the University of Alaska, United States, held an expedition to Sabah aiming to locate the tallest tropical tree in the world. They went to various places of interest in Sabah including to Danum Valley. The specialist group climbed giant trees using rope techniques and measured each of it using measure tapes from top down. Being located on the verge of Tawau town, no one expected the tallest trees to be found in Tawau Hills Park. The park was the last destination explored by this group. To the amazement to many parties including us, towards the end of their expedition, this group managed to measure more than 12 individual trees with height above 70 meters tall inside Tawau Hills Park. The top ten tallest individual trees in Sabah are located at Tawau Hills Park. The expedition ended with the conclusion that the tallest tropical tree of the world is situated in Tawau Hill Park. That particular tree is now our heritage tree from the family of dipterocarps, named Seraya Kuning Siput (*Shorea faguetiana*) measured at 88.35 meter from its base. The tree comparable to the Eiffel tower in ecotourism sense, is only 1 kilometer away from the park headquarters. The old tree has experienced branch breaking and is subjected to fungal infection, termite and other diseases. It may fall at any time, most of us have seen it, tourist should grab the chance of visiting this particular giant tree.

Canopy Walkway

In 2006, a canopy walk way was built at this park as a man made tourist facility. The aim was to diversify tourist attractions from the traditionally acclaimed waterfalls based picnic and recreation activity, to the one that based on nature attraction and forest exploration. Provision of canopy walkway was aimed to bring the premium tall forest canopy to park visitor. Having a monkey view when one strolling the canopy is an exciting experience. This is due to the fact that the majority of wild animals including insects spent most of their time in the canopy. Entering their territory will propagate chances of their encounter at a site where they feel safe and less fearful of human presence. To some visitor equipped with camera, this is the ideal place for wildlife photography.

Our previous experience in putting a canopy walkway in Poring, Kinabalu Park has indicated the popularity of this facility among visitor. The walkway possesses a power to attract visitor. Considering that fact, a visitor can tolerate a substantial long walk to get to the walkway site. And by doing so, opportunity of encountering passing arboreal wild animals along the access trails is also enhanced. Remote location of the walkway helps to keep wild animals to be remained at the walkway area with minimal human disturbance. Such approach also help to disperse visitors from the main recreation sites that characterized by riverine and waterfall areas.

Challenges of Forest Canopy

While the idea of building the canopy walkway was considered a right decision, there are many challenges faced by us in keeping the walkway in good condition. The old rain forest of Tawau Hills Parks is comprised of old trees that tend to break down. This situation exposed the walk way structure to damage and exposed the users to accidental hazards. Similarly, at a site where annual rainfall is around 3,000 mm to 4,000 mm, humid forest quickly degrades the structure. These are risks and costs that we have to bear in laid the facility and the need for its high cost of maintenance.

Future development

It is a revenue stream for a sustainable development of the park. We projected that in years to come, park areas will become the main if not the only natural sites available to tourist both domestic and foreign. As such big number of visitor will create excessive number of tourist and the carrying capacity will be exceeded in due course. As such venture into more natural sites and adventure activity are important. The forest canopy exploration is one of suitable programme for the tourist. Utilization of canopy resources based on research findings has potential for sustainable development projects.

Apart from walkway of a suspended rope, other exploration methods are hot air, tree top platform, free standing metal bridge, industrial crane, sky bridge. These methods are among possible ways of exploring the forest canopy. The cost and practicality of usage are main concern for a profitable endeavour.

Conclusion

The existence of forest canopy in its premium condition at Tawau Hills Park is simply priceless and is our gift to the world. It is our pillar of tropical ecosystem services in Sabah and globally. Such protected area is our last frontier of the tropical rain forest on our ageing planet earth. It is our hope for future exploration in the tropical rain forest canopy.

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[譯文] 沙巴斗湖國家公園的森林樹冠生態

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沙巴國家公園

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摘要

由於地理位置在赤道附近，婆羅洲的生物豐富程度舉世聞名，例如保護原始雨林超過三十年的斗湖國家公園(Tawau Hills Park)。因其豐富的動植物相，1970 年代起迄今有許多科學研究。園區內的自然環境也提供了各種動物豐富的食物。熱帶雨林的高大冠層裡有豐富的動植物相，非常適於生態研究，特別是樹冠層研究。而世界上最高的熱帶雨林樹木，88.35 公尺的望天樹(*Shorea faguetiana*)就位在斗湖國家公園內。為了區分傳統觀光客和生態觀光客，國家公園裡也建造了樹冠層走道，吸引公園參觀者前往高樹的樹冠層。斗湖國家公園的原始森林樹冠層是世界上無價的禮物。

前言

沙巴位在婆羅洲北部，因位在赤道上，其生物豐富度舉世聞名。婆羅洲中間的區域是高地，由於地形起伏造成氣候、礦物和土壤型態的差異，也造成許多不同的自然資源分布。沙巴受到神山(Mount Kinabalu)的影響，造就了多樣化的資源和自然環境的發展。這些原始雨林的自然景觀提供了沙巴、神山、斗湖、克洛克山脈(Crocker Range Park)等國家公園設立的理由。

高地區域位於人類活動範圍之外，被劃分出來並設為保護區。50 年前神山國家公園設立之後，其他的國家公園陸續成立，例如 1979 年設立的斗湖國家公園以及 1984 年設立的克洛克山脈國家公園。在這些保護區內，自然資源的保護持續了 50 年以上；然而保護區外的森林則受到各種人類發展的影響。隨著人類族群數量的穩定成長，許多雨林只存在於村莊的邊緣並且易於進入開發。高品質的雨林和良好的森林覆蓋僅存在於那些完整保護的地區。

這篇論文將討論沙巴斗湖公園裡的森林樹冠層。國家公園能夠保育生物並維持生態系統功能，期望在未來能針對永續保育有更深的探索。

斗湖國家公園

斗湖國家公園是沙巴三個陸地國家公園之一，位在沙巴州的東南角，面積約為半個新加坡大小，1979 年為了保護低地熱帶雨林及集水區而設立。其豐富的動植物相及自然環境提供了重要的生態系統。除此之外，斗湖國家公園中的集水區域也是附近鄉鎮如斗湖、 仙本那(Semporna)和 庫納克(Kunak)的主要水源。

位置

斗湖國家公園位在沙巴州的東南角落，總部位在北緯 4 度 23.873 分及東經 117 度 53.274 分，是長期生態研究地區。此區域的特色是學術步道系統、植物樣區、氣象站及各種設施。特別是步道系統，能提供研究者探索整個廣大的區域。目前其他研究活動的步道也陸續建設中。

斗湖國家公園的北邊是 Kalumpang 保育林，周圍其他的區域則是廣大的棕櫚樹和可可亞種植地(圖一)。斗湖國家公園也是沙巴東南角仍然有森林分布的區域，位於火山土壤之上，並由原生及次生的龍腦香科森林組成。其中有些林地曾在 1970 年代遭受擇伐。

長期生態研究

科學研究是保護區經營及生態觀光的基礎。在設立為國家公園之前，1970 年代就有許多地方開始進行科學研究。由於過去至少 35 年的保護，斗湖國家公園內會有一些科學考察，通常考察結束時會發現許多無法解答的問題。這促使了更多針對特殊問題的研究。除了在動物誌及植物誌上的基本資源之外，也會進行標本的採集及生態研究。

龍腦香科巨木的樹冠層是斗湖國家公園內的特點之一。超過 70 公尺以上的大樹繁茂生長，高大的樹冠層和複雜的結構提供了動植物許多不同的生態棲位。在幾個研究案例裡，因為測量上的差異，森林樹冠層的分類成為一個難以解決的問題。不同於其他鄰近的森林區域，大樹和老樹提高了從地面到森林頂端的高度，巨大的樹冠層同時也是地面土壤的厚實覆蓋。

靈長類研究

目前關於靈長類的研究有三個計畫正在執行：靈長類的生態隔離、婆羅洲長臂猿的餵食生態學(feeding ecology)和恆河猴及葉猴的比較生態學(comparative ecology)。國家公園提供了動物各種豐富的食物，同時也提供了大量的空間棲息和躲避掠食者。豐富的動植物相以及巨大的熱帶雨林樹冠層，提供未來的生態研究一座優良的野外實驗室，特別是針對樹冠層的研究。

如果想要有效率地經營國家公園，科學研究的成果會是必要的資料。斗湖國家公園受益於蓬勃的學術活動，特別是過去 20 年來對於靈長類的研究。在長時間、有系統地追蹤猴子的活動之後，對於國家公園總部附近的動物種類和習慣有了良好的認識。馴服的野生動物(例如猴子)是生態旅遊的資產，因為遊客會喜歡這些動物。知道野生動物的活動範圍和習性會對於生態旅遊計畫的發展有莫大的助益。

紅毛猩猩(*Pongo* pygmaeus)、象鼻猴(*Nasalis larvatus*)和白葉猴也都會出現在國家公園裡。

鳥類研究

在斗湖國家公園裡，最顯而易見的野生動物其實是鳥類。國家公園非正式的處徽是馬來犀鳥，因為它是最常出現在總部附近的大型飛鳥。犀鳥需要依賴老樹和大樹築巢、覓食和擇偶，而斗湖國家公園的原始熱帶雨林就是最好的生存環境。持續地保護森林棲地有助於維持犀鳥的健康和族群數量。

最近在斗湖國家公園的鳥類研究由康乃爾大學的溫克勒(David Winkler)教授領導，選擇幾種樹冠層鳥類研究餵食生物學。這是一項頗具挑戰的任務，因為大多數的鳥類都選擇在很高的樹冠層築巢，取得他們的蛋進行必要的測量是非常困難的事情。然而，許多研究結果是無法估價的資產，這些結果指出鳥類在熱帶雨林裡的生存策略。

世界上最高的熱帶雨林樹種

在過去調查的文件裡，保存了一些不是非常精確的林木測量。真實的森林有著更高的樹冠層，是國家公園裡的美麗風景。生態學上，它提供了森林的地面和樹頂之間豐富的空間分層。2006 年，阿拉斯加大學的戴爾(Roman Dial)博士帶領的繩索攀爬團隊，為了找出世界上最高的熱帶樹，探索了沙巴國家公園內各式各樣的地方，甚至包括了單濃谷(Danum Valley)。這個特殊的團隊透過繩索技巧攀爬了巨大的樹木，並且用測量繩從頂端垂下測量樹高。令人驚訝的是在研究結束時，這個團隊在斗湖國家公園境內量測了超過 12 棵超過 70 公尺的大樹。沙巴境內前十高的獨立木都位在斗湖國家公園。這個考察的結論是：全世界最高的熱帶樹木，88.35 公尺高的望天樹 (*Shorea faguetiana*)，就位於斗湖國家公園。這種特別的樹現在是世界遺產樹，就生態旅遊的觀點來看和艾菲爾鐵塔一樣高，而且只距離總部一公里遠。然而，老樹的枝條會逐漸枯死並且容易受到真菌、白蟻和其他疾病的危害，隨時可能倒塌，觀光客必須抓緊機會參觀這棵特別的巨木。

樹冠層走道

2006 年，國家公園建造一條為了吸引觀光客的樹冠層走道。主要是為了區分在瀑布區、為了野餐和遊樂的傳統觀光客，和為了自然景觀及森林探索的生態觀光客。當人類像是猴子一樣在樹冠層裡散步的時候，是很特別的經驗和觀感。由於很多野生動物大多生活在樹冠層，人類進入牠們的活動範圍能增加看到他們的機會，同時，待在樹冠層時動物也會覺得比較安全，比較不畏懼人類的存在。對於那些愛好攝影的觀光客來說，這也是野生動物攝影的理想地方。

根據之前的經驗，在神山國家公園波令遊憩區設置的樹冠層走道是非常受觀光客歡迎的設施。樹冠層走道的吸引力，能讓觀光客願意徒步一段長距離路程到走道所在的地方；並藉由進入樹冠層走道，偶然遇見棲息在樹上的野生動物。樹冠層走道設置在離人類活動區域較遠的地點也會使野生動物留在走道區域，受到較少的人為干擾。這些設施可以幫助分散主要遊憩區(例如河邊或是瀑布附近)的觀光客。

樹冠層的挑戰

決定要建造一條樹冠層走道時，要面對許多的挑戰，必須使走道保持在良好的狀態。而斗湖國家公園的古老雨林有許多老樹看起來有倒塌之勢，使得走道暴露在設施損毀和遊客受傷的危機下。除此之外，雨林的年雨量大約是 3000 到 4000 釐米，潮濕的森林也會造成步道的腐朽。國家公園必須提高維修的經費以應付這些風險和支出。

未來發展

樹冠層走道是國家公園的穩定收入來源。未來計畫開放國內外旅客參觀自然區域，屆時將湧入大量的觀光客，可能會超出地區環境的乘載量。是故必須分散遊客進入不同的自然環境，而森林樹冠層的探索是一項合適的計劃。根據研究指出，對於永續發展而言，樹冠層是極有潛力的資源。

除了以懸吊繩索構成走道以外，還有其他探索樹冠層的方法，例如熱氣球平臺、金屬立橋、工業起重機、天空橋梁等等。但造價和實用性是收益的主要考量。

結論

斗湖國家公園內的原始森林樹冠層是無價的自然資源，是全球及沙巴共有的熱帶生態系統，也是未來探索熱帶雨林冠層的希望。

The Comparison of Insects from Canopy, Understory, and Shrub Layers by Different Sampling Methods in Mid-montane Xuejian Reserved Forest

利用不同取樣方法比較雪見中海拔地區樹冠層、冠下層及矮灌層的昆蟲

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摘要

本研究應用數種方法對雪見地區長尾尖葉櫧、木荷、杏葉石櫟等 3 種優勢植物進行昆蟲調查，將馬氏網及吊網升至 20 公尺高的樹冠層(canopy)收集昆蟲一星期，針對木荷施以噴霧法收集樹冠昆蟲，也應用掃網分別對樹冠層、冠下層(understory)及灌木層(shrubs)進行取樣。噴霧法是當中最有效的方法，對薊馬尤為有效。這些樹種的調查都顯示雙翅目是主要組成，其次為寄生蜂及甲蟲。掃網部分則顯示，森林表層的灌木層捕獲的昆蟲遠多於樹冠層；多尺度空間分析也顯示，樹冠層、冠下層及灌木層的科級昆蟲數量組成截然不同。食性功能分析則顯示，樹冠層掃網捕獲的昆蟲以植食性為主，而冠下層及灌木層則以次級消費者及分解者為主。

關鍵詞：樹冠層、昆蟲相、吊網、馬氏網、噴霧法

Abstract

Different insect sampling methods were applied on three dominant plants, i.e., Castanopsis cuspidata, Schima superba, and Lithocarpus amygdalifolius, in Xuejian recreation area. For insects of canopy layer, hanging trap and malaise trap were set up at ca. 20 meters above the ground for one week; and in addition, fogging method was used on S. superba canopy. Sweeping net was employed for insects of canopy, shrubs as well as understory layers. Fogging method was proved to be the most efficient, particularly for thrips. Of all the insects captured from the three trees with these sampling methods, dipterans were the most abundant, especially by hanging trap, followed by wasps and beetles. More insects were captured by sweeping net from the shrubs layer and the least from canopy. Multidimensional scaling analysis revealed that the spatial distribution of insects, in family level, was significantly different among canopy, understory and shrubs layers. Functional group analysis showed that the canopy contained a higher proportion of primary consumers while more secondary consumers and decomposers were found in the understory and shrubs layers.

