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破碎地景中鳥類群聚組成及棲地偏好

Avian Community Composition and Habitat Preferences
in Fragmented Landscape



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自從高中在生物研究社學習辨識蟲魚鳥獸開始，至今完成一本生態學的碩士論文，已經過了九個年頭。我很高興，能夠一路走來讓自然生態研究從我的興趣，變成我的主修科目、專長，而未來能進而成為我的職業與志業。能從事自己喜歡的工作是非常幸福快樂的，能有這樣的機會，我中心感謝曾經指導、引導、支持、協助我的每一位長輩、前輩與朋友，願意與大自然共同參與我的生命。口試的結束，同時也代表研究生涯暫時告一段落。感謝夏禹九老師、李培芬老師、許富雄老師願意審視我的研究論文，並且給予我許多值得寶貴建議以及再三審慎思考的癥結，讓我研究論文得以更加精美完善。同時感謝奧山利規老師在統計分析上的協助與建議；感謝丁詩同老師在我申請參與研討會的補助時給我極大助力的推薦信，以及每次在 BACT 活動中的合作與無形中的啟發；感謝林貞瑋學姐及傅淑瑋學姐於 2005 至 2007 年先行蒐集了完整詳細的野外資料，這份論文才能有多元的分析方向與發展空間，因此我才有更充裕的時間專注於資料的分析與寫作。

今天我能有現在的研究表現，首先要由衷的感謝袁孝維老師、丁宗蘇老師與沈聖峰學長，將我從一個學習既有學問的大學生，成為一個嘗試以科學方法回答問題的研究生。星期四的下午，在林一教室拿到林業概論的課程大綱，看到其中一項「森林野生動物 袁孝維副教授」（當時是副教授），就是我高中在社團裡玩物喪志的主題，便期待著那一週的到來。那時我不理會下一節微積分的小考，只顧著辨識出投影片中野生動物的名字。課後，袁老師跟我說，蟲魚鳥獸之名很基本也很重要，但除此之外，對自然生態的現象不應僅只於知其然，更須進一步知其所以然，並且懂得用科學方法做研究以回答問題。自此，袁老師不僅邀請我參與野生動物研究是的味庭及協助學長姐的野外調查工作，也不吝於讓我使用研究室的器材。到了大三，袁老師全力支持我申請國科會大專生研究計畫並撰寫學士論文，讓我在進入研究所之前，就能有一次執行研究的經驗。像是參加碩士生涯戰鬥體驗營，而不會在真正的碩士生涯中措手不及。雖不至於如魚得水，但至少能穩紮穩打，按部就班的向前走。袁老師給我的是學士班到碩士班的轉變，也累積許多難能可貴的研究執行經驗。

在生物多樣性概論的課後，我想著以華萊士線為題的報告。幾天後恰巧在系館遇到了丁老師，順口提了如何找相關文獻的問題。隔日上課前，丁老師找我去辦公室，抱了一整疊文獻給我，在相關的章節夾了書籤。第一次遇到如此積極熱忱的老師，覺得沒把文獻讀完好好寫份報告，還真是對不起老師啊。即使大學期間不是丁老師的導生，丁老師依舊熱情不減的提供我求學所需的文獻、器材與各種寶貴的研究建議。研究所之後，丁老師除了持續給予我執行碩士論文所需的指導、建議與討論之外，更不斷地幫助我往更高的層級上邁進。畫了一千多張鳥類分佈圖，讓我熟悉世界地理與鳥類分佈、分類狀況；各項的野外調查工作，讓我累積許多野外工作經驗。最珍貴的是，2009 年夏天在美國的兩場研討會，直接參加生態研究的一級戰區，更是開拓了我在研究與認識世界的眼光與遠見。這段時間下來，丁老師給我的協助不僅止於碩士階段的完成，也不吝提供各種資源讓我對將來出國申請博士班的規劃做準備。丁老師的協助在我的研究生涯中，無疑是一股莫大的助力。此外，兩位老師在我的學士與碩士生涯中，不斷的邀請我擔任各種教學形成的助教，無形中令我的教學解說得經驗的能力也在學生生涯中提昇。同時，賞鳥也成為我與兩位

老師之間共有的休閒活動，常常出差一路下來，工作、研究、教學、賞鳥同時執行。使得我與兩位老師除了師生關係之外，也是教學研究的戰友、賞鳥的鳥友。

在執行國科會大專生計畫，冠羽畫眉的研究團隊中，許多研究及野外工作的實際執行方面的細節，都是由沈聖峰學長來指導與提醒的。那時剛踏出研究生涯的第一步，對於研究的一切都得從頭開始。學長不僅不厭其煩的耐著性子從文獻搜尋、閱讀論文、資料分析、論文撰寫指導之外，也分享了許多執行研究及出國求學的心路歷程。其中最大的收穫是從「做研究是一連串的挫折感」到「解決問題的方法，不外乎就是毅力和經驗(知識)」。當時救硬碟的過程，從頭到尾把這兩句話體驗了一遍。這個經驗如同一把屠龍寶刀，讓我在將來的研究生涯中能夠更勇敢的面對問題與挫折，再嘗試各種可能的方法解決問題。此外，學長常常談到如何「問一個好問題」，這個部份談了很多次，現在還無法體會其精髓，也許還需要更多經驗才能夠體悟吧。

九個年頭的起點來自於建中生物研究社，讓我的高中生涯精彩又不留下遺憾。雖然常常假正事之名行玩樂之實，搞得課業成績亂七八糟，但是無形中培養起來的物種辨識能力與技巧，成為研究與調查工作上的優勢條件。感謝當時許多學長們：傳凱、國雄、富凱、建融、逸祥、盈宏、昱中、小虎、維民、達叔、魚一隻、A 奎、A 泰、老頤、樸煜、大雄王、資棟，所傳授與分享給我們的知識(?)、經驗(?)與教誨(???)。尤其感謝大學長傳凱，在人文、自然科學領域都帶給我許多值得反思的觀點與想法，成為我許多事物上諮詢與討論的對象。還有好幾次瓦拉米、花東縱谷的旅行，我們老是說有空要再去一趟花東，結果到現在還是流標，任真的希望有機會在一塊去花東走一走啊！感謝何老頤，上次通 MSN 時提到「十年的交情不是叫假的啊！」，我才發現哇靠已經第十年了。從建中生研、自然保育社，一直到你轉讀社會科學，再一起從 summer!! 團中拼研究所畢業。這段時間共同的興趣與回憶，快樂或不愉快的都好，總之真的經歷很多值得回憶、討論與玩味的種種。希望希望日後能共同由「都市生態學」與「城市與自然」朝自然與社會科學通融的方向努力奮鬥。感謝同屆的擦蘇、咻平、嚕邦，我們四個人從高一開始跟著動物組一塊在新店烏來到處闖蕩，雖然畢業後各自往不同的領域發展（有人又回頭了 XD），還是很高興高中生涯中有你們這些不可多得的好友。