Keywords: Canopy, Insect fauna, Hanging trap, Malaise trap, Fogging method.

前言

樹冠層(Canopy)是森林生態系當中光合作用最旺盛的處所，在生態系的運作上有著重要的角色，其多樣性組成常是森林生態系的研究重點。學者認為樹冠上的生物種類受樹種、森林型態、生物本身特性、環境因子及其它一些偶發性事件的影響。以環境因子來說，一棵樹有關的樹冠層內外圍、冠下層(Understory)、灌木層(Shrub)等其所受的光照、風力強度及所含濕度等多有不同，都會影響其生物相(Parker 1995) 。Srinivasa et al. (2004)應用噴霧法(Fogging)比較樹冠層無脊椎動物，發現熱帶森林內優勢樹種龍腦香科的 Vateria indica 及 Dipterocarpus indicus，其節肢動物組成大不同；Vateria indica 以雙翅目最為多樣，Dipterocarpus indicus 則是蜘蛛，兩樹種的鞘翅目量雖多，但歧異性都低。另有學者指出，森林型態會影響昆蟲的組成及多樣性，最優勢的樹種並非植食性昆蟲最多樣的樹種，同樣的樹種在不同地區也會有不同的昆蟲組成(Ribeiro et al. 2005)。此外，颶風的衝擊，對昆蟲及鳥類的組成及數量有無可恢復的影響(Johnson and Winker 2010, Sklodowski and Garbalinska 2011)。以螞蟻為特定對象的研究則指出，樹冠層間若有高度聯結，其螞蟻相會較豐富多樣(Powell et al. 2011)，而樹冠層及森林底層的螞蟻相則有相類似的組成(Weiser et al. 2010)。Chen and Chang (2007)在南仁山的次生林研究則指出，迎風面及背風面的樹冠層與樹冠下層的覆蓋面積截然不同。

在樹冠層上活動的生物，有些是固居的，有些只是偶爾經過或與固居者有互動，這些不同特色生物的收集及觀察方式各有不同。像鳥類的調查，可用望遠鏡，但高達 20 公尺以上的樹冠層昆蟲，常用的掃網採集法即無法應用。因此，在昆蟲方面開發出了各類的調查方法，如噴霧法、馬氏網、吊網、吊燈陷阱、黏蟲紙網、剪枝條(Basset et al. 1997)，其中噴霧法是最直接有效的方法(Paarmann and Stork 1987, Lowman and Wittrnan 1996)，Blanton (1990)更指出噴霧法對寄生蜂類群尤為有效，但也有學者認為此方法會對樹冠層上的昆蟲相造成無法復原的衝擊；Floren and Linsenmair (1997)就曾指出，噴霧後 7 個月的調查顯示，其上的昆蟲組成數量截然不同。因此，馬氏網及吊網較常被採用於樹冠上昆蟲組成及棲群動態的研究，而吊燈陷阱則對鱗翅目蛾類有很好的誘捕成效(Preisser and Smith (1998)。這些調查方法收集下來的昆蟲樣本，因昆蟲分類專家的限制，鮮有全面細分到種的研究，多針對特定昆蟲進行分析，其中步行蟲、螞蟻、蠡蟴、蚊蠅、樹皮下甲蟲及附生植物內的土棲昆蟲最為常見(Stork et al. 1997, Srinivasa et al. 2004, Ellwood and Foster 2004)。

雪見地區位於雪霸國家公園西北隅的泰安鄉，海拔在 1800 公尺上下，屬暖溫帶重濕氣候(Su 1984)。轄區林相組成為複雜的闊葉林，維管束植物高達 600 種，為櫟林帶（Quercus Zone）植群，有三至四層的結構，以樟科及殼斗科等優勢樹種的樹冠層為最上層；樹冠下層夾雜著有

落葉樹種，主要有尖葉槭（Acer kawakamii）及栓皮櫟（Quercus Variabilis）；而林下灌木層的草本植物則以蕨類(Pteridophyta spp.)及五節芒(Miscanthus floridulus)為主(歐1996，傅 2009)。唐等人(2002)曾於雪見地區以腐肉、福馬林、黃色黏蟲紙及馬氏網等方法進行昆蟲相之調查研究，發現捕獲昆蟲會因調查方法及季節而異，其中以馬氏網所捕獲種類及數量最多。唐等(2008)同樣於雪見地區進行環境生態監測，並與 2002 年的調查結果比對，發現黃色黏蟲紙陷阱昆蟲捕獲量有減少的情形，且部分樣區因人為干擾而昆蟲變少。唐等(2002, 2008)以地表灌木層為主的調查，並無法類推樹冠層及樹冠下層的昆蟲組成；Preisser and Smith (1998)就曾指出，應用馬氏網及吊燈陷阱都顯示灌木層的昆蟲數量為樹冠層之 8 倍；但螞蟻的研究則顯示，樹冠層及森林底層的螞蟻相有相類似的組成(Weiser et al. 2010)。

雪霸國家公園鑒於樹冠層昆蟲相的重要性，委託徐等人(2010)在觀霧地區進行樹冠層昆蟲調查，探討不同林型環境或樹種間昆蟲相組成之變化差異，進而探討各類昆蟲功能群組成及其所扮演的角色，利用長竿捕網進行抖落及網捕等方法調查，發現以尺蛾科(Geometridae)類群最為優勢，鞘翅目則為金花蟲科(Chrysomelidae)，但其長竿捕網並無法捕獲 20 公尺以上的樹冠層昆蟲。傅等人(2011)更進一步於雪見地區搭建樹冠平臺，並針對樹冠平臺以吊網及枝條套網進行昆蟲調查，發現雙翅目數量最多，並有大量膜翅目無螯蜂及纓翅目的薊馬。

本研究基於雪見地區已建立的樹冠平臺，進行雪見地區樹冠層的昆蟲相調查分析。以優勢植物物種為對象，評估吊網、馬氏網、掃網、噴霧等取樣方法於樹冠層昆蟲的收集效能，並與樹冠下層及灌木層掃網而來的昆蟲比對，建立臺灣中海拔山地區樹冠層昆蟲的組成特性。

材料與方法

一、調查時間

雪霸國家公園雪見遊憩區為四季分明的中海拔山區，故於 2013 年各季，即 3 月、6 月、9 月及 12 月調查採集樣。

二、調查樹種

雪見遊憩區周邊林相的代表樹種，具有 20 公尺以上的樹冠的大喬木，即木荷（Schima superba，SS）、杏葉石櫟（Lithocarpus amygdalifolius，LA）及長尾尖葉櫧（Castanopsis cuspidata，CC）各一棵調查採樣。

三、調查方法

應用吊網、馬氏網及掃網等取樣方法進行樹冠層的昆蟲採樣，另針對有樹冠層平臺的木荷進行噴霧法(Fogging)的取樣，也針對樹冠下層及森林底層的灌木層進行掃網收集；所得之昆蟲均裝於 8 號夾鍊袋中，標記採集日期、地點及方法，帶回實驗室進一步處理。採集方法簡述如下:

(1) 樹冠層掃網(Canopy layer sweeping net)：於 21 公尺高的木荷樹冠平臺上，用長竿掃網針對木荷、杏葉石櫟及長尾尖葉櫧，分別掃取 22 網，代表該樹種樹冠層周圍之昆蟲。

(2) 樹冠下層掃網(Understory layer sweeping net)：用 20 尺長竿捕網於離地 8 公尺的樹冠下層林木掃網採樣，每一樹種選 3 個方位各掃取 22 網，代表該棵樹樹冠下層周圍之昆蟲。

(3) 灌木層掃網(Shrubs layer sweeping net)：於樹冠層下周圍 2 公尺以下之矮灌木及地表植物掃網採樣，每一樹種下選取 3 個方位各掃取 22 網，代表該樹種下周圍灌木層之昆蟲。

(4) 吊網(Hanging trap)：於樹冠層下，用繩索將吊網升至 20-25 公尺高的樹冠層收集昆蟲；配合掃網，每一樹選 3 個方位各升起一個吊網陷阱，內置放發酵的鳳梨皮誘引昆蟲，代表該棵樹樹冠層之昆蟲，放置的誘捕期間為一星期。

(5) 馬氏網法(Malaise trap)：選擇合適的樹冠層位置，用繩索將馬氏網升至樹冠層 20-25 公尺的高度收集昆蟲；因馬氏網體積龐大，每棵樹僅升一馬氏網，代表該棵樹樹冠層之昆蟲，放置的誘捕期間為一星期。

(6) 噴霧法(Fogging method):僅針對木荷 21 公尺高的樹冠層平臺於六月進行一次的噴霧法燻落昆蟲，於樹底平鋪四塊 3 x 3 公尺的白色帆布承接掉落的昆蟲。噴霧的時間為 5 分鐘，含賽酚寧(Cyphenothrin) 5.5%、異治滅寧(d-Tetramethrin) 0.75%及協力精(Piperonyl Butoxide) 8%，並輔以助煙劑稀釋 5 倍。

四、標本處理、鑑定及採集記錄:

(1) 分蟲；按採集日期、地點、方法、採集者等資料進行標本編號。

(2) 鑑定；以各目、科及形態種為分類依據，填寫鑑定資料。參考昆蟲分類及圖鑑相關書籍進行鑑定。此外，更建立各昆蟲個體之體長資料，應用 Gruner (2003)提出各類昆蟲之體長及體重的轉換公式(表 1)，以評估其相對之生物量。

(3) 輸入 Excel 製作資料庫，應用 Excel 製作各類圖表。

(4) 分析該地區各優勢植物的各目及各科昆蟲組成、變動及優勢類群。

(5) 分析各採樣法間的各目、各科昆蟲數量之異同，並應用軟體 PAST (Hammer et al. 2001)分析昆蟲多尺度空間分布(Multidimensional Scaling, MDS)及相關之多樣性指數。

結果與討論

一、樹冠層各採集法採得的昆蟲總量比較

此次調查因噴霧法僅於 6 月應用於昆蟲收集，分析比對該季的樣本共得 15 目 162 科 22841 隻昆蟲，以雙翅目最多，其次為鞘翅目、膜翅目及半翅目，其中吊網的雙翅目遠高於其它昆蟲，主要為果蠅，高達 11603 隻。若將果蠅去除，噴霧法雖僅針對木荷樹冠層執行一次，在各目的收集上仍是最高，尤其是半翅目、雙翅目、膜翅目及鞘翅目，較特別的是纓翅目薊馬及嚙目的蟲子，數量遠多於其它採集法。掃網僅有木荷樹冠平臺 22 網的採集資料，相較於調查時間為一星期的吊網及馬氏網少甚多。馬氏網的結果顯示，雙翅目佔多數，數量遠多於居次的半翅目、膜翅目及鞘翅目，其餘各目數量都不多。吊網的部分除去果蠅科仍以雙翅目數量最多，但半翅目數量不若其它兩方法多(表 1，圖 1)。

二、各採集法捕獲之常見各目昆蟲科別組成

針對捕獲的優勢昆蟲各目的科級分析顯示，雙翅目在馬氏網、吊網及噴霧法都可見到很高的黑翅蕈蚋。若將吊網 11603 隻果蠅去除，黑翅蕈蚋遠多於其他各科，其餘如蕈蚋科、黃潛蠅科、舞虻科、家蠅科、水蠅科及毛蚋科數量也不少。馬氏網部分則是超過一半的蠓科為最多，其次為癭蚋科、搖蚊科、黑翅蕈蚋科及果蠅科。噴霧法而來的昆蟲並未有馬氏網及吊網單科優勢的現象，蠓科、舞虻科、搖蚊科、黑翅蕈蚋科、黃潛蠅科及果蠅科量都不少(圖 2)。

吊網的鳳梨誘引對半翅目幾乎沒有誘引效果，僅有 9 隻，掃網甚至有 54 隻的數量。馬氏網則對常蚜科及葉蟬科有不錯的捕獲能力，噴霧法則有超過 1000 隻的捕獲量，除常蚜科及葉蟬科外，有極高數量的盲椿科及不少的木蝨科。掃網部分則未有特別的科別出現(圖 3)。

膜翅目也是在吊網的捕獲情形較少，但有很高數量的金小蜂科寄生蜂。馬氏網則以釉小蜂數量較多，而噴霧法則是遠多於其他調查方法，如同 Blanton (1990)在北美的研究，噴霧法對具翅有飛行能力的寄生蜂類群尤為有效；其中以釉小蜂科最多，而數量居次的有繭蜂科、廣肩小蜂科、跳小蜂科、姬蜂科及金小蜂科，其它如蜜蜂總科、卵細蜂科級分盾細蜂科也不少，較常被拿來研究的蟻科則數量不多(圖 4) (Powell et al. 2011, Weiser et al. 2010)。

鞘翅目在幾個採集法當中被捕獲的特性與膜翅目類似，也是吊網的捕獲量最少，但其內有很高的出尾蟲科昆蟲，顯見此類蟲對鳳梨皮的誘引有偏好性。馬氏網捕獲的鞘翅目昆蟲科別也不少，但僅有隱翅蟲數量較多。噴霧法則明顯高出甚多，高達 1500 隻，以金花蟲科、隱翅蟲科及象鼻蟲科量較多，其餘各科數量都不是很多。值得注意的是捕獲的鞘翅目昆蟲高達 59 個科別，較雙翅目的 35 科及膜翅目的 32 個科高出甚多(圖 5)。

三、各採集法捕獲之各目之優勢昆蟲科別

為判別各採集方法採得的各科昆蟲數量的優勢度(family dominance)，依 Engelmann (1978)的優勢度等級定義區分為 6 個等級，即真優勢(eudominant)為該物種個體數量佔群聚總個體數的 32.0~100%、優勢(dominant)為個體數量佔群聚的 10.0~31.9%、亞優勢(subdominant)為個體數量佔群聚的 3.2~ 9.9%、劣勢(recedent)為個體數量佔群聚的 1.0~3.1%、亞劣勢(subrecedent)為個體數量佔群聚的 0.32~0.99%、稀有(sporadic)為個體數量小於群聚總個體數的 0.32%。本研究各採集法，僅吊網的果蠅科(90.8%)具真優勢的特性，但果蠅科明顯是偶發性的結果，其它季節並未見如此多的果蠅；若不列入果蠅科，吊網的黑翅蕈蚋也具真優勢的特性(表 3)。優勢特性的昆蟲則見於馬氏網的蠓科(26.6%)及掃網的木蝨科(14.8%)及葉蟬科(12.8%)。而亞優勢的昆蟲則於各採集法都有不少，馬氏網的黑翅蕈蚋科、癭蚋科、隱翅蟲科及搖蚊科，吊網上有家蠅科、蟻科、蚊蚋科、、等 9 個科，掃網的常蚜科、釉小蜂科、舞虻科、廣腹細蜂科、縞蠅科、繭蜂科，噴霧法的管薊馬科、常蚜科、等 9 個科(表 3)。較特別的是採集數量最多的噴霧法並未有真優勢及優勢特性的科別，但是介於 3.2%~9.9%的亞優勢則高達 9 個科，可見噴霧法取樣方法各優勢科別豐度的捕獲特性與其他方法截然不同。

四、各採集法於 3 個樹種間捕獲昆蟲之各目、科及個體數量比較

樹冠掃網因僅掃 22 網，故所得昆蟲目別、科數及個體數量均少；噴霧方式(Fogging)取樣法得到最多的 15 目、146 科、7 千餘隻；吊網的數量雖然也達 5 千隻，但目級及科別的數量並不多，此為果蠅科有上萬隻所造成；馬氏網雖僅捕獲 300-1200 隻，但其科別數量達 90 個。若比較 3 個樹種間的捕獲情形，鳳梨吊網(HNT)的杏葉石礫除果蠅數量較少外，其目別及科級的組成特性與其他兩樹種類似；馬氏網誘集法在木荷上明顯較多，以長尾尖葉櫧最少(表 4)。因此噴霧法除外，各樹種均顯示，馬氏網取得最多的目別與科數，而吊網對果蠅科有特別的誘引能力。

五、三個樹種間各樹層掃網捕獲昆蟲之組成差異

多尺度空間分布分析顯示，掃網而來的昆蟲科級組成及數量在各樹種的樹冠層、冠下層及灌木層截然不同，顯示各樹種間的昆蟲組成差異小於各樹層間的變異(圖 6)。灌木層(紅色)昆蟲組成在 3 個樹種間雖也存有很大的變異，但仍與冠下層(綠色)及樹冠層(藍色)分開來；冠下層與樹冠層的昆蟲組成也顯然有差別，但兩樹層在樹種間各自較為相似。

針對木荷掃網所獲得之各科昆蟲個體數及轉換的生物量，進行樹冠層、冠下層及灌木層之多尺度空間(MDS)分析，也顯示這三個樹層結構捕獲的昆蟲有截然不同的組成，Stress 數值接近於 0，顯示區辨性很高（圖 7A）；其中灌木層 3 個採集點(紅色)有很大的歧異，各據一方，但仍與冠下層 3 個採集點(綠色)及樹冠層(黑色)離很遠，而冠下層及樹冠層組成則較近。將資料轉換成各科的累計生物量也顯示出類似的結果（圖 7B）。

六、各樹種不同取樣法的昆蟲數量及組成

木荷噴霧法所得的昆蟲數量及其經過轉換的生物量均遠多於其他採樣方法。噴霧法外，在 3 個樹種中，都以吊網法捕獲最多昆蟲，其次為馬氏網，樹冠層因僅掃 22 網量明顯低(圖 8)，杏葉石礫吊網因果蠅科數量少，故較其他兩個樹種少。以昆蟲各目數量來看，各樹種吊網上的雙翅目遠多於其餘各目(圖 9)，木荷的噴霧法雖也是雙翅目最多，但鞘翅目、膜翅目、半翅目數量也很多；馬氏網的捕獲特性較不一，於木荷上仍以雙翅目為主（圖 9A)，但杏葉石礫上則以鞘翅目捕獲最多（圖 9B）。

在木荷各樹層掃網組成上，常見目別的科級昆蟲組成具有不同的特性。灌木層有較多的雙翅目、膜翅目及鞘翅目，其中雙翅目的黑翅蕈蚋科、膜翅目的釉小蜂科及廣腹細蜂科、鞘翅目的隱翅蟲科及金花蟲科佔優勢；樹冠層則是半翅目最多，以木蝨科及葉蟬科為優勢。此外，膜翅目的釉小蜂科及鞘翅目的金花蟲科於冠下層及樹冠層數量也不少(圖 10)。

七、各樹種各樹層間掃網昆蟲多樣性指數分析

無論是 Shannon 或 Simple 多樣性分析都顯示，樹冠層掃網所得的昆蟲多樣性較低，灌木層最高，均勻度分析也顯示灌木層最低(圖 11)。此一結果與多數熱帶地區樹冠層有較高多樣性的結果相反，雪見地區處海拔 1800 公尺，屬溫帶特性的氣候環境或許是原因之一。Preisser and Smith (2009)應用馬氏網及吊燈陷阱調查溫帶地區森林昆蟲，即指出灌木層的昆蟲數量 8 倍於樹冠層之昆蟲。

八、各樹層間掃網昆蟲數量季節變動

3 樹種各季節掃網昆蟲的捕獲數量都顯示，灌木層有著較高的捕獲量(圖 12)，在 3 月份量最高，之後遞減，12 月份數量不一定最少。此結果與夏天溫度較高應有較高捕獲量的常理相反，可能與溫帶適應物種有關，因在 3 月大量羽化；圖 10 木荷的灌木層即顯示含有大量的黑翅蕈蚋、

癭蚋、縞蠅、隱翅蟲、釉小蜂等耐寒特性的昆蟲。樹冠層的昆蟲數量最少，但其與冠下層數量在各季節波動都不大，此兩層的昆蟲數量都在 12 月較少，6 月及 9 月居多。

九、各樹層捕獲昆蟲之食性組成分析

將各樹層各科昆蟲以食性功能特性分析，植食性為初級消費者，肉食性及寄生性為次級消費者，腐食性為包括植物性分解者及動物性分解者。因此，植食性初級消費者主要昆蟲為半翅目、鞘翅目及直翅類各科昆蟲；肉食性有脈翅目、雙翅目的虻科及蠓科、鞘翅目的步行蟲及瓢蟲，寄生性昆蟲以膜翅目為主；而彈尾目、嚙目、雙翅目多數的蚊蚋蠅為分解者主要組成。

先前分析已顯示各樹層的昆蟲數量及科別組成不一樣，因此將不同樹層的昆蟲食性功能組成各別分析探討。從個體數量組成來看，樹冠層以植食性的初級消費者居多，分解者最少(圖13)；而樹冠下層及森林底層的灌木層彼此有較相似的食性功能組成，即植食者較少，次級消費者與分解者數量較多且彼此相當。此結果顯示不同樹層的微環境可能對昆蟲的食性功能組成有影響，樹冠層為枝葉茂密的棲所，提供較多的食物給初級消費者，其流通光亮的棲所特性也不適合喜陰暗潮濕的分解者棲息；而灌木層位森林底層，其陰暗潮濕的微環境與樹冠層截然不同。

唐等(2002, 2008)針對雪見地區昆蟲相之調查研究，與本研究同採馬氏網調查方法，但其陷阱位於森林地表的灌木層，並非離地 20 餘公尺高的樹冠層；因此，其等發現 16 個目之昆蟲，與本研究 17 個目相當，可能已反應出雪見地區目級昆蟲的最大數量；Preisser and Smith (1998)應用馬氏網的調查曾指出，樹冠層與灌木層的昆蟲數量及組成截然不同。徐等(2010)曾調查中海拔觀霧地區的樹冠層昆蟲，其針對鱗翅目採用的採剪法與抖落法與本研究取樣法不同，不適合比較其間異同。傅等(2011)於雪見地區用吊網、套網收集樹冠上的昆蟲，共採得 9 目 528 隻昆蟲，明顯少於本研究結果，但該報告也指出雙翅目佔最多，約有 81%；傅等人的研究也指出有偶發性的大量無螫蜂出現，本研究 6 月吊網果蠅科達 10000 多隻亦屬偶發特性。Rinker et al. (2001)指出，從森林底層到樹冠層、不同地區的樹冠層、各類取食功能群等等與樹冠層有關的研究，若採集方法及研究目的不一致，難以有效比較分析其間異同。

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表 1. 昆蟲各目體長資料的生物量轉換(Gruner 2003))。

Taxon \ Parameter	a	b
Blattodea	0.0313	2.385
Orthoptera	0.0180	2.720
Psocoptera	0.0136	3.115
Coleoptera	0.0336	2.347
Hemiptera	0.0441	1.934
Homoptera	0.0234	2.536
Lepidoptera	0.0271	1.769
Hymenoptera	0.0139	2.383
Diptera	0.0153	2.573
Collembola	0.0056	2.809
Neuroptera	0.0070	2.739
Tricoptera	0.0179	2.318
Thysanoptera	0.0139	2.383

* Weight= a × $Length^b$; W= mg , L: mm。

表 2. 各採集法採得的各目昆蟲個體及科別數量

Order	目名	MLT	SWP	HNT	Fogging	Total
Hemiptera	半翅目	168	54	9	1187	1418
Diptera	雙翅目	1365	31	12446	1979	15821
Hymenoptera	膜翅目	262	35	152	1474	1923
Coleoptera	鞘翅目	362	9	80	1599	2050
Orthoptera	直翅目	1	1	0	40	42
Dermaptera	革翅目	0	0	0	57	57
Neuroptera	脈翅目	11	5	2	44	62
Blattaria	蜚蠊目	0	0	0	18	18
Collembola	彈尾目	38	0	0	17	55
Phasmida	竹節蟲目	0	0	0	1	1
Psocoptera	嚙蟲目	41	5	1	213	260
Thysanoptera	纓翅目	37	4	1	856	898
Lepidoptera	鱗翅目	60	4	88	81	233
Mantodea	螳螂目				2	2
Siphonaptera	蚤目				1	1
Total		2345	148	12779	7569	

表 3. 各採集法捕獲之各目優勢昆蟲科別及百分比

	MLT	SWP	HNT	Fogging
真優勢			黑翅蕈蚋(32.4%)	
優勢	蠓(26.6%)	木蝨(14.8%)		
		葉蟬(12.8%)		
亞優勢	黑翅蕈蚋(9%)	常蚜(8.1%)	家蠅(8.3%)	管薊馬(8.4%)
	癭蚋(7.3%)	釉小蜂(6.7%)	螞蟻(6.2%)	常蚜(7.3%)
	隱翅蟲(5.7%)	舞虻(6.1%)	蚊蚋(6%)	搖蚊(5.1%)
	搖蚊(5.4%)	廣腹細蜂(4.1%)	黃潛蠅 (5.4%)	金花蟲(4.9%)
		縞蠅(3.4%)	蕈蚋(5.4%)	釉小蜂(4.7%)
		繭蜂(3.4%)	出尾蟲(5.4%)	黑翅蕈蚋(4.4%)
				隱翅蟲(4.1%)
				象鼻蟲(4%)
				舞虻(3.6%)

HNT(吊網)為果蠅科去除後的相對百分比。

表 4 各採集法於 3 個樹種間捕獲昆蟲之各目、科及個體數量

	MLT			SWP			HNT			Fogging		
	目	科	個數	目	科	個數	目	科	個數	目	科	個數
木荷(SS)	10	89	1284	8	13	44	6	32	5405	15	146	7569
長尾尖葉櫧(CC)	9	56	307	7	24	65	6	38	6094			
杏葉石礫(LA)	9	74	754	8	17	39	6	32	1280			