自然保育社，我們自稱假保育之名行玩樂之實的社團。保育社並不單單僅只於「自然」與「保育」，保育社裡聚集著來自各系四面八方的朋友，學了許多在教育體制下學不到的。單車環島、登山、旅行、天文、議題、社會科學等…這些內容與經驗都是從保育社開始學起的。感謝自然保育社的各位：黃蓉、彥豪、丁禕、泰華、偉光、昆典、育豪、縈瑩、鈺敏、凱安、俊男、柏豪、仁棣、以博、彥樺、斐悅、盈宏、永暉、慈恩、宜瑾、宜家、脆皮、靜娟、翊展、皖文、祖濬、盈潔、致羗、振益、涵靈、馨頤、定敏、彥君、琬純、其蓁、之儀、嫻君、小光、婕瑜、琛哥、栗子、馥如、老頤、嘉耘、澤先、宜君、樸煜、怡吟、軒毓、映淳、家怡、鼻亨、雅婷、貞儀、芳庭、俐君、宣衡、庭光、以旋、傳佳、飛筆、育豪、理哲、尚慧、涵茹、阿京、祐昇、品奴、誼珊、智偉、思怡、劉鎮、博仁、鳳翎、瀚峽、奕嘉、美儀，還有烏來的老林和瘦瘦…(怎麼這麼多人啊!!)，不僅是議題討論的對象，也是喜歡奔向大自然的同好夥伴，造就了我繽紛又多樣的大學生涯，如同生物多樣性一樣。此外，保育社給我最大的啟發，就是從許多不同的角度看事情的眼界，豐富了我許多看事情的心態與想法，否則我可能還只是一個總是侷限在自己的領域

中看待這個世界的學生。其中最重要的，我終於在畢業前夕理解到「保育生物學是一門科學，但只是保育議題的一部分。也就是說，保育議題不是科學，不能完全用科學的眼光和標準來審視。因此，誇大的彰顯議題的手段，自然會存在其中，如果能有效幫助保育議題達成目的，也就不必太過度在意是不是要用科學的標準來審視了。」這是畢業前保育社的各位在討論國光石化時無形中帶給我的體悟，恐怕讀一百次保育生物學課本也讀不出來，是我在想法上很重要的轉折與體認，謝謝保育社的大家！

感謝「野生動物研究室」與「生物多樣性研究室」的各位學長姐、夥伴、學弟妹在野外出差時的照顧與經驗的傳授、合作與分享，以及咪庭時的討論與建議。第一次擔任幫手是在金門栗喉蜂虎的研究，感謝力平學長、佩妤、明淵、元均願意照顧與帶領一個還很菜、什麼都不懂不太會得大學生。參與冠羽畫眉小鳥隊時，第一次蒐集自己要的研究資料，感謝當時一同合作架巢、追鳥的小鳥隊：聖峰、愷愷、阿燙、棒棒、穎慧、史特龍、凱中、湘靜、文宜，還有這段期間上來幫忙的栗子、智偉、涵茹、傳佳，在梅峰的兩個月有辛苦有樂趣，誠然是一段難忘的經驗與回憶，謝謝你們！感謝曾經在 401 的各位：怡良學姐在研究上的討論與文獻的提供；熊大、惟仁、修銘、菜蟲、勁廷、可言、田婕、佩蓉在研究與統計上的建議；馥蔓在研究與 GIS 上的協助；Devil 總是不遺餘力的搶救電腦與印表機及 COSTCO 的邀約；勁廷加的火鍋燒烤宴；可言不定期的提供各式各樣的食物得以維持做研究所需的體力(ㄊㄨㄨㄨ)。感謝 308 共同奮鬥的凱中、湘靜、文宜、陳球、婉如、惠冰、威廷，除了參與咪廷之外，常常提供我串門子的空間與時間，以及在賞鳥上面的分享與較勁。

感謝分佈在森林系 B93 各大研究室的夥伴們永信、姿麟、旨价、青蛙、芽芽、滢茜、削邊、Y 伯、國父、搖滾蛋、三鐵、小苗、建仲、禽獸、雅筠、小元、信甫、立昇，讓我有是沒事都能忙裡偷閒去、喝杯茶、聊聊天。還有每一次的 momo-paradise 聚會，談起大學時代跟林場實習的點點滴滴，總是都有聊不完的話題。我很喜歡畢業典禮那天，大家一起坐在林一教室裡假裝上課的照片，希望還能有機會一起坐在教室裡上課聊天睡覺啊。也感謝森林系的學弟妹們：阿斯、玫瑰、部長、廉潔、JUJU、王翎、函蓁、芳儀、何昀、羚榛、惟珽、思怡、阿蓮、智海。B97 重建了壘球隊，讓我研究之餘又多了一個可以享受的休閒活動。也很高興從林業概論、森多、野動等幾個實習（可惜沒有林場實習）、一起共事合作系上活動能遇到有趣又活潑的你們。

森林生物多樣性概論，感謝每一位在森多助教：小珠一路很有耐心的帶我們學習助教的工作，耳提面命的的碎碎念讓我們代課能更快上手；熊大、育霖跟公公一起設計行程、課程內容、作業等討論，以及不定期的「桃福啊！」、「出來面對啊！」（籃球機和保健中心量體重）；感謝每位曾經跟我一起出隊的助教們：熊大、育霖、公公、婉如、恩保、威廷、忠義、培欣、宜俊、皖文、阿京、涵茹、小乙、獅子、宗霖、阿丁，感謝你們一路上的協助與合作，得以讓課程進行的更順利也更圓滿。還有最重要的是每一位被我帶到的 213 個森多學生，（抱歉沒有把各位的名字都列出來，但是寫到這裡我又把每班實習手冊前面的名字與照片拿出來看過一遍）很高興能擔任你們的助教，寫到這裡說得還是那些好像在哪裡看過的老話。你們提到第一次接觸到野外環境的興奮與感動，跟我在生研社的前一兩年是一樣的，第一次拿起望遠鏡看小鳥、第一次摸蛇摸青蛙的日子。在忙碌且充滿挫折的研究生活中，這一份感動與興奮總是容易忘記。但是這些記憶，

每一次都會被各位修森多的學生表現出來的樣子給喚醒，而回憶起以前第一次接觸自然的喜悅。感謝各位不斷提醒我壓力再大、遇到瓶頸時的時候回想起初衷，繼續努力。

感謝最親愛的婉玲，五年多來，我真的非常非常的快樂，回憶也非常的美麗，總是給我無限的陪伴、照顧與支持。現在當兵服役，妳還是耐著性子站崗等我放假、退伍。我的興趣與工作總是讓我往外跑，感謝妳總是包容我讓我去追逐那些山啊、樹啊、鳥啊等等。也很感謝妳常常陪著我的喜好去旅行遊玩，從雪山翠池開始，這些年我們去了很多很美的地方，希望接下來還能夠一起去世界的各個角落，發現這個世界的美。感謝有妳，有妳真好。

最感謝的是我的家人：爸媽和弟弟。從小開始就給我無限的自由讓我無限的任憑自己的喜好去發展。從高中開始玩這些玩到玩物喪志，包容我表現相當糟糕的課業。一直到大學、研究所期間動不動就要往外、往山上跑三五天。您們的愛、支持與鼓勵，讓我可以無後顧之憂的將我的興趣轉化成我的成就與志業，好讓你們不再為我操心。去美國參加研討會的時候，即便我已經自己申請補助，老爸還是堅持給我足夠的旅費，也感謝大伯父、二姑姑在這趟旅行時支助我旅費，讓我能無顧忌的旅行拓展視野。您們給我的每一分錢我都不會揮霍浪費，會審慎的投資在我所需的刀口上。謝謝爸媽！