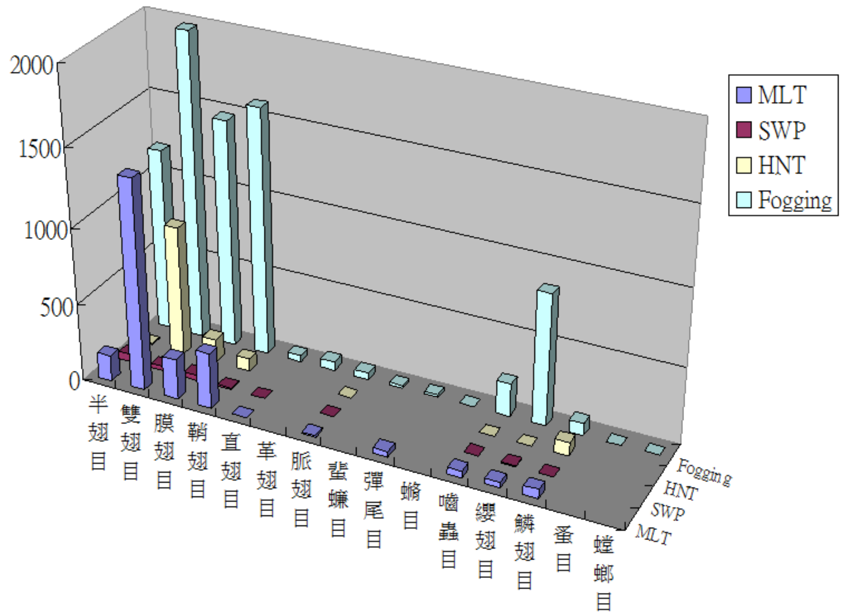


圖 1. 馬氏網(MLT)、掃網(SWP)、吊網(HNT)及噴霧法(Fogging)捕獲的各目昆蟲數量分布。

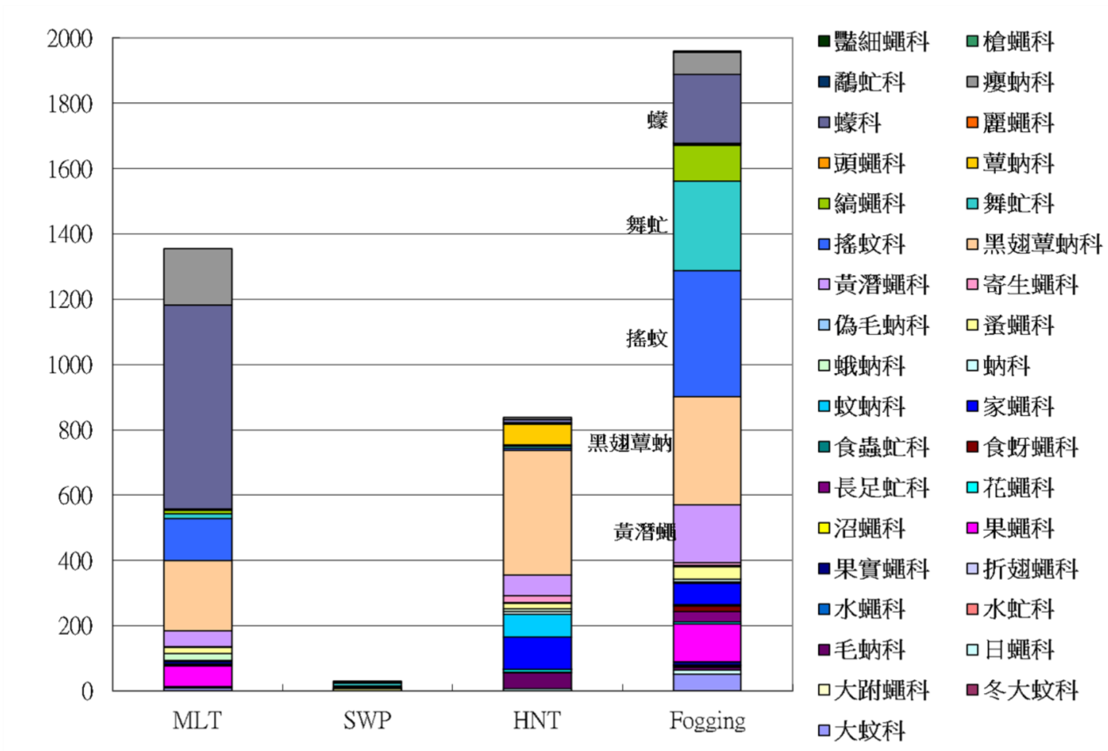


圖 2. 馬氏網(MLT)、掃網(SWP)、吊網(HNT)及噴霧法(Fogging)捕獲的雙翅目各科昆蟲相對數量，主要科別標示於圖上。

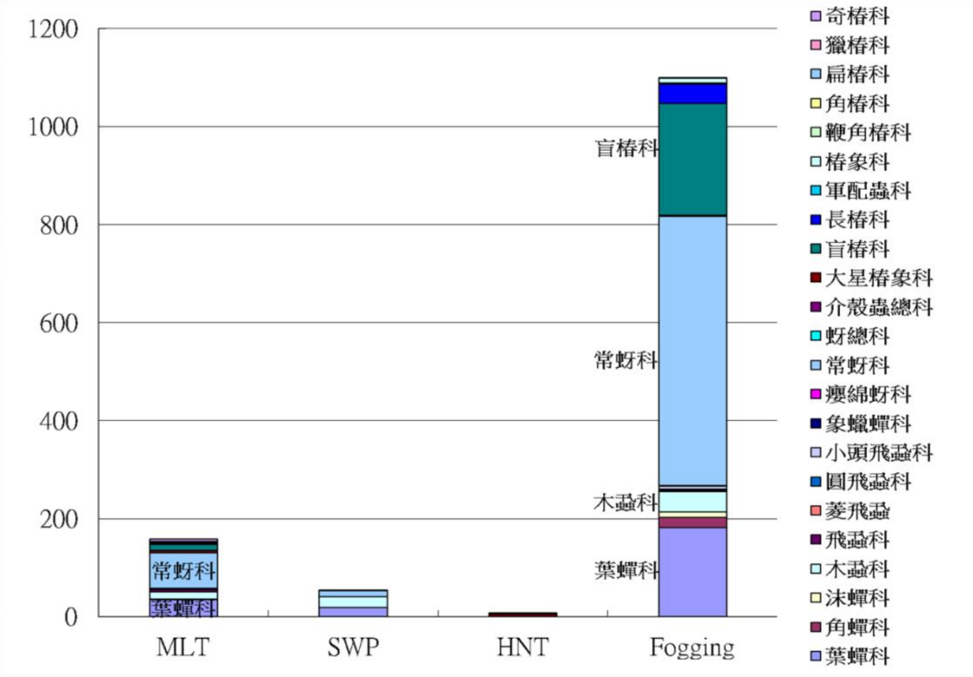


圖 3. 馬氏網(MLT)、掃網(SWP)、吊網(HNT)及噴霧法(Fogging)捕獲的半翅目各科昆蟲相對數量，主要科別標示於圖上。

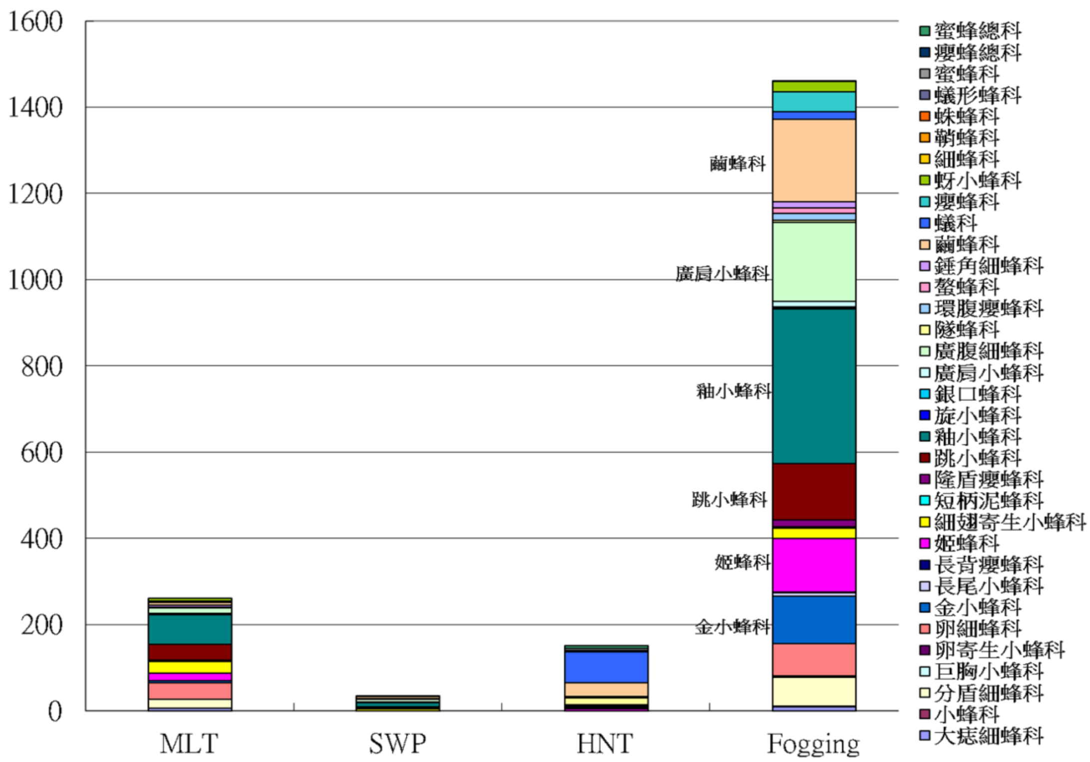


圖 4. 馬氏網(MLT)、掃網(SWP)、吊網(HNT)及噴霧法(Fogging)捕獲的膜翅目各科昆蟲相對數量，主要科別標示於圖上。

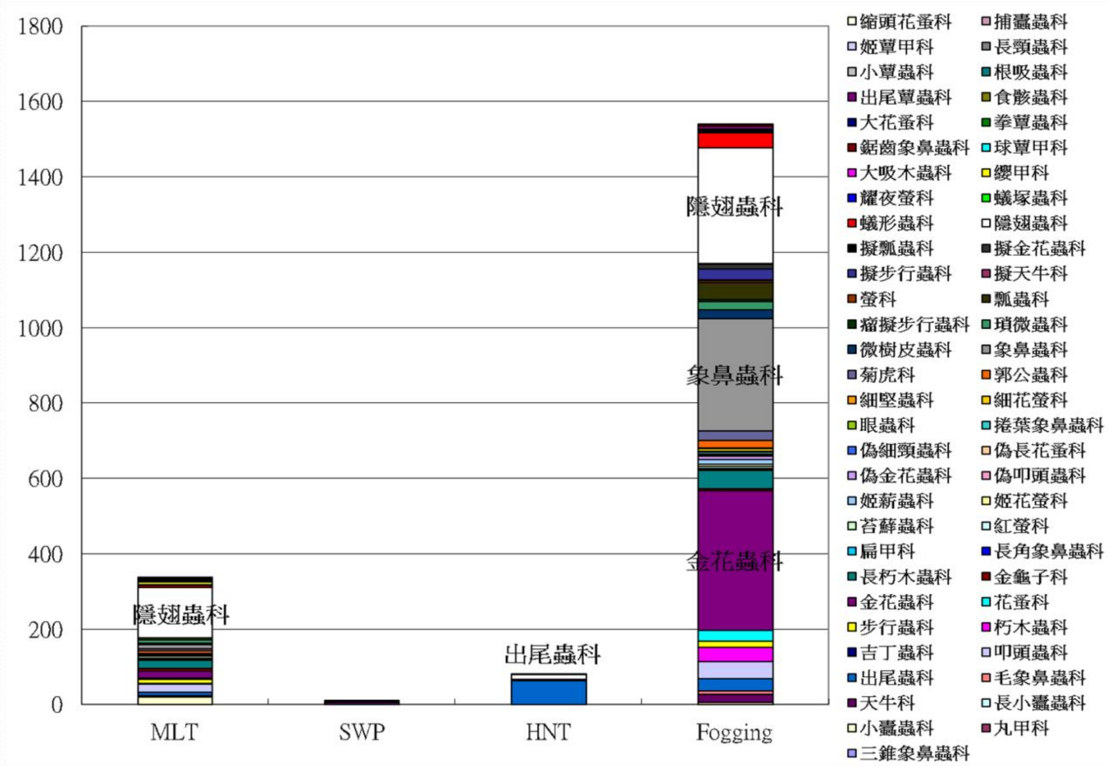


圖 5. 馬氏網(MLT)、掃網(SWP)、吊網(HNT)及噴霧法(Fogging)捕獲的鞘翅目各科昆蟲相對數量，主要科別標示於圖上。

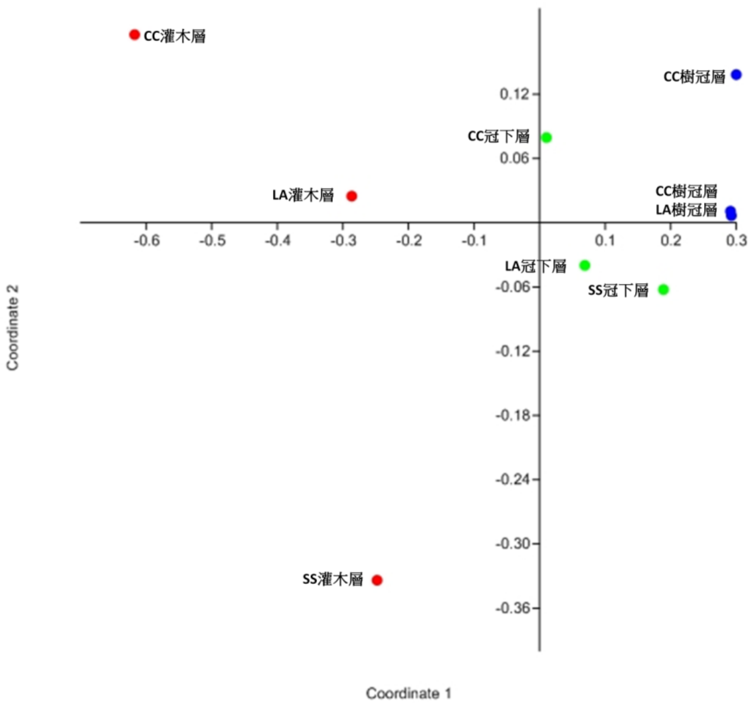


圖 6. 三個樹種間灌木層(左邊 3 紅色點)、冠下層(中間 3 綠色點)及樹冠層(右邊 3 藍色點)各科昆蟲數量之多尺度空間(MDS)分析。

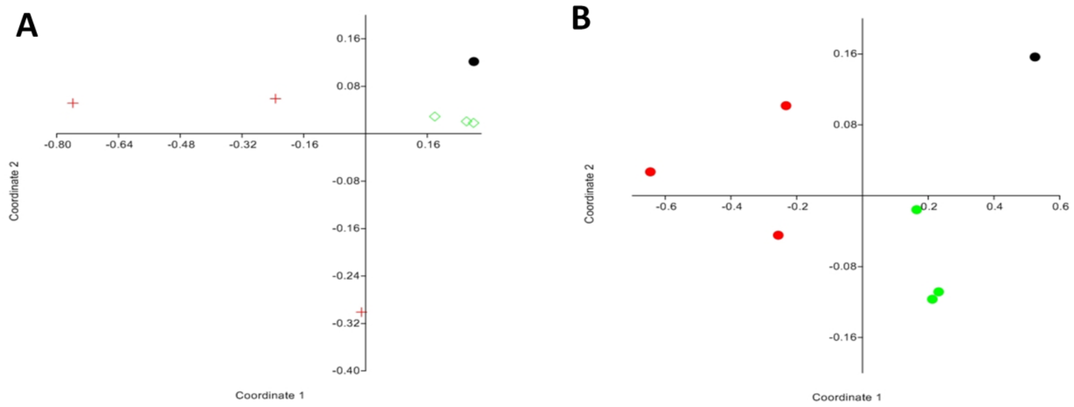
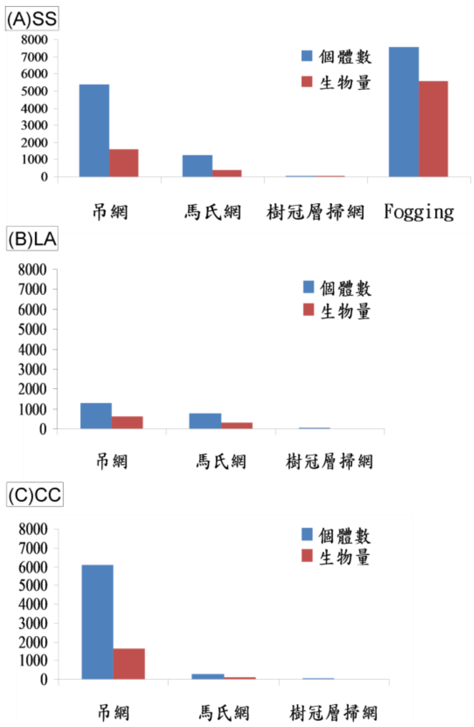


圖 7. 木荷灌木層(紅色”+”)、樹冠下層(綠色”◇”)及樹冠層(黑色”●”)各科昆蟲數量之多尺度空間(MDS)分析結果(A)。木荷灌木層(左邊 3 紅色點)、冠下層(第 IV 象限綠色點)及樹冠層(第一象限黑色點)各科昆蟲數量轉換為生物量之多尺度空間(MDS)分析結果。



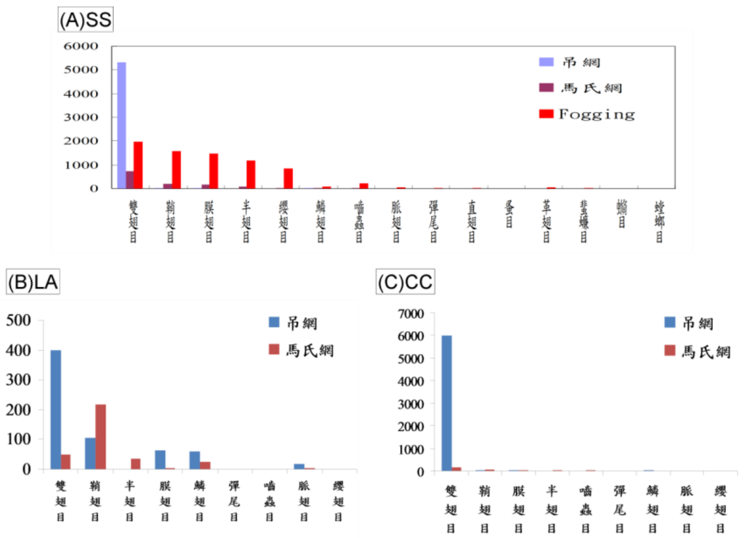


圖 8(上左). 木荷(SS)、杏葉石櫟(LA)、長尾尖葉櫧(CC)的吊網、馬氏網、掃網法及噴霧法，於樹冠層昆蟲的捕獲數量及轉換的生物量結果。

圖 9(上右). 木荷(SS)、杏葉石櫟(LA)、長尾尖葉櫧(CC)的吊網、馬氏網、掃網法及噴霧法，於樹冠層各目昆蟲的捕獲數量及轉換的生物量之結果。

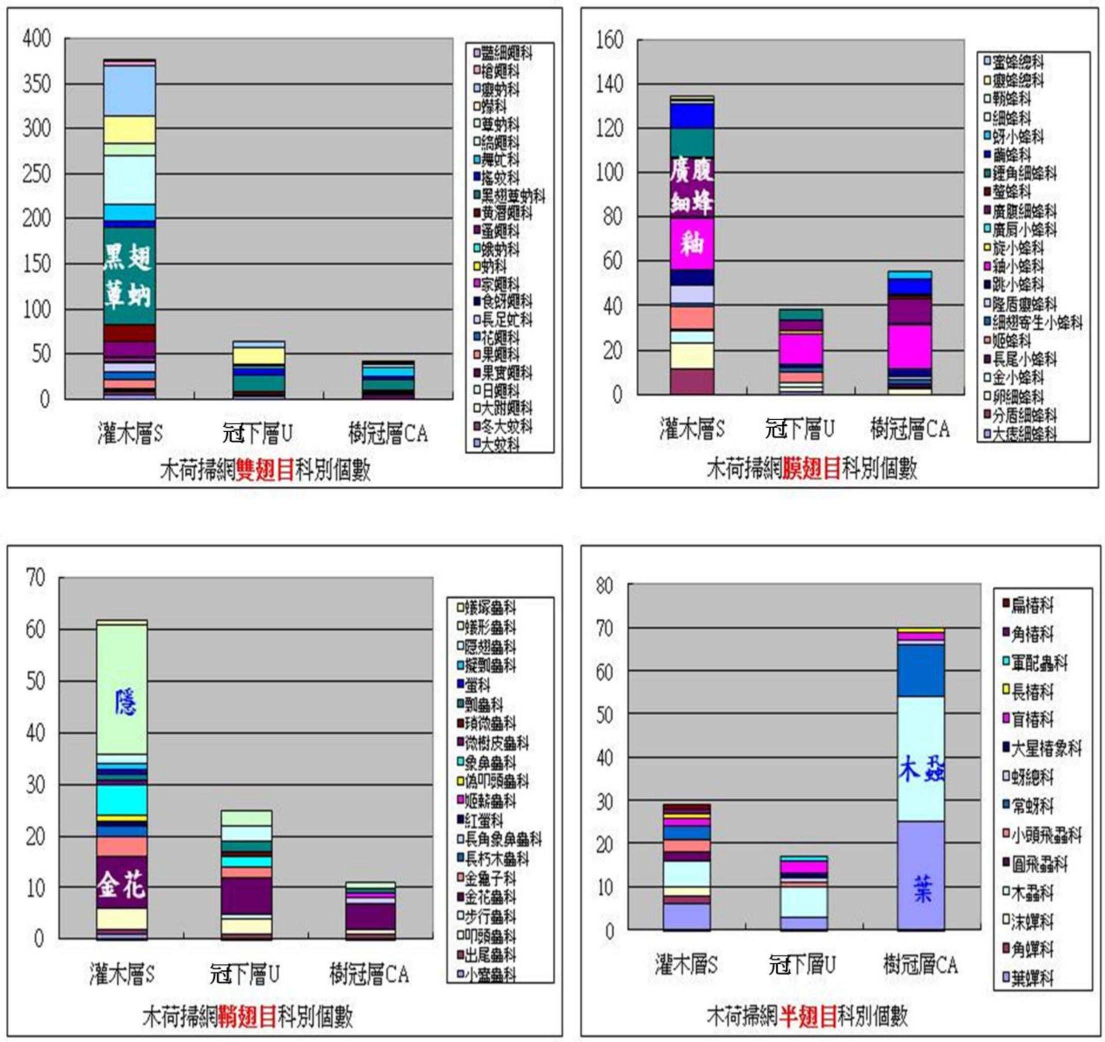


圖 10. 木荷掃網法於灌木層(S)、冠下層(U)及樹冠層(CA)捕獲優勢目別昆蟲(雙翅目、膜翅目、鞘翅目及半翅目)的各科昆蟲相對數量，主要科別標示於圖上。

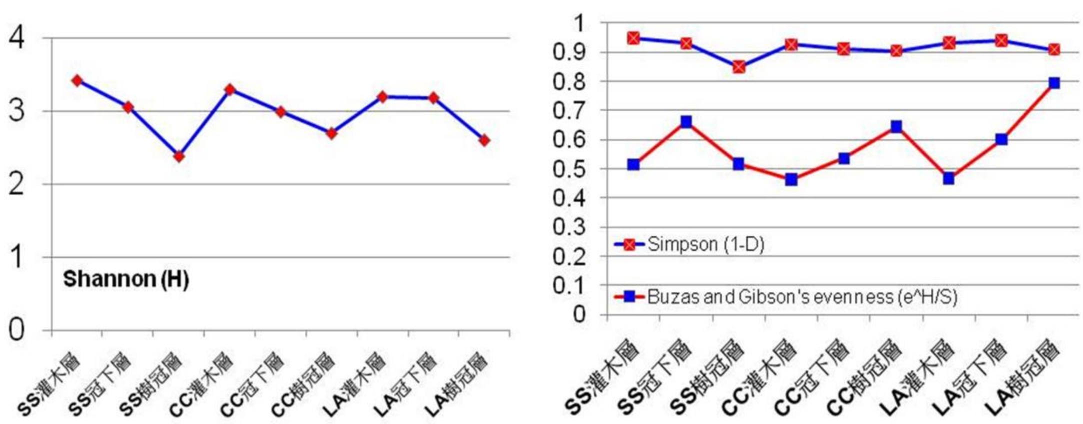


圖 11. 木荷(SS)、長尾尖葉櫧(CC)、杏葉石櫟(LA)之灌木層、冠下層及樹冠層各樹層掃網的昆蟲多樣性指數(Shannon and Simpson)及均勻度(evenness)比較。

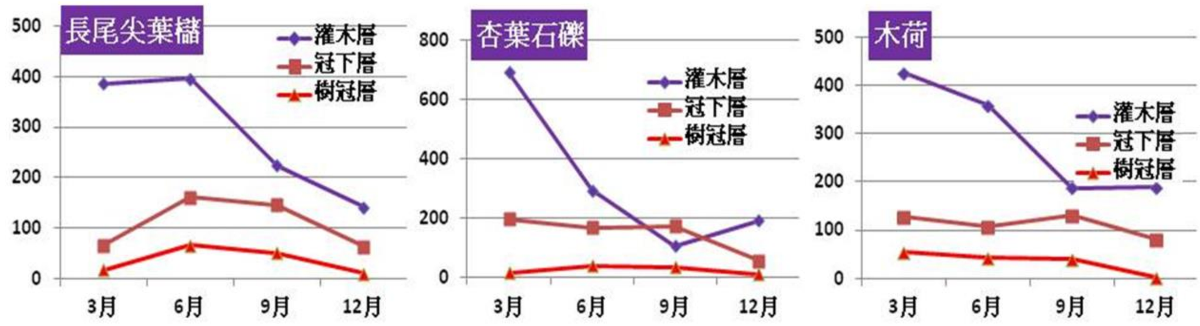


圖 12. 長尾尖葉櫧、杏葉石櫟、木荷之灌木層、冠下層及樹冠層各樹層掃網的昆蟲數量於個季節間的變動比較。

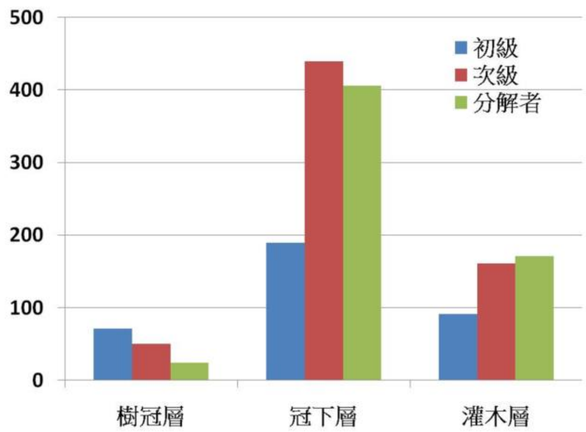


圖 13. 樹冠層、冠下層及灌木層各樹層掃網捕獲昆蟲之食性組成分析。

Fogging a Subtropical Forest of Central Taiwan: a Study of Arboreal Beetle Assemblages and Recolonization

臺灣中部亞熱帶森林噴霧採集：探討樹棲步行蟲群聚與再拓殖

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www.entomol.nchu.edu.tw/dept/teachers/mmyang/teacher.htm

摘要

瞭解本地及全球生物多樣性的渴望，已在世界各地催生並致力於達成此目標。臺灣是生物多樣性倡議的積極參與者，例如臺灣生物多樣性資訊入口網(TaiBIF)、臺灣物種名錄(TaiBNET)、臺灣生命大百科(TaiEOL)、臺灣生命條碼(TaiBOL)等。而這些規劃的其中一個主要元素就是各標本館的標本蒐藏，這些蒐藏提供生物多樣性可從中被檢視、比較、描述及瞭解的材料。由於昆蟲種數佔了現今生物種數的半數以上，所以其蒐藏更顯得重要。但不幸的，相較於本地的多樣性，臺灣的昆蟲標本蒐藏明顯不足，而且在過去保存較不易，這對任何想研究當地昆蟲相的研究者具有相當的困難性，且此問題不僅限於本地、更是整個東方區、甚至世界亞熱帶地區的問題。以步行蟲為例，臺灣目前蒐藏量非常不足，檢視主要的標本館之步行蟲標本，蒐藏的個體僅數千件，而所包含的物種遠少於已定名之 476 種的一半。我們在臺灣中部的山區(惠蓀林場) 嘗試藉由噴霧採集法達到快速增加臺灣節肢動物蒐藏量的目標，透過這項技術對於環境不會造成長期影響，也是目前廣泛認為最有效、快速的無脊椎動物採集法。此項研究將對於臺灣樹冠層之生物多樣性提供初步瞭解，為未來較大尺度的樹冠層研究調查建立重要基礎資料，並提供不同領域學者之合作交流平臺。我們的初步探討的目標涵蓋：瞭解來自多棵樹種在兩個不同海拔高度(600 與 2000 公尺)的甲蟲在屬級的季節分布；檢視藉由樹冠噴霧法在臺灣中部地區所採集的步行蟲物種；以及進一步檢視當無脊椎動物從一棵樹清除後，甲蟲再拓殖的潛在季節性差異。

Abstract

The desire to know our local and global biodiversity has spawned initiatives worldwide that are aimed towards fulfilling this goal. Taiwan is an active participant in biodiversity initiatives such as TaiBIF, TaiBNET, TaiEOL and TaiBOL. One major component of projects like these are museum collections. These collections provide the material from which biodiversity can be examined,

compared, described and understood. Because insects make up over half of the currently known diversity, their collections are of particular importance. Unfortunately, insect collections in Taiwan are insufficient in comparison to its diversity and have, in the past, been difficult to maintain. This can be very problematic for anyone wishing to study the insect fauna here. This is not only a problem at the local level but also for entire Oriental region, as well as, subtropical areas worldwide. Ground beetles (Coleoptera: Carabidae), for example, are very poorly represented in collections. There are no more than a few thousand individuals, representing less than half of the currently recognized 476 species in the major collections around Taiwan. We aim to work towards this goal through rapidly increasing arthropod collections in Taiwan by means of insecticidal fogging in the central mountain area (Hui-sun Forest Area). This technique is ideal because it is considered to have no long-term environmental impact and it now widely considered the most efficient and rapid arthropod collecting technique. This project will provide an important first look into the diverse canopy fauna of Taiwan. In addition, it will provide base data for future large-scale canopy projects and a platform for collaboration with workers from many fields. Initial projects that will result from this canopy fogging includes: an examination of the seasonal distribution of Coleopteran genera collected from several trees species at two altitudes (600 and 2000m); an examination of carabid species collected from fogging in central Taiwan; and a look into the potential seasonal differences in beetle recolonization into trees recently cleared of invertebrate fauna.