寫到最後了，寫給自己吧，算是快速的把九年的自然生態生涯給從頭到尾回想了一次。同時，也才發現，學生生涯也就這樣暫時告一段落了。離開了台大，想起來剛入學時要進來這裡好好的挖寶藏，回過頭來看，付出了很多，收穫也很多；只是，每到了一個階段，總是會覺得自己欠缺的還很多，該學得還有很多。可惜歲月不待人，時間就是這樣把我往下一個階段推去，也就硬著頭皮面對下一個階段所需面臨的挑戰。雖然未來充滿不確定，但是，這個世界真的很大，我努力讓自己活著沒有遺憾。我會努力讓自己變成一個自動自發的主體、追求夢想的魯夫、主宰球場勝負的投手、勇敢邁向叢林的鹿野忠雄、華萊士、達爾文與斯文豪。這本碩士論文的完成，算是一個暫時性逗點。台灣的教育體制下，好像差不多接近尾聲了；但是對學術生涯而言，這卻才只是剛開始的一小步，要走的路還很長，也許不會有結束或終止的那一天。但是我很享受於這樣追求知識與世界的忙碌之中，這樣一整個感覺就是很充實很棒，每天都在期待著明天的挑戰。樂在研究的「樂」字並不表示「輕鬆」，而是能夠克服一切的挫折，並且樂於突破現況。無論如何，

感謝各位願意走進我的生命，也願意讓我走入各位的生命裡。

非常感謝各位的關心、支持與鼓勵！我的碩士論文寫完了！耶！！

摘要

棲地破碎化對生物多樣性的效應對所有的物種並不一致，且不易釐清。若研究只在廣（地景）尺度下檢視群聚組成，則細微的反應容易被忽略。因此，在細（區塊）尺度下探討個體層級的反應亦相當重要。在群聚的層級，於破碎環境中的區塊之間檢驗地景結構（區塊面積、形狀複雜度、相鄰區塊、棲地類型）與植群結構（垂直枝葉結構、植群組成）對鳥種豐富度的效應與交互作用。在個體層級，則分別檢驗不同物種、繁殖狀態（在地繁殖者、鄰地繁殖者、冬候鳥種）、以及生態同功群（食蟲者、雜食者）鳥類的棲地偏好。最後則比較不同繁殖狀態的鳥類在不同棲地類型的區塊中是否具邊緣效應。研究地（國立臺灣大學梅峰山地實驗農場）區分成 286 個區塊及六種棲地類型（建築、耕地、天然林、果園、人工林、水池）。2005 年到 2007 年的三個繁殖季中，所有被觀察到的鳥類個體（66 種、1,1740 個紀錄點）的位置皆記錄於地圖上，所有區塊的植群結構則在 2007 年測量。

在群聚層級，棲地類型和植群結構對鳥種豐富度的影響大於區塊面積。在建築、耕地、人工林及水池，該區塊與天然林和人工林區塊的相鄰長度為維持鳥種豐富度的重要因子。在果園、天然林與人工林中，植群結構則為維持更高的鳥種豐富度的重要因子。在個體層級，大多數的鳥種偏好天然林與人工林，但是仍然有些鳥種偏好非森林的棲地。不同物種、繁殖狀態以及生態同功群的鳥類個體，對垂直枝葉結構與植群組成的偏好皆不盡相同。在地繁殖者的紀錄點密度顯著的高於鄰地繁殖者與冬候鳥種。在建築與耕地中，任何繁殖狀態的鳥類個體紀錄點密度沒有顯著的邊緣效應。然而，在地繁殖者在果園、天然林與人工林中，與冬候鳥種在天然林中，邊緣距離帶的紀錄點密度顯著地高於內部。這些結果暗示地

景結構、垂直枝葉結構與植群組成的多樣度是在破碎環境中維持高生物多樣性的重要因子。破碎的區塊可以依面積和植群結構分類。植群結構單純的區塊（無論面積大或小），首要是增加其植群結構的複雜度。植群結構複雜的大區塊對於吸引鳥類個體與維持高鳥種豐富度而言是較好的狀態，但是無法吸引某些偏好非森林棲地的鳥種。

關鍵詞：鳥種豐富度、邊緣效應、棲地破碎化、棲地偏好、臺灣、植群結構



Abstract

Effects of habitat fragmentation on biodiversity are not universal to all species and are difficult to be clarified. If only examining community composition at broader (landscape) scale, it will be easy to neglect some delicate responses. It is important to conduct research on individual level and at finer (patch) scale. This study was aimed to examine the effects and interactions of the attributes of landscape structure (patch area, shape complexity, neighboring patches, and habitat type) and vegetation structure (vertical foliage structure, and floristic composition) to bird species richness among patches in a fragmented environment. On individual level, the habitat preferences of different bird species, reproductive statuses (local breeders, neighboring breeders, and wintering species), and ecological guilds (insectivores and omnivores) among diverse landscape components were also examined. Finally, edge effects to different bird reproductive statuses in different habitat types were compared. The study site, Meifeng Highlands Experimental Farm of National Taiwan University, was classified into 286 patches and six habitat types (buildings, fields, native forests, orchards, plantations, and ponds). The locations of all observed bird individuals (66 species, 11,740 registration spots) were mapped during three breeding seasons from 2005 to 2007. The vegetation structures of the 286 patches were measured in 2007.

On community level, the effects of habitat types and vegetation structure on bird species richness were stronger than patch area. For patches of

buildings, fields, plantations and ponds, the length of adjacent native forests and plantations were the important factors to sustain bird species richness; in orchards, native forests and plantations, vegetation structure were the important factors to sustain higher bird species richness. On individual level, most species preferred native forests and plantations, but there were still some species preferred non-forest habitats. Different species, reproductive statuses, and ecological guilds preferred different situations of vertical foliage structure and floristic composition. The registration spot densities of local breeders were significantly higher than neighboring breeders and wintering species. In buildings and fields, the registration spot densities of different reproductive statuses did not show significant edge effects. However, the registration spot densities of edge buffer zones were significantly higher than the interior ones in orchards, native forests, and plantations for local breeders, and in native forests for wintering species. These results suggested that diversity of landscape structure, vertical foliage structure, and floristic composition were important factors to sustain higher biodiversity in fragmented environments. Fragmented patches can be classified by area and vegetation structure. For patches with simple vegetation structure (no matter large or small), it is important to increase the complexity of vegetation structure. Large patches with complex vegetation structure are the best to attract bird individuals and sustain high bird species richness, but invalid to some species which prefer non-forest habitats.

Keywords: bird species richness, edge effects, habitat fragmentation, habitat preferences, Taiwan, vegetation structure

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CHAPTER 1

Introduction

Habitat fragmentation has been one of the most serious threats to biodiversity in many parts of the world (Wilson, 1992; Collinge, 1996; Turner, 1996; Debinski and Holt, 2000) at all spatial scales (Lord and Norton, 1990; Dirzo and Raven, 2003). The main process of habitat fragmentation is habitat loss results in habitat isolation (reviewed by Fahrig, 2003). In general situations, habitat loss is removing habitats form landscape, which is the most manifest phenomenon and produces various spatial patterns. However, in habitat fragmentation, habitat loss not only decreases patch area but also creates small isolated patches at the same time (reviewed by Fahrig, 2003). The spatial arrangement of fragments affects the population and community dynamics in fragmented environments (Hanski and Gaggiotti, 2004). Therefore, habitat fragmentation has become one of the important issues in conservation and management (Tilman *et al.*, 1994; Meffe and Carroll, 1997; Margules and Pressey, 2000; Balmford *et al.*, 2005; Zipkin *et al.*, 2009).

Habitat loss is recognized to the major threat to biodiversity during the process of habitat fragmentation (Wilson, 1992; Tilman *et al.*, 1994; Fahrig, 2003; Collinge, 2009). Generally, each individual has minimum patch area requirements. Therefore, smaller patches have lower biodiversity than larger patches (Debinski and Hlot, 2000). Fahrig (2003) reviewed negative effects of habitat loss on direct and indirect measures of biodiversity. The direct

measures of biodiversity includes species richness (Schmiegelow and Mönkkönen, 2002), population abundance and distribution (Debinski and Holt, 2000), and genetic diversity (Wilson and Provan, 2003). The indirect measures of biodiversity includes population growth rate (Keller and Waller, 2002), species interactions (Steffan-Dewenter and Tschardtke, 1999) and breeding success (Donovan *et al.*, 1995). All these effects reveal that habitat fragmentation not only changes the quantity and quality of the landscape but also alters biodiversity.

Isolation of habitat breaks apart of habitats and increases edge effects (Lovejoy *et al.*, 1986). Edges are generally defined as boundaries between two different habitat types. Initially, in game management, Leopold (1933) used “edge effects” to describe edges provide diverse resources from both adjacent habitat types, and then sustain higher diversity and abundance of game species in fragmented landscapes. Edges have been traditionally considered as the sites of higher productivity and higher biodiversity (Leopold, 1933; Harris, 1988; Yahner, 1988). However, as more anthropogenic edges produced, the negative side of edge effects attracts more attentions (Gates and Gysel, 1978; Lovejoy *et al.*, 1986) because edge effects have found to greatly decrease the population size of some interior species (Wilcove, 1986; Saunders *et al.*, 1991; Mills, 1995). Therefore, these anthropogenic edges are often viewed as undesirable landscape components (Harris, 1988; Saunders *et al.*, 1991; reviewed by Ries *et al.*, 2004).

However, effects of habitat fragmentation are considered not universal to all species (Andrén, 1994). Habitat fragmentation not only reduces patch

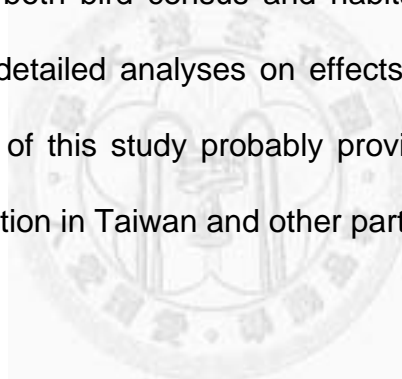
size but also creates new habitat types at the same time. The fragmented landscape is similar to mosaic landscape (reviewed by Fahrig, 2003). In the concepts of spatial heterogeneity theory (MacArthur and MacArthur, 1961), the more complex the arrangement of landscape components is, the more micro-habitats and ecological niches to habitat-specific species can afford. Besides, many species require more than one kind of habitat type for survival and reproduction (Law and Dickman, 1998). Therefore, fragmented environments usually contain higher species richness and increase the immigration rate of new species. In other words, habitat fragmentation attracts new species to the region (Andrén, 1994) and increase beta diversity, the species diversity across all habitats (Whittaker, 1960).

As detailed above, effects of habitat fragmentation on biodiversity might be positive, negative, neutral or mixed. However, it is difficult to clearly conduct census or investigation works of wildlife communities and vegetation structure at broader scale. Rotenberry (1985) also suggested that the finer scale (within-habitat type) investigations are better to untangle the mechanisms of wildlife-habitat relationships.

In this study, Chapter 2 was aimed to understand the effects and interactions the attributes of landscape structure and vegetation structure to bird species richness on community level; Chapter 3 was aimed to understand the effects of habitat types, patch area, and vegetation structure to attract various bird species, reproductive statuses (local breeders, neighboring breeders, and wintering species), and ecological guilds (omnivores and insectivores) at a bird individual perspective; Chapter 4 was aimed to

understand the responses of different reproductive statuses of birds to habitat edges at a bird individual perspective.

This study was conducted in a 50 ha study site with fragmented landscape surrounded by primary broad-leaved forests. The locations of all observed bird individuals were mapped during three breeding seasons from 2005 to 2007. The landscape of the study site was classified into 286 patches and six major habitat types (buildings, fields, native forests, orchards, plantations, and ponds). The vegetation structure (vertical foliage structure and floristic composition) of each patches were measured in 2007. This immense magnitude of both bird census and habitat measurement enables in-depth detection and detailed analyses on effects of habitat fragmentation on biodiversity. Results of this study probably provide insightful conclusions for biodiversity conservation in Taiwan and other parts of the world.



CHAPTER 2

Effects of Habitat Fragmentation on Bird Species Richness

Abstract

Habitat fragmentation has been one important issue on conservation in recent decades. The attributes of landscape structure (patch area, shape complexity, neighboring patches, and habitat type) and vegetation structure (vertical foliage structure, and floristic composition) had been respectively referred to the important factors to sustain bird species richness, but not universal to all species. This chapter was aimed to understand the effects and interactions of these habitat attributes to bird species richness in a fragmented environment at finer scale. The study site, Meifeng Highlands Experimental Farm of National Taiwan University, was classified into 286 patches and six habitat types (buildings, fields, native forests, orchards, plantations and ponds). The locations of all observed bird individuals (66 species, 11,740 registration spots) were mapped during three breeding seasons from 2005 to 2007. The vegetation structures of all patches were measured in 2007.

The species-area relationship functions of bird species in native forests and plantations were significantly differed from other habitat types; but showed no significant difference between native forests and plantations.

Native forests had significantly higher plant family richness in canopy layers than plantations, but no significant difference in sub-canopy layers. In generalized linear regression analyses, attributes of vegetation structure were more important than attributes of landscape structure in the habitat types with complex vegetation structure; the length of adjacent native forests were forwarded first in the habitat types with simple vegetation structure. Path analysis suggested patch area and sub-canopy plant family richness were important to sustain higher bird species richness. Patch area is still a major factor to sustain native biodiversity in fragmented landscapes. However, in small patches, increasing the complexity of vegetation structure is a key management strategy to sustain higher native biodiversity.