Introduction

The desire to understand our local and global biodiversity has spawned initiatives worldwide. Taiwan is an active participant in biodiversity initiatives such as TaiBIF, TaiBNET, TaiEOL and TaiBOL. One major component of projects like these are museum collections. These collections provide the material from which biodiversity can be examined, compared, described and understood. Because insects make up over half of the currently known terrestrial biodiversity, their collections are of particular importance. Unfortunately, insect collections in Taiwan are insufficient in comparison to its diversity and have, in the past, been difficult to maintain. This can be very problematic for anyone wishing to study the insect fauna here. In fact, working insect collections are not only a problem at the local level but also for the entire Oriental region, as well as, subtropical areas worldwide. Ground beetles (Coleoptera: Carabidae), for example, are very poorly represented in collections. There are no more than a few thousand individual specimens, representing less than half of the currently recognized 476 species in the major collections around Taiwan. We aim to rapidly expand the arthropod collections in Taiwan with the use of insecticidal fogging in the central mountain area (Hui-sun Forest Area). This technique is ideal as it is considered to have no long-term environmental impact and it now widely considered the most efficient and rapid arthropod collecting technique. This project will provide an important first look into the diverse canopy fauna of Taiwan. In addition, it will provide base data for future large-scale canopy projects and a platform for collaboration with workers from many fields. Initial projects that will result from this canopy fogging include: an examination of the seasonal distribution of Coleopteran genera collected from several trees species at two altitudes (600 and 2000m); an examination of carabid species collected from fogging in central Taiwan; and a look into the potential seasonal differences in beetle recolonization into trees recently cleared of invertebrate fauna.

Canopy sampling

Effective sampling of canopy dwelling arthropods has been studied, tested, and refined over the past ~30 years. By far, the most effective and important of these methods is insecticidal knockdown, commonly known as "fogging" or "misting". Canopy fogging is a collection method in which an insecticidal "fog" is released into the air column below the canopy of a specific tree. The chemicals rise up into the canopy where they paralyze and knockdown the insects onto a sheet or funnels to be collected and preserved. Fogging is now widely considered a very useful tool for expediting the understanding of species richness and diversity. It is also a valuable tool for collecting cryptic, unique and rare species which only dwell in canopies and are not easily collected by hand or alternative methods.

Over the past several decades, the environmental impact of canopy fogging has also been well studied and continuously improved upon. Today, the chemicals utilized for insecticidal knockdown are typically natural botanical pesticides such as pyrethrins. Pyrethrins are known to be safe for vertebrates, breakdown quickly in nature and do not accumulate in the environment.

Procedure

To gain a more robust understanding of the canopy fauna of Taiwan we are currently sampling insects from two altitudes (600, 2000m). This will allow for comparisons of altitudinal preferences of taxa to be made. At each altitude, trees will be sampled 12 times per year to help determine the seasonality of the canopy inhabiting taxa. As well, select trees are being sampled shortly after fogging events (15 and 30 days) to develop a better understanding of arthropod recolonization after zero population has been attained. At each altitude, two trees that were common in the area and did not have canopies that overlapped with other trees, were selected (Fig. 1).

Shortly before each fogging event, tarps are set out under the entire canopy of the candidate tree (Fig. 2). All tarps are set out just prior to the fogging event to avoid condensation build-up that can make collection more difficult. Tarps are raised along their sides with wooden steaks to stop fallen insects from escaping, and as well, stop terrestrial fauna from coming onto the tarps. Each fogging event takes place in the early evening hours between 19:00-20:00 and when the air is still. This allowed the fog to rise straight up into the canopy air column of the selected tree only. For each fogging event, an ultra low volume (U. V. L.) fogging machine was used with a natural pyrethrin insecticide. The fogger is started (Fig. 3) and runs for at least 10 minutes per tree to ensure an even and complete fogging of the entire canopy. After fogging has taken place, insects are allowed to fall from the canopy for 3 hours before collecting the specimens from the tarps. Insects are then collected from the tarps (Fig. 4) using soft paintbrushes, placed into labeled jars of 70% alcohol and transported back to the lab for sorting.

After each fogging event, collected material is sorted (Fig. 5) to insect order. All beetles (Coleoptera) are separated for identification to family and morphospecies. All of the ground beetles (Carabidae) collected from this study will be examined, identified, and new species will be described. All additional material will be labeled and databased with all pertinent data, placed into vials of alcohol and refrigerated until it can be examined further.

Ground beetles in Taiwan

Ground beetles play an important role in the forest ecosystems they inhabit. They are numerous in species and often high in numbers, providing both a major food source for other forest fauna, and as well, contributing to ecosystem stability as generalist predators. In areas where carabid assemblages are taxonomically well known, they can be used effectively in biodiversity studies and to develop conservation measures. For these reasons, accurate and up-to-date taxonomic knowledge of this beetle family is extremely desirable. Unfortunately, over the past 130 years, few workers have studied the ground-beetle fauna of Taiwan. The latest checklist of Carabidae from Taiwan indicates that a total of 467 taxa belonging to 34 tribes. An examination of the major insect holdings in Taiwan has revealed that the carabid fauna (and many other arthropod groups) are poorly represented in Taiwan's collections. The majority of ground-beetle specimens that are currently in these collections were collected by means of pit-fall trapping or hand collecting. Historically, these have been the most common methods of collecting but it is now known that these techniques do not effectively sample insects dwelling in trees. Because of this, it can be assumed that the total ground-beetle fauna of Taiwan is underrepresented and potentially much larger than previously thought. With this major gap in knowledge realized, it became clear to us that steps should be taken to properly sample this untouched biotic frontier.

Preliminary findings

The first seasonal samples for this project were taken in late August and early September of 2013. Sorting and processing the thousands of individual insects is very time consuming and laborious. In fact, it takes hundreds of hours to sort and organize the beetles from just one fogging event! This must be done before pinning, labeling, dissection and identification can take place. Due to the time investment required, we are still in the early stages. So far, all members of the ground-beetle family (Carabidae) have been sorted, processed, and identified. In terms of this group, some interesting preliminary observations have been made. A total of 520 carabid beetle specimens were collected during the winter and autumn sampling period. There were representatives from 6 tribes, 25 genera, and 37 morphospecies. The most speciose tribes were Lebiini (23 morphospecies) and Platynini (10 morphospecies). These two tribes were also the most numerous in individual specimens, which could be expected as both groups are known to have members that are arboreal or semi-arboreal in nature. Interestingly, a few individuals were also collected from tribes (Scaritini and Chlaenini) that are considered to be primarily ground dwelling. Apparently, these species are using the trees but in what capacity still remains unclear.

So far, higher diversity (~65%) has been recorded at the lower altitude (600m) than the higher altitude (2000m). This is what we would expect to see and believe that this trend will continue across the seasons. As well, after identifying all species it has become apparent that at least 6 of the carabid species (~15%) are either new records for Taiwan or new to science. This is perhaps a little lower than we had anticipated however, of the 37 species collected, 9 of the identified species are both very uncommon in collections (Fig. 6) and were collected in numbers ranging from 5 to 25 individuals with the aid of insecticidal fogging.

We believe it is clear that the material collected from this project will help us develop a better understanding the canopy fauna of Taiwan's forest systems. It will also greatly expand our knowledge of the underrepresented Oriental and subtropical faunas. As this portion of the fauna becomes more well known, we will have the ability to draw comparisons among other biodiversity systems and a more clear picture of Taiwan's total canopy arthropod diversity will emerge

Support

We are thankful to the National Science Council of Taiwan, Dr. Nan-Jang Lo, The Experimental Forest Management Office of NCHU and the members of Systematics and Evolution laboratory, National Chung Hsing University, for their cooperation and continued support.
This project is funded by NSC grant # 102-2621-B-005-001



Fig 1 (left). High elevation (2000m) candidate tree for fogging, *Neolitsea variabillima* (Hayata).

Fig 2 (middle). Ground tarps are set-up before each fogging event.

Fig 3 (right). Insecticidal "fog" rising up into canopy.



Fig 4 (left). Insect material being swept and placed into alcohol for transport back to laboratory.

Fig 5 (middle). Insect material being sorted and organized.

Fig 6 (right). Twenty-nine specimens of uncommon ground beetle (Coleoptera: Carabidae) *Horniulus andrewesi* Jedlicka, 1932, captured with insecticidal fogging.

Construction of Canopy Access Systems

淺談樹冠層走道的設置

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Research in the canopies of forests (Lowman and Wittman 1996) around the world has been limited by the logistical constraints safe and easy access. Of the many methods used to gain access to field sites only a few allow several people to be in close proximity in the canopy for significant periods of time. Observation platforms and canopy bridges are used to overcome these limitations but the design in cost of such structures often exceed research budgets. Compared to suspension bridges the canopy bridges discussed here are lighter and easier to construct and install can be placed higher in the canopy. Walkways can also be integral to forest conservation by creating local income streams through ecotourism (Lowman 2009).

Walkway systems

One of the first things to be decided is how long will the system be in use? There are two main ways of attaching bridges and platforms to trees. One is to encircle the tree with cables (Fig. 1) and the other is to use bolts and penetrate the tree (Fig. 2). The entire tree health and growth issue can be minimized if the budget allows for the construction of towers. However even with a tower the placement with respect to nearby trees roots can be an issue.

If the system is to be temporary, i.e. less than 1 or 2 years, then girdling the tree is the preferred method. This may be in response to a short-term research project, the need to move to another site or even a special event (conference or symposium).

The primary reason is that the tree won't grow much in this short period of time and thus won't be significantly affected by the increased pressure caused by the girdle (or more appropriately the offset blocks used to keep the girdling cables from strangling the tree). Then at the end of the project the girdling cables can be removed without any remaining issues affecting the tree's future health. To use girdling cables for a longer time the owner must relocate the offset blocks to new positions on a yearly basis. Since this is tantamount to rebuilding the bridges this necessary maintenance is rarely if ever done. This leads to the poor health and early decay of the tree thus limiting the useful life of the canopy access system.

If the system is to be permanent, i.e. more than a few years, then bolting is the preferred method of attachment. The main reasons for a permanent canopy access system are long term research (decades are possible), ecotourism or a combination of both.

When thinking about drilling into a tree to use galvanized bolts, most people erroneously think of a similar hole in their body when considering the potential damage to the tree. However most of a tree trunk (and the large branches) is simply structural support and not living. The cambium layer just under the bark is indeed damaged, but the wound is then snuggly fit with a galvanized bolt. The tree responds as it does to any similar natural wound and begins to heal and seal around the bolt (Fig. 2). If the bolts are properly installed the tree eventually will totally encase them. This is simply addressed by added some type of extension to the bolt, such as a rapid link or shackle.

It is important to look at articles in peer reviewed publications when determining best methods to attach hardware to trees. The ANSI (American National Standards Institute) and ISA (International Society of Arboriculture) standards are based on industrial testing and research on the physiology of trees. Specifically ANSI A300 part 3 - Supplemental Support Systems refers to drilling holes for lags or through bolts and specifically forbid "girdling the trunk, limb or branch”. ISA also has many publications regarding tree climbing, tree health, pruning techniques, cabling and bracing and safety backed by decades of bracing and guying using bolts.

A canopy access system typically incorporates some combination of platforms, bridges and a means of access (Lowman and Bouricius 1995). A canopy bridge as discussed here consists of an overhead user safety cable, two handrail (backup) cables and two more in the treadway. The treadway consists of short wooden planks laid orthogonal to and on top of the supporting cables evenly distributed along the entire length. These planks (treads) and attached directly to support cables using galvanized bolts, bar washers and nuts. Even few feet a 3/16 inch stainless steel aircraft cable is used to connect the treadway support cables to the 3/8 inch SS aircraft cable handrails. The verticals are all the same length and this allows the cables of the treadway to hang freely and assume the mathematical shape known as a catenary curve. The ends of the cables are attached to tree trunks or large branches with eyebolts and other hardware. These trees are also stabilized with guy cables attached to some type of ground anchor.

This bridge design requires users to wear a climbing harness and to be tethered to the overhead safety cable. This makes the system less expensive but typically not user friendly enough for a high throughput of users. The addition of side netting (included in the $300 per foot cost) removes the need for a harness and the overhead cable as well.