Keywords: bird species richness, habitat fragmentation, mosaic landscape, patch area, Taiwan, vegetation structure

摘要

近十幾年來，棲地破碎化已經成為保育上的重要議題。許多研究已經分別指出地景結構（區塊面積、區塊形狀複雜度、相鄰區塊、棲地類型）與植群結構（垂直枝葉結構、植群組成）會影響鳥種豐富度，但是對各鳥種的影響並不一致。本研究目的在於瞭解上述因子在細尺度的破碎化環境中對鳥種豐富度的影響以及因子間的交互作用。研究地點（國立臺灣大學梅峰山地實驗農場）區分成 286 個區塊以及六種棲地類型（建築、耕地、天然林、果園、人工林、水池）。2005 到 2007 年的三個繁殖季中，所有被觀察到的鳥類個體（共 66 種、11,740 個紀錄點）的位置皆記錄於地圖上，所有區塊的植群結構則於 2007 年測量。

天然林和人工林中，鳥種的物種面積關係式與其他的棲地類型有顯著的差異，但是在天然林與人工林之間沒有顯著的差異。在樹冠層中，天然林的植物科豐富度顯著的比人工林來的高，但是在次冠層中則沒有顯著的差異。一般線性迴歸分析的結果顯示：在植群結構較複雜的棲地類型中，植群結構因子比地景結構因子重要；在植群結構較單純的棲地類型中，相鄰天然林區塊的長度則最重要。路徑分析顯示區塊面積與次冠層的植物科豐富度是維持較高的鳥種豐富度的主要因子。在破碎化的地景下，區塊面積仍然是一個維持生物多樣性的主要因子。然而，在面積較小的區塊中，增加植群的複雜度是維持較高生物多樣性的關鍵經營方針。

關鍵詞：鳥種豐富度、棲地破碎化、地景鑲嵌體、區塊面積、臺灣、植群結構

Introduction

With increasing development of natural environments, habitat fragmentation has been one important issue on biodiversity conservation in recent decades (Tilman *et al.*, 1994; Margules and Pressey, 2000; Dirzo and Raven, 2003; Balmford *et al.*, 2005; Zipkin *et al.*, 2009). At community level, species richness is the clear and obvious object for researches and biodiversity conservation (e.g. Yoccoz *et al.*, 2001; Schmiegelow and Mönkkönen, 2002; Watson *et al.*, 2004; Zipkin *et al.*, 2009). For conservation and management strategies of habitats, it is critical to understand how interactions of ecological factors affect species richness in fragmented landscapes.

Effects of habitat fragmentation on species richness are not universal (reviewed by Fahrig, 2003) In general, habitat fragmentation illustrates a process during which a large expanse of habitat transformed into small isolated patches (Wilcove *et al.*, 1986; Forman, 1995), produces more habitat edges and enhances edge effects (Lovejoy *et al.*, 1986). However, habitat fragmentation sometimes diversifies landscape components and increases habitat types (reviewed by Fahrig, 2003). This means the fragmented landscapes sometimes are similar to mosaic landscapes. In the concept of spatial heterogeneity theory (MacArthur and MacArthur, 1961), the more complex the arrangement of landscape components is, the more micro-habitats and ecological niches to habitat-specific species can afford.

Besides, many species require more than one habitat type for survival and reproduction (Law and Dickman, 1998). Therefore, fragmented habitats could contain higher species richness and increase the immigration rate of new species. In other words, habitat fragmentation could attract new species to the region (Andrén, 1994) and increase beta diversity, the species diversity across all habitats (Whittaker, 1960). In mosaic landscape (Forman, 1995; Wiens, 1995; Bennett *et al.*, 2006), the ecological factors are classified into two categories: attributes of landscape structure and vegetation structure. Attributes of landscape structure includes patch area (Waston, 1835; Arrhenius, 1921), shape complexity (Laurance and Yensen, 1991; Collinge, 1996), landscape configuration and habitat type, (Bennett *et al.*, 2006). Attributes of vegetation structure (MacArthur and MacArthur, 1961; Lee and Rotenberry, 2005) includes vertical foliage structure and floristic composition.

Habitat loss, decreasing patch area, is the most direct and negative effects to species richness (Andrén, 1994; Tilman *et al.*, 1994; reviewed by Fahrig, 2003). The process of habitat fragmentation is one kind of habitat loss that results in habitat isolation (van den Berg *et al.*, 2001; reviewed by Fahrig, 2003; reviewed by Collinge, 2009). In general, species richness increases with patch area (Waston, 1835; Arrhenius, 1921, Gleason, 1922). This relationship between area and species richness that can be described by the power function called species-area relationship (SAR, Formula 1).

$$S = c A^z \quad \text{(Formula 1)}$$

Where S is the number of species, A is the area, and c and z are constants fitted to the data (MacArthur and Wilson, 1967; Wilcox, 1980; Rosenzweig, 1995; Gotelli, 1995). On the logarithmic form of Formula 1:

$$\log S = \log c + z \log A \quad (\text{Formula 2})$$

Where $\log c$ is the intercept and z is the slope of this linear function. The z -value means the increasing rate of species richness with area (MacArthur and Wilson, 1967; Wilcox, 1980). There are three explanations for SAR: the passive sampling hypothesis (Arrhenius, 1921; Connor and McCoy, 1979), the habitat heterogeneity hypothesis (Terborgh, 1977; Boecklen, 1986; Rosenzweig, 1995), and the island biogeography theory (MacArthur and Wilson, 1967). The passive sampling hypothesis describes that increasing the sampling area more individuals are sampled, then higher probability to sample new species. The habitat heterogeneity hypothesis suggests that larger patch contains more micro-habitats or ecological niches than the smaller one, so species richness of the larger one should be higher than that of the smaller one (many species are habitat specialist). Island biogeography theory states that species richness based on the equilibrium between the rate of species immigration and extinction. Larger island has higher probability of encountered by dispersing individuals than smaller one. Larger island contains more ecological resources to sustain more valid populations for a longer time than smaller one. According to these explanations, larger patch supports higher species richness. In the point of view of individual, each

individual requires minimum patch area, based on their life history. Habitat loss would definitely decrease population size. In case the patch area is below the minimum requirement of a population, the population would extirpate (Lande, 1987; Venier and Fahrig, 1996).

Shape complexity is determined by the interaction between patch area and perimeter. It is an indicator to the amount of core habitat area and edge of patches (Laurance and Yensen, 1991). The patches with higher shape complexity have greater amount of core habitat area and edge. Larger core habitat area contains more species, especially to interior species. The more edges increase the probability of the patch encountered by moving individuals (Collinge and Palmer, 2002).

In mosaic landscape, the landscape configuration also strongly influences the species richness of a patch and neighboring patches (Bennett *et al.*, 2004; Bennett *et al.*, 2006). Nearest-neighboring distance is the distance to the nearest conspecific habitat patch, the commonest index for estimated isolation (Bender *et al.*, 2003). The patch with shorter nearest-neighboring distance is located in landscape containing more habitat types than the patch with longer nearest-neighboring distance (Tischendorf, 2001). Jasson and Angelstam (1999) reported that the occurrence of Long-tailed Tit (*Aegithalos caudatus*) was positively related to the amount of habitat within 1 km², and negatively related to the distance between habitat patches.

Vegetation structure usually greatly determines the diversity and abundance of many bird species in terrestrial habitats (MacArthur and

MacArthur, 1961; Cody, 1985; Block and Brennan, 1993; Morrison *et al.*, 2006)

The relationship of habitat structure and avian community has been developed to the vegetation-habitat concept (Wiens, 1989), an important part of theory in avian ecology (Block and Brennan, 1993). Vegetation structure can be distinguished to two basic and obvious aspects: vertical foliage structure (or vegetation physiognomy); and floristic composition (the composition of plant taxa). For vertical foliage structure, MacArthur and MacArthur (1961) constructed foliage height diversity-bird species richness (FHD-BSR) hypothesis, it suggested bird species richness (BSR) increases with complex foliage height diversity. According to habitat heterogeneity hypothesis, complex vegetation structure contains more ecological niches for more bird species. On the other hand, floristic composition increases with the evolvement of vertical foliage structure, makes higher plant species richness (Halpern and Speis, 1995). Different plant species provide different ecological resources (especially food resources) to attract more different species and increases the species richness. Above of all, the habitat patch with complex vertical structure provides more cover, foraging and reproductive opportunities for more species (MacArthur and MacArthur, 1961; Carey *et al.*, 1999; Hunter, 1999).

In mosaic landscape, patch area, shape complexity, neighboring patches, and vegetation structure obviously influence species richness. Because effects of habitat fragmentation on species richness might be positive, negative, neutral, or mixed (reviewed by Fahrig, 2003; Ries *et al.*, 2004), this means its effects are not universal to all species. Not only studying

on these effects to species richness respectively is important, but also understanding the interactions of these factors. However, at landscape scale, it is difficult to conduct census or investigation works of wildlife communities and vegetation structure. Rotenberry (1985) referred that the finer scale (within-habitat type) investigations are better to untangle the mechanisms of wildlife-habitat relationships. At a perspective of individuals, species richness of different patches is based on the responses of individuals to environment, behavioral strategies and morphological constrains of individuals (Cody, 1985; McCollin, 1998). Therefore, the habitat selection model should base on three assumptions: (1) competition increases with increasing population density; (2) the selective strategies are based on the highest fitness; (3) the individual is free to enter any habitat (Fretwell and Lucas, 1970).

As detailed above, this chapter was aimed to understand the effects and interactions of the attributes of landscape structure and vegetation structures to species richness at a finer scale. This study was conducted in a 50 ha farm with fragmented landscape. The locations of all observed bird individuals were mapped during three breeding seasons from 2005 to 2007. The landscape of study site was classified into 286 patches of six major habitat types. Vertical foliage structure and floristic composition of each patch were measured in 2007. To understand how mosaic landscape sustains high bird species richness among fragmented patches, the effects of patch area, neighboring patches, habitat types, vertical foliage structure, and floristic composition to bird species richness were examined.

Methods

Study site

The study was conducted in Meifeng Highlands Experimental Farm of National Taiwan University in Nantou County, central Taiwan (24°05'N, 121°10'E; mean altitude: 2,150 m a.s.l.; 50 ha). It is located within primary broad-leaved forests dominated by Fagaceae and Lauraceae. The climate of study site is similar to temperate zone. The annual average temperature was 12.5 °C, the highest monthly temperature was 16.3 °C in July, and the lowest one was 5.3 °C in January (Meifeng Meteorological Station, data from 2003 –2007). Average relative humidity was 84.8% and the annual precipitation was 2,383 mm. The study site was established for horticultural research purposes in 1961. It was a 50 ha area mostly consisted of fragmented Japanese Cryptomeria (*Cryptomeria japonica*) plantations with various temperate-fruit orchards, horticultural fields, green-houses, and meadows. The landscape is highly fragmented, with well-developed road systems, so researchers could easily and quickly approach everywhere. These characters made the farm as an ideal place to map observed bird individuals.

Attributes of landscape structure

To quantify the study site, the aerial photo of the study site was used to draw an 1:1000 work map by ArcGIS 9.2 (ESRI, 2006). The 50 ha study site

was classified into 286 patches of six major habitat types (Figure 2-1). These habitat types were determined by the actual situations during 2005 –2007, included: buildings (31 patches, 7.75% area of the study site), fields (45 patches, 18.25%), native forests (124 patches, 39.44%), orchards (15 patches, 14.00%), plantations (61 patches, 19.63%) and ponds (10 patches, 0.93%). These patches were the unit of the habitat structure investigation. The patch area and perimeter were calculated from the classified landscape map by ArcGIS 9.2. To examine the effects of neighboring habitat type to BSR, the sum of length of adjacent patches (categorized by habitat types) and the distance to nearest patch of same habitat types were measured for each patch by ArcGIS 9.2. The nearest distance meant the distance between the nearest points on the boundaries of the two patches of same habitat type. The number of adjacent habitat types and the shape index (McGarigal and Marks, 1995; Formula 3) of each patch were calculated.

$$\text{shape index} = \frac{0.25 \times P}{\sqrt{A}} \quad (\text{Formula 3})$$

Where P is the perimeter of the patch, A is the patch area. The shape index equals to 1 for a square patch, and increases when the shape of a patch becomes more complex (McGarigal and Marks, 1995). All landscape attributes of the 286 patches were listed below.

1. Patch area,
2. Patch perimeter,
3. Shape index,

4. The number of adjacent habitat type,
5. Adjacent buildings: the total length bordering adjacent building patches,
6. Adjacent fields: the total length bordering adjacent field patches,
7. Adjacent native forests: the total length bordering adjacent native forest patches,
8. Adjacent orchards: the total length bordering adjacent orchard patches,
9. Adjacent plantations: the total length bordering adjacent plantation patches,
10. Adjacent ponds: the total length bordering adjacent pond patches,
11. Distance to building: the distance to nearest building patch,
12. Distance to field: the distance to nearest field patch,
13. Distance to native forest: the distance to nearest native forest patch,
14. Distance to orchard: the distance to nearest orchard patch,
15. Distance to plantation: the distance to nearest plantation patch,
16. Distance to pond : the distance to nearest pond patch.

Attributes of vegetation structure

The vegetation structure (vertical foliage structure and floristic composition) of each patch was recorded on March to June, 2007. For the vertical foliage structure, the mean height of vegetation, the area percentage of foliage coverage, and the number of foliage layers were estimated by sighted observing and a pole with meter scales. The product of the area percentage of foliage coverage and the number of foliage layers was the estimation of the foliage volumes of different layers (canopy layer, sub-canopy

layer, shrub layer, and ground layer) of vegetation height.

1. Canopy layer: the tree foliage of top 1/3 height of native forests, plantations, and orchards.
2. Sub-canopy layer: the tree foliage of middle 1/3 height of native forests, plantations, and orchards.
3. Shrub layer: the tree foliage of lower 1/3 height of native forests, plantations, and orchards, excluding ground layer.
4. Ground layer: the foliage below 30 cm of height. The area percentage of foliage coverage and the number of foliage layers were estimated by sighted observing.
5. Litter: the area percentage of litter coverage was ranked from 1 –10 by sighted observing, higher number meant denser one.
6. Log and snag: the number of log and snag (diameter above 10 cm) in one 10 × 10 m gird of each patch was counted. If the patch area was less than 100 m², the whole patch was observed.