Design considerations

Why choose a cable support bridge or suspension bridge? In a cable support bridge the load bearing cables are underneath treadway allowing for higher placement in the tree. This means the treadway must follow the catenary curve (Fig. 3) and thus always has a sag associated with it. In a suspension bridge the load bearing cables are above the treadway and over your head at each end of the bridge. This means that the treadway must be lower in the tree to ensure a strong end attachment. However by varying the length of the vertical support cables the treadway can actually be level.

Prior to the design phase an onsite survey visit must be made so appropriate trees can be selected and accurate measurements can be made in and between the trees. This typically requires two experienced climbers with at least one ground support person and can take 2 to 4 full days depending on the number tree selected, their location, height, architecture and so on. Trees are climbed to measure the diameter of the trunk and branches at platform height, identify support branches (distance, angle and size) and measure the distance between the trees in the canopy. Additionally local sources of appropriate materials can be located and investigated during this visit as well.

To design and construct a walkway one must know the attributes of all materials use such as the tensile strength of the cables and the weights of all component parts. For our treadways we prescribe a safety factor of 5:1 (WRTB 1993) or higher. To achieve the safety factor the tension on cables must be either measured or calculated. To permit easy negotiation the slope of the treadway should not be too large i.e., less than 25 degrees from the horizontal at any place on the treadway. The first choice for supporting cables is 3/8 inch stainless steel aircraft cable; however calculations may reveal the required safety factor cannot be met or the angles at the ends of the treadway are too great. In this case, a higher tensile strength (thicker) support cable must be used. Different choices for the other attachment hardware, including eyebolts, cable clamps, thimbles, turnbuckles, etc. will be required. Perhaps different trees or building towers might become necessary. Once the final specifications are determined, a complete system is designed and the construction cost determined. Upon approval all materials are ordered and transported to the site. Once all materials are on site, the construction crew arrives with the tools needed to start the project. Then the construction of the canopy access system begins without material related delays, but still dependent upon local weather conditions.

Construction considerations

Designing a specific catenary curve requires two parameters, one of which is the horizontal distance between the two ends, defined as the span (Bouricius et al. 2002) and the other is the live load desired. The most practical way to ensure during construction that a treadway meets its design specification is to measure the sag in the treadway cables while unloaded. A line of sight method using a portable laser level works well. The sag can be set during the construction by varying the length of the support cables. This is accomplished by adjusting the cables through cable clamps and the eyebolts bolts at one end of the treadway. The use of turnbuckles can also be used at one end of the treadway cables to facilitate final adjustments of the sag.

The means of entering the canopy access system is driven by cost and the type of user. Towers with stairs are the most user-friendly but also the most costly. Other means in order of decreasing expense but increasing effort of getting to the canopy include climbing ladders bolted to the tree trunk, being pulled up in a block and tackle using a bosun's chair, or even climbing a rope. Sometimes the location of the canopy access system presents the option of using the topography of a ridge and access is possible by simply connecting the first platform to the ground on the side of a hill or cliff.

Cost estimates

An on-site survey visit cost ranges from $2000 to $6000 and plus travel expenses, which are highly variable depending on the country and the location within the country. Due to the custom nature and size of each canopy project, access and location costs are highly variable and time dependent. The most expensive scenario is a client who simply wants to have a complete system built without any interaction on their part. A cost estimate then must include all travel, room and board, labor, customs fees, transportation costs and materials cost. Estimates are $300 per foot of completed treadway; platforms range from $2000 to $10,000 depending on size and complexity; towers with stairs are roughly $10,000 dollars for every 10 feet in height. These costs are negotiable with input and help from the client, who is also typically able to provide room and board, local laborers and appropriate locally available materials, especially the lumber.

Ongoing Maintenance

After the construction phase has been completed there is a need for training of the local staff that will be responsible for the day to day operation of the canopy access system. This not only includes climbing techniques, but also what to look for in the health of the trees (including adjacent trees that could potential fall onto the bridges, platforms or guy cables).

Additionally an ongoing inspection and maintenance program must be in place in order to maximize the useful life of the canopy access system. It is important to check the tightness of bolts and clamps especially in the first several years as lumber dries and the structure responds to the weather, specifically wind, rain and sun. It is recommended that an outside consultant (not an employee of the system owner) perform at least an annual inspection.

Over time the trees will grow and some deck boards may need to be trimmed to keep from impacting the tree's growth. Some treads and other wooden members will need to be replaced due to rot, insect attack or animal chewing damage. Depending upon the environmental conditions the lumber may also need periodic sealing or painting.

As the platform trees and adjacent trees age some branches will naturally die and need to be pruned to facilitate the tree's healing process. This also eliminates any potential damage to the system as well as minimizing the threat to users of being struck by a falling dead branch. Lianas also need to monitored to ensure that they do not have a significant impact on the health of system trees.

In summary every canopy access system needs routine maintenance just like any other structure and this should be included within the planning budget.

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Fig 1. Girdling with offset blocks

Fig 2. An eyebolt being overgrown by the tree

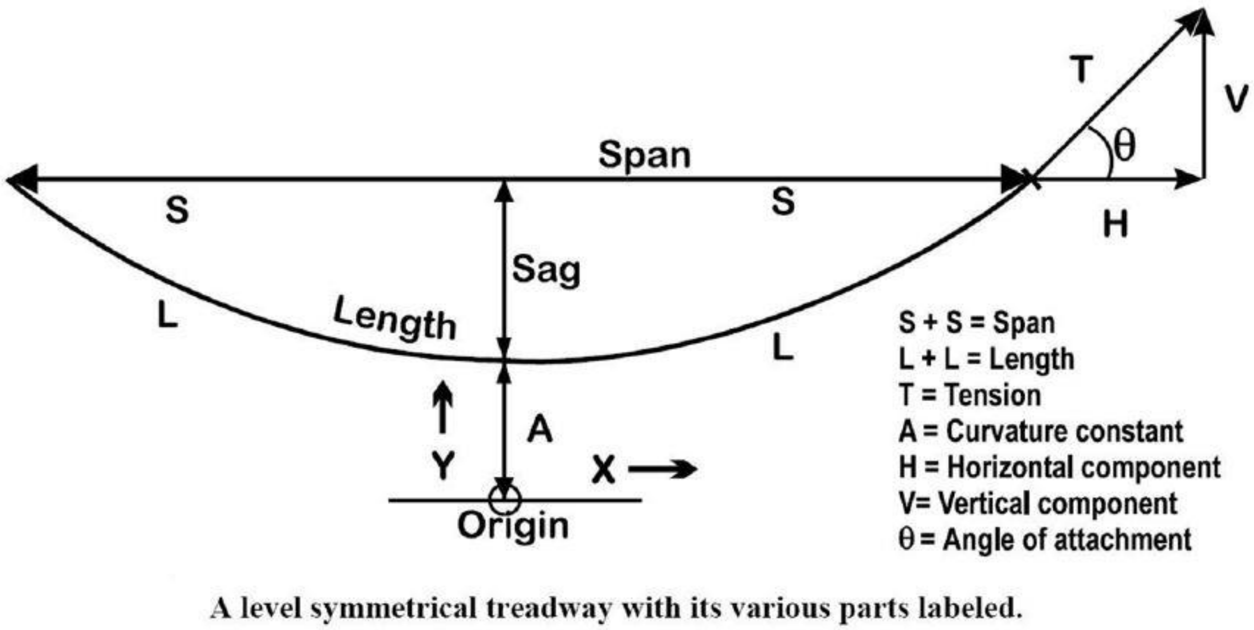

Fig 3. Catenary curve

[譯文] 淺談樹冠層走道的設置

菲力普‧惠特曼 博士

冠層走道建造協會

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全世界森林樹冠層的研究都受限於進入的系統。有許多到達樹冠層的研究方法都只能讓少數的人們在特定的時間進入冠層。觀察平臺以及樹冠層走道則可以克服這些問題，但造價昂貴，常受限於研究經費。和懸吊式的橋樑比較，在這篇文章裡討論的樹冠層走道較為輕便而且容易建造。樹冠層走道也可以同時兼顧森林保育和當地居民的經濟收入。

樹冠層走道系統

我們需要決定的第一件事情是：這個系統需要使用多久？在樹上設立平臺及橋樑有兩種主要的方式：一種是用繩索環繞著樹幹(如圖一)，另一種則是使用栓釘釘入樹幹。如果預算足夠的話，建立樹塔是比較能夠顧及到樹木健康及生長的方式，但必須注意樹塔和樹根之間的距離。

如果這個系統是暫時性的，大約 1 到 2 年或更短，在樹上綁繩索是比較好的方法。這種方法比較適合短期的研究計畫或是特殊事件(例如研討會)，因為樹木在短時間內不會長得太快，暫時纏繞樹體不會有明顯的影響(或是在繩索和樹木之間設置緩衝墊以避免勒死樹木)。在計畫結束後就可以移除繩索而不會影響樹木未來的生長。如果要用這種方法使用較長時間的話，研究者就需要每年移動纏勒的部位；但由於移動等同於重新設置，所以常常沒有認真遵守，就會影響樹木健康以及提早衰老。

如果這種系統是常設的，時間在多年以上，則傾向使用螺絲或栓釘固定。這種永久系統維持時間比較長，適合研究人員以及生態觀光客。把鐵製螺絲鑽進樹幹的時候，許多人以為將在樹體上造成一個小洞並且傷害樹木，但絕大部分的樹木主幹都是早已死亡的結構性支撐。樹皮底下的形成層確實會受到損傷，但傷疤會立刻包覆鐵製螺絲。樹木會對螺絲產生的反應就像是對其他自然產生的傷疤一樣，最終會在螺絲的周圍癒合(圖二)。如果螺絲正確地嵌入樹幹，樹木就會包覆它。在螺絲之外也可以結合銬環或是連結系統。ANSI(American National Standards Institute) and ISA (International Society of Arboriculture)公布的標準都經過工業的試驗以及樹木生理學的研究，特別是 ANSI A300 part 3-補足支撐系統，提到在樹上釘入螺絲的方法並明令禁

止纏繞樹體及枝幹；ISA 也有許多關於攀樹、林木健康、修枝技巧、繩索和支撐以及安全措施的著作。

樹冠層的進入系統主要包含了平臺、橋梁和一些進入方法。在這裡討論的樹冠層橋梁包含了一條在頭頂上的確保繩索，兩條扶手的繩索和踩踏步道(tread way)。踩踏步道包含了交錯的短木板以及分布在整條走道上的支撐繩索，短木板會用鐵製螺絲等元件直接連接支撐繩索。十六分之三英寸的全新鋼纜就可以用來連結踩踏步道的繩索和八分之三英寸的全新鋼纜扶手。垂直方面的連結則都一樣長，這可以允許行人自由抓握且可以形成一條懸垂線。繩索的終點會連結到樹的主幹或是大型的枝條，有環首螺栓或其他硬體。這些樹也會用大型支索以某些形式固定在地面上。

這種橋樑系統造價較便宜但是無法同時乘載很多使用者，因為需要穿著攀爬的鞍帶並且勾住頭頂上的確保繩索。但若在兩側加裝網袋就可以免除鞍帶和頭頂上的安全繩索。

設計考量

為什麼要選擇支撐橋樑或懸吊橋樑呢？在支撐橋樑中支撐的繩索是在踩踏步道之下，這表示踩踏步道必須要遵循懸吊線(圖三)並且總是下彎的。在懸吊橋樑裡支撐繩索是在踩踏步道之上，同時另一端都繫在頭頂上的支點。這表示踩踏步道會低於樹高以確保有較強的終點支撐。踩踏步道也依據不同長度的垂直支撐繩索而有所分級。

在設計之前，必須要實地勘察以選擇合適的支撐樹木，並精確丈量樹木之間的距離。主要會由兩個有經驗的攀樹者和至少一個地面工作者，依選擇樹木的數量、位置、高度、形狀等等現場狀況工作 2 到 4 天。工作內容包含在樹上測量主幹的直徑以及平臺附近的枝條大小，決定支撐的枝幹，以及測量這些樹在樹冠層中的距離。此外當地的自然資源也需要一併調查。

要設計和建造一座空中走道，必須要知道所有材料的用途，例如繩索的拉張力和所有組成元件的重量。以走道來說我們規定的安全因素條件要是 5:1 或更高。為了達到這個安全條件，繩索的張力不能只是簡單的測量或計算，步道的斜度不能過大，必須低於 25 度。例如支撐繩索的首要選擇是八分之三英吋的全新鋼纜，但計算之後通常會發現無法達到安全條件的標準，或是末端的角度過大；這時候就會使用更高張力的繩索。不同的連接裝置硬體的選擇，包括環首螺栓、繩索螺絲鉗、頂針、套筒螺母等等，也是考量的一環。一旦最終的規格定案，就能設計一套完整的系統，並且決定建造的價格。同時，會訂購核准的材料並運送到建造地。待材料都送達建造地後，建造團隊會帶著工具開始整個計畫。除了有時受到氣候因素影響之外，建造工作通常就會準時開始。

建造考量

設計一個特殊的懸垂線需要考慮兩個變數：端點間的水平距離和承載需求。為了確保建造期間踩踏步道會符合設計，在支撐踩踏步道的繩索還沒有下凹受力之前，可使用攜帶式雷射光用視覺觀察或測量。下凹的程度可以在建造時藉由各種長度的支撐繩索設定，並用環首螺栓和螺絲鉗在兩端點調整。套筒螺母則可以固定於踩踏步道的其中一個端點，便於做下凹程度的最後調整。

進入冠層系統的方法視預算和使用者類型而定。有階梯的樹塔是最符合大部分使用者的方式，但造價很昂貴。其他的方法如鎖在主幹上的梯子、軌道和水手椅、或甚至用繩索攀樹，能夠減少製作經費,但會增加進入冠層的難度。有時冠層進入系統的設置會利用山坡地形的特點，可以直接用簡單的連接系統從第一個平臺到達山谷或懸崖的地面。

經費估計(美金)

實地勘查的經費從 2 千到 6 千元不等，旅費則依據不同的國家和地點另計。由於當地環境以及計畫的規模，進入建造地點的花費會依時間而有所不同。經費的估算包含了旅行、食宿、工錢、報關費、運送費以及材料費。踩踏步道的部分每英尺 3 百元，平臺則依據大小和複雜度從 2 千到 1 萬元不等，有階梯的樹塔則大約是每十英尺高 1 萬元。

使用時的維修

建造完成之後需要訓練當地員工日復一日的操作。除了攀爬技術之外，還必須監測樹木的健康(鄰近樹木也有可能倒塌壓到橋樑、平臺或支撐繩索)。

定期檢查和維修計畫也是必要的，以盡量延長樹冠層進入系統的使用年限。很重要的是要確定螺絲和螺絲鉗的緊密度，特別是剛開始的前幾年木材會逐漸乾燥並受到風、雨和太陽等氣候影響。除此之外，每年必須要有一次外部單位的檢測。

隨著時間過去，樹木逐漸長大，有些甲板就需要修整才不致妨礙樹木生長。有些踏板和其他木製元件需要更換(因為腐壞、昆蟲攻擊或是動物啃咬)。根據環境條件木材也需要週期性的更換或是上漆。

當支撐平臺的樹木以及鄰近樹木長大後，有些枝幹會自然死亡，必須進行修枝以促進樹的療癒過程；也需要移除有可能傷害整個系統的枝條以減少使用者被枯枝打到的風險。木質藤本也需要監測以確保不會對整個系統之內的樹木造成健康上的影響。

總而言之，每個樹冠層進入系統都需要定期維修，這也是預算的一部分。

Poring Canopy Walkway, is a Recreational and Educational Facility that is Attracting Many Visitors.