For floristic composition, the plant family richness in canopy and sub-canopy layers were investigated in one 20 × 20 m sample gird in each patch. For those patches with area less than 400 m², the whole patch was investigated. There were 23 plant families from canopy layer, 36 families from sub-canopy layer, and 21 families were both recorded (Appendix 1). The foliage volumes of each family were ranked to the 1 –10 scale by sighted observing (higher number means denser one). The locations of the important food resource for birds, such as Taiwan cherry (*Prunus campanulata*) and Eastern debregeasia (*Debregeasia edulis*), were mapped. All attributes of

vegetation structure were listed below.

1. Mean vegetation height,
2. Foliage volumes of canopy: the estimation of foliage volumes of canopy layer,
3. Foliage volumes of sub-canopy: the estimation of foliage volumes of sub-canopy layer,
4. Foliage volumes of shrub: the estimation of foliage volumes of shrub layer,
5. Foliage volumes of ground: the estimation of foliage volumes of ground layer,
6. Total foliage volumes: the estimation of total foliage volumes; it was the sum of the estimation of foliage volumes of canopy, sub-canopy, shrub and ground layers.
7. Coverage of litter: the area percentage of litter coverage was ranked from 1 –10, higher number meant denser one,
8. Log and snag: the number of log and snag (diameter above 10 cm) in one 10 × 10 m gird,
9. Canopy plant family richness: plant family richness of canopy layer,
10. Sub-canopy plant family richness: plant family richness of sub-canopy layer,
11. Total plant family richness : plant family richness of whole patch.

Attributes of avian community

The locations of all observed bird individuals were mapped during three breeding seasons from early-March to late-July of 2005 (censused weekly for

consecutive 20 weeks), early-April to mid-June of 2006 (censused weekly for consecutive 12 weeks), and late-March to late-May of 2007 (censused weekly for consecutive 15 weeks). Parts of the individuals were captured by mist netting and color-banded for individual identification and morphological measurement from March to August of 2004 and March to September of 2005. The census of birds began around 30 minutes before local sunrises and finished in 3.5 hours. Censuses were omitted and redone on another day when the bird singing decreased abruptly during census time. The census routes along the road and trail systems (Figure 2-2) were designed to survey any location in the study site within a distance of 40 m. For reducing the bias of time (Hall, 1964; Hayes *et al.*, 1986), censuses took different combination of routes and directions every time. The researcher kept the walking speed about 1 km per hour. The locations of all bird individuals seen or heard were recorded on the map (Figure 2-3). In order to make the census more efficient, each name of bird species were coded. All activities of territorial displaying (singing, calling, and fighting) and attributes of bird individuals (age, gender, movements, and color rings) were also noted as special symbols, based on the system of International Bird Census Committee (Robbins, 1970), on the working maps. There were 66 bird species from 11,740 registration spots, included 15 local breeders (LB; the species bred in study site), 29 neighboring breeders (NB; the species bred in the primary broad-leaved forests near the study site but not in the study site) and 22 wintering species (W; the species never breed in study site or neighboring region, either latitudinal or altitudinal migrants) (Appendix 2).

Statistical analysis

In order to examine whether if the distribution pattern of each species and BSR was random, a set of randomized distribution spots were generated for each species. The randomized distribution spots were selected from a pool generated by ratio of the area of each habitat type (buildings 8%, fields 19%, native forests 40%, orchard 14%, plantations 20%, and ponds 1%). The number of randomized distribution spots of a species was equal to the number of its registration spots in the study site. The randomized distribution spots of all species were compiled to generate the randomized BSR of each habitat type. Generalized linear regression analyses by SYSTAT 12.0 (SYSTAT, 2007) were used to compare SAR function of BSR among six habitat types. I first tested whether if the constants of the SAR functions of different habitat types differ then examined the influences of vertical foliage structure and floristic composition on the constants of SAR functions.

To examine the effects of attributes of landscape structure and vegetation structure to BSR, forward variable selection of generalized linear regression analysis was done for each habitat type. In the whole study site, the effects of attributes of landscape structure and vegetation structure, and the effects of habitat types were analyzed separately. For the effects of attributes of landscape structure and vegetation structure, BSR was the dependent variable; all attributes of landscape structure and vegetation structure were the independent variables. For the effects of habitat types, BSR was the dependent variable; patch area and six habitat types were the independent variables.

Results

The actual BSR of various habitat types significantly differed from random one (Paired *t*-test, $p < 0.05$; Figure 2-4). Native forests (60 species) and plantations (47 species) contained higher BSR than buildings (15 species), fields (34 species), orchards (30 species) and ponds (6 species).

The SAR functions of BSR were compared by different habitat types. BSR was dependent variable; patch area was independent variable. The SAR functions of native forests and plantations were significantly different from buildings (both $p < 0.001$), fields (both $p < 0.001$), orchards (both $p < 0.001$) and ponds (both $p < 0.001$; Figure 2-5). However, there were no significant difference between the SAR function of native forests and plantations ($p = 0.859$; Figure 2-5). The SAR functions of orchards and fields had significant difference with buildings (both $p < 0.001$) and ponds (both $p < 0.01$), but no significant difference between orchards and fields ($p = 0.947$; Figure 2-5). There was also no significant difference between the SAR functions of buildings and ponds ($p = 0.923$; Figure 2-5).

The SAR functions of canopy and sub-canopy plant family richness in native forests and plantations were compared. The patch area was independent variable, and the canopy and sub-canopy plant family richness were dependent variable separately. The canopy plant family richness of native forests and plantations significantly differed from each other in SAR functions ($p < 0.05$; Figure 2-6). Nevertheless, the sub-canopy plant family

richness of native forests and plantations were not significantly different in SAR functions ($p = 0.38$; Figure 2-7).

In the generalized linear regression analyses (forward selection) to examine the effects of the attributes of landscape structure and vegetation structure (listed in Methods) of the whole study site on BSR, total plant family richness was forwarded first, followed by patch area, total foliage volumes and the number of adjacent habitat types (Table 2-1a). For the effects of the six habitat types and patch area on the BSR of the whole study site, patch area was forwarded first, followed by native forest habitat and plantation habitat (Table 2-1b).

Generalized linear regression analyses were used to examine the effects of the attributes of landscape structure and vegetation structure of each habitat type on BSR. For buildings, the sum of the length bordering adjacent plantation patches was the only significant factor for BSR (Table 2-2). For fields, the sum of the length bordering adjacent native forest patches was forwarded first, followed by the estimation of foliage volumes of shrub layer and patch area (Table 2-3). For native forests, the sub-canopy plant family richness was forwarded first, followed by the sum of the length bordering adjacent native forest patches, the estimation of foliage volumes of canopy, and the distance to nearest native forest patch (Table 2-4). For orchards, only total plant family richness was forwarded (Table 2-5). For plantations, patch area was forwarded first, followed by the sum of the length bordering adjacent native forest patches and the distance to nearest native forest patch (Table 2-6). For ponds, the sum of the length bordering adjacent native forest

patches was forwarded first, followed by the sum of the length bordering adjacent field patches and the distance to nearest plantation patch (Table 2-7).