教育及觀光功能兼具的沙巴波令樹冠走道

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Introduction

The canopy walkway at Poring Hot Springs in Kinabalu Park was the world's first canopy walkway installation for conservation through nature tourism in 1988 (Illar & Gabriel, 1988). The walkway was opened for use on May 02, 1990. Construction of this facility was funded by ICR's grant and with initiative and technical advice from Dr. Illar Muul (President and founder of Integrated Conservation Research (ICR)- an international non-profit organization) and in collaboration with Sabah Parks and the State Government of Sabah. The canopy walkway is spread between six of the area's largest rainforest trees such as Dipterocarps and 'Manggaris' Kompassia excelsa to ensure stability and safety. At 157.6 metres in length, the canopy walkway at this location is essentially a rope and steel cable suspension bridge that zigzags through the canopy and is composed of a series of 5 meter aluminium ladders bolted together and suspended horizontally from cables. Laced with polyster ropes, the open rungs are covered with boards for walking. Fish netting encloses the sides of the walkway for safety. The canopy walkway is an experience unequaled in the rainforest! At a height of over 40 meters, it is accessible to all and requires no special skills or equipment and provides a view of the rainforest from the treetops, the best vantage point for observing wildlife and vegetation. Passing over the canopy across a hanging bridge is a memorable experience and a challenge for those trying to overcome their fear of heights. Because safety is of the utmost importance daily inspections, performed according to Standard Operating Procedures (SOPs) will be done to determine the security of the walkway before it is opened to the public.

The goal of canopy walkway

The construction of a canopy walkway aims at three main purposes which make it a viable option for ecologically and economically sustainable tourism development. First, it is an educational facility. Visitors are exposed to the amazing conditions and life in the forest canopy and it is our hope that they then realize the importance of working together for the conservation of the environment and the natural forests. Secondly, as a tourism facility, which attracts vast numbers of domestic and international tourists interested in wildlife and the rainforest while remaining environmentally friendly, and cost-effective to construct. Third, as a facilities for scientific research.

Accomplishments

In Sabah, Malaysia, the parks have begun to receive much more government support and new parks are being established. Tourism, including nature tourism, has flourished and now ranks as the third highest source of foreign exchange. At its peak, tourism exceeded more than five hundred thousand visitors per year to Sabah Parks facilities. Such a volume of visitors requires convenient facilities to access every single place of attraction. The largest portion of growth in nature tourism is made up of local Malaysians who have become more aware of their natural heritage while their disposable income has increased. Increased international tourism influences the economy in a multitude of ways especially in the state of Sabah, Malaysia.

Table. The number of tourists visits Poring Hot Springs Station.

Year	**No of Visitor visit Poring Station**	**No of Visitor visit Canopy Walkway**	**%**	**Local visitor visit canopy walkway**	**International visitor visit canopy walkway**
2010	318,284	137,844	43.4	65,860	71,984
2011	341,881	167,769	49.1	87,120	80,649
2012	347,217	148,980	43	79,456	69,524
2013	363,268	179,299	49.4	84,959	94,340
Total	**1,063,650**	**633,892**	**59.6**	**317,395**	**316,497**

Strategy

Sabah Parks is non-revenue oriented as a State Government Agency. Instead, it works for conservation management on its own and also with businesses, local entrepreneurs, and other conservation groups to integrate development with the best available information on preserving biodiversity. The founding premise of the Sabah Parks management master plan is that "high species diversity provides opportunities for economic diversification". Economic diversification is the basis for long-term economic stability and for better opportunities for having an element of control in, rather than being a victim of, the marketplace. Yet, rainforests are still being cut for agriculture and other monocultures which are likely to cause extinction of species in the future, with the loss of forests on which they depend. Sabah Parks manages for ecologically sustainable economic development of intact tropical rainforests. Conservation of natural forests will favor economically valuable species of plants and animals, as a step toward conserving lifetime rainforest with high species diversity.

Approximately 75% of animals in the tropics spend the majority of their time in the canopy. Canopy walkways provide tourists with the opportunity to observe high canopy species that are difficult to view from the ground. Additionally, some animals appear to be less fearful of people on the canopy walkway than they are when close to people on the ground. Lastly, we have made efforts to habituate wildlife, especially primates and big mammals, to use the canopy walkway area. Thus far, we have been successful in this endeavor. The progress of this work has shown a positive result. It is hoped that, in time, observation of wildlife will be easier and enhance attraction to visitors.

Challenges

Various outstanding areas of research can be done in the canopy, but the current number of expert researchers in this very specific field is very limited.

"Doing Well by Doing Good"

Acknowledgements

We express our gratitude to the Director of Sabah Parks Dr. Jamili Nais, and Mr. Paul Basintal (former Director) and Mrs Rimi Repin (Research and Education Division Coordinator) and to all Parks' Officers and staff for their support to my participation in this seminar... Finally, thanks to Dr. Illar Muul and Mr. Gabriel Sinit (former park Manager) in the provision of vital information that supports these articles.

Main References (Figure 1)

1. Dr. Illar Muul, Presidents and founder of ICR as a project adviser and consultant of the construction of the Canopy Walkway at Poring, Sabah, Malaysia.
   Illarmuul@integratedconservationresearch.org
2. Mr. Gabriel Sinit. A former Park Manager, who led the world's first canopy walkway installation team for use for conservation through nature tourism (Kinabalu Park, Sabah, Malaysia) in 1988. Specialists in the construction of the tropical Canopy Walkway. He was a consultant in the construction of the longest canopy walkway at Pahang National Park in Peninsular Malaysia.
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[譯文]教育及觀光功能兼具的波林・沙巴樹冠層走道

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前言

沙巴國家公園的波令樹冠層走道是世界上第一條以生態旅遊進行保育為目的建造的冠層走道，啟用於 1990 年五月。由於 ICR((President and founder of Integrated Conservation Research)的贊助、Illar Muul 博士的建議，以及沙巴國家公園和政府的合作，這條樹冠層走道才得以建立。為了確保安全，走道建立在六棵巨大的龍腦香樹和樹王木(*Kompassia excelsa*)之上，全長 157.6 公尺，由繩索和鋼纜構成懸吊系統，之字形穿過樹冠層，並由五公尺長的鋁梯相連而成踏板。梯級上覆蓋木板並以聚酯纖維的繩索連結，便於行走；走道的側面則以漁網圍住。行走在樹冠層走道是與眾不同的經驗，不須藉由特殊工具和技術就能進入 40 公尺高的樹冠層，提供了行者特殊的視野，並能近距離觀察野生動植物。同時，穿過樹冠層的懸吊繩橋也是試圖克服懼高的挑戰。而最重要的則是安全；為了確保民眾的安全，每天開放參觀前都需要照著標準操作程序檢查走道狀況。

樹冠層走道的目標

1. 教學：透過參觀樹冠層的美好經驗讓民眾了解保護自然環境的重要性。
2. 觀光：在盡量不破壞環境的條件下吸引觀光客增加經濟收入。
3. 科學研究。

目前成就

在沙巴，國家公園署開始收到較多的政府補助，並設立更多的國家公園。而旅遊業(包含生態旅遊)愈來愈發達，現在已經是收入來源的前三名。每年有超過 50 萬人次造訪沙巴國家公園，所以需要更方便的設施以增加各個地方的入園吸引力。馬來西亞國人佔了生態旅遊中很大一部分人口，隨著所得增加，他們開始關心自己擁有的自然遺產。而逐年增加的外國觀光客在很多方面上影響了沙巴的經濟發展。

經營策略

沙巴國家公園是非收益導向的州政府機構，結合了保育、經營、商業、在地企業以及環保團體，期望能透過保護物種多樣性達成經營多樣性，以維持長期經濟穩定以及控制市場機制。如果為了農業及其他單一栽培作物砍伐熱帶雨林，可能會在未來成為物種滅絕的受害者。沙巴國家公園以永續發展的概念經營原始熱帶雨林，除了有利於具有經濟價值的動植物，同時也保護了熱帶雨林的物種多樣性。

熱帶雨林裡大約有 75%的動物會在樹冠層生活。比起待在地面上，動物在樹冠層活動時比較不會恐懼人類，而樹冠層走道最大的優點正是可以離開地表觀察野生動物。國家公園目前也持續努力讓野生動物習慣出沒於樹冠層走道的區域，特別是靈長類和大型哺乳類。期望未來能更加容易觀察野生生物，並因此提高對觀光客的吸引力。



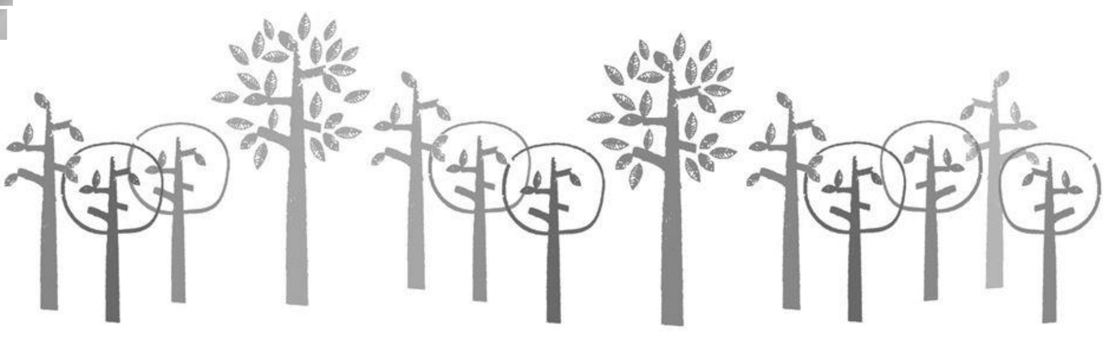
Figure 1 (left). Dr. Illar Muul (left) and Mr. Gabriel Sinit (right).
Figure 2 (right). Canopy Walkway at Poring, Sabah, Malaysia.

MEMO

----------International Symposium of Canopy Ecology Conservation----------

森林樹冠層

生態保育國際研討會



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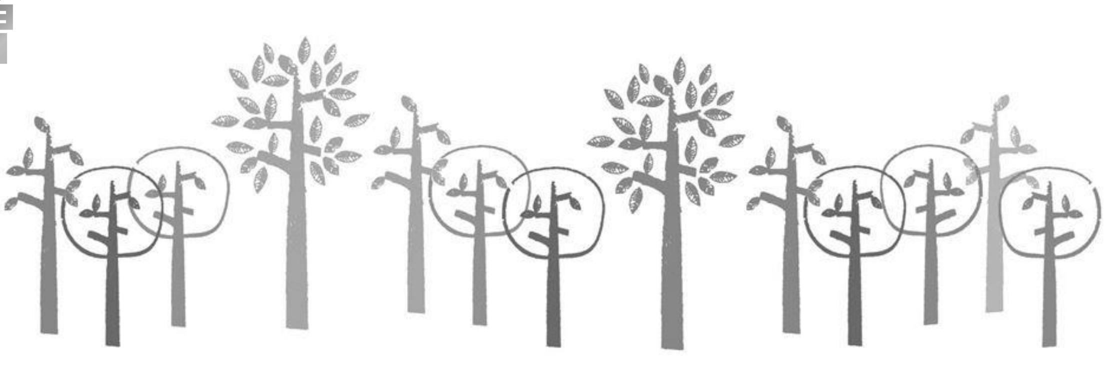

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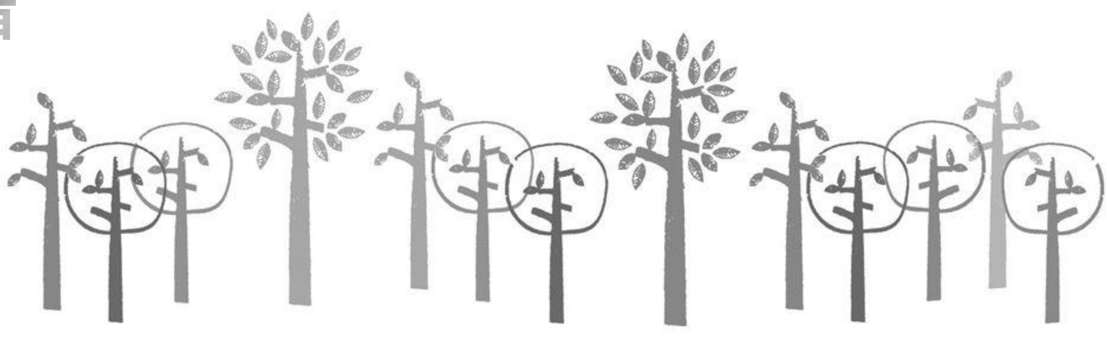

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