The correlation coefficient of simple correlation between sub-canopy plant family richness and BSR in native forests and plantations was not significantly different ($p = 0.408$; Figure 2-8). In simple correlation, BSR was dependent variable, and the sub-canopy plant family richness was independent variable. There was no significant difference between native forests and plantations in the correlation coefficient of simple correlation.

Path analysis showed that patch area and sub-canopy plant richness significantly affected BSR (Figure 2-9). In path analysis, patch area was exogenous variable, canopy and sub-canopy plant family richness were intervening causal variables of endogenous variable, and BSR was dependent variable of endogenous and intervening causal variables (Figure 2-9). "Patch area", "canopy plant family richness", "sub-canopy plant family richness" and "BSR" were set to the manifest factors, the errors of each manifest factors were set to the latent factors. Patch area ($p < 0.01$) and sub-canopy plant richness ($p < 0.01$) were significant factor to BSR

Discussion

The regression function of actual BSR was significantly different with randomized one. It implies that the distribution of BSR and the registration spots did not distributed randomly. If the bird individuals had no habitat preference at all, the registration spots should distributed randomly, and the BSR of each patch should perfectly follow area relationship. Therefore, this result suggests bird individuals prefer certain habitat characters what might confer greater fitness for them (Block and Brennan, 1993).

Generalized linear regression analyses suggested local vegetation structure was the most important variable for BSR. Patch with higher plant species richness should contain more diverse food resources and attract more insects, thus attracting more bird species (Holmes and Robinson, 1981). The high foliage volumes forms high coverage for birds to avoid predators and bad weathers (Wilson and Comet, 1996). These characters of vegetation attracted more bird individuals enter the patch, resulted in higher BSR.

The buildings and ponds were difficult to attract bird individuals since both habitat types contain few food resources and vegetation shelters. The fields sometimes bare-grounded and attracted some bird species, such as White Wagtail (*Motacilla alba*) and Oriental Tree-pipit (*Anthus hodgsoni*). With some small shrubs or tall grass presented in fields, some bird species which active in shrub layer may be attracted in, such as Steere's Liocichla (*Liocichla steerii*), Strong-footed Bush Warbler (*Cettia fortipes*) and Vinous-throated

Parrotbill (*Paradoxornis webbianus*). In orchards, the vegetation structure was composed by simple vertical foliage structure and low floristic composition. There were almost only single fruit tree species planted in an orchard. When the orchards contained some foraging plants for birds, those plants were usually the key to attract birds. The fields and orchards were under agricultural and horticultural management: removing non-economical plant, and using insecticide and herbicide. These managed methods also affect the vegetation structure and biodiversity negatively (Rands, 1986).

The SAR functions of birds in native forests and plantations significantly differed from those in buildings, fields, orchards, and ponds; but there was no significant difference between native forests and plantations. Between native forests and plantations, the SAR functions of plants of sub-canopy layer were not significantly different; the correlation coefficients of the sub-canopy plant family richness and BSR showed no significant difference. The results implied the plant diversity of sub-canopy was a key factor for the similar BSR between native forests and plantations. In general, native forests contained higher foliage volumes and plant species richness than plantations, therefore the diversity of wildlife was usually higher. In the study site, most plantations have not received silvicultural managements for decades. Most silvicultural management dramatically change the vegetation structure, affect the environment, and usually result in lower species richness of plants and wildlife (Hansen *et al.*, 1991; Zurita *et al.*, 2006; Magura *et al.*, 2008). Without silvicultural management, the plantations had begun secondary succession. Paillet *et al.* (2010) reported BSR was higher in unmanaged forests than in

managed forests, but varied between different taxa. Therefore, abandoning silvicultural management made there was no significance of floristic composition in sub-canopy layers between plantations and native forests; thus made the SAR functions of birds in plantations not significantly differed from native forests.

Generalized linear regression analyses suggested patch area and the neighboring native forests played an important role to sustain BSR in plantations. The effects of landscape configuration were stronger than the vegetation structure in plantations. It means BSR in the plantations which located within native forests may be higher than those in isolated plantations. For the effects of habitat types and patch area on BSR, patch area was forwarded first, followed by native forests and plantations. When the bird individual density was too high in a native forest patch, some of the individuals would move into neighboring plantations, attracted by the plants in sub-canopy layer of plantations. The plantations of Japanese cryptomeria were introduced for wood products few decades ago in Taiwan. Therefore, there are no frequent interspecies interactions between Japanese cryptomeria and native biodiversity, might made the plantations were not the first preferred habitat to native bird individuals.

The effects of the vegetation structure in canopy layer and sub-canopy layer to BSR were different. In the generalized linear regression analyses of native forests, the sub-canopy plant family richness was forwarded first, followed by the foliage volumes of canopy. Path analysis suggested the canopy plant family richness did not affect BSR significantly. This result

supported the vegetation structure in sub-canopy layer played more important role than canopy layer in sustaining diverse bird community in native forests and plantations. In general, the species richness of plant in sub-canopy layer is higher than canopy layer, because some plant species are seldom dominant in canopy layer (Spies, 1998). The vegetation structure in sub-canopy layer was important to birds, because most bird species foraging around the sub-canopy layer, less bird species only active in canopy layer in this study. Vargas-Contreras *et al.* (2009) observed the frugivorous bat abundance follows with the fruit mass positively in understory, because the fruit density in understory is higher than canopy layer. This implied the floristic composition of sub-canopy layer provided more food resources than canopy layer to attract wildlife. The diverse floristic composition also makes more complex vertical foliage structure, so there were two major functions of sub-canopy: providing food resources and shelters. The function of canopy layer may mainly provided shelters, so the effects of canopy layer to increase BSR were weaker than sub-canopy layer.

Species richness increases with area, but this area factor was not dominant in this study. Patch area was only forwarded in the analysis of the whole study site, fields and plantations, and its effects were weaker than the effects of vegetation structure. The standard coefficients of patch area were negative, because patch area of native forests and plantations (higher suitability for birds) were usually smaller than buildings, fields, orchards and ponds (lower suitability for birds). This character make the effects of patch area were contrary to the conventional prediction of SAR: species increases

with area (Herrando and Brotons, 2002; Santos *et al.*, 2002). The effects of patch area to BSR were strongly affected by the complexity of vegetation structure. Kallimanis *et al.* (2008) reported the SAR functions are affected by increasing habitat heterogeneity in many ways, but commonly increase the slope of SAR functions. The complex vegetation structure provides specific benefits (food resources and shelters) to bird individuals directly, but patch area does not always. In general, larger patch with complex vegetation structure is the best to sustain biodiversity. Excluding the best situation, to sustain higher BSR, smaller patch with complex vegetation structure was better than the larger patch with less vegetation structure. It was difficult to sustain higher BSR in a patch with very simple vegetation structure, such as buildings, fields, and ponds, even though the area was large.

Shape complexity were never forwarded in any generalized linear regression analyses. It suggested that shape complexity was not an important factor to BSR in this fragmented environment. Shape complexity affects the amount of core area and edges of patches (Laurance and Yensen, 1991). However, it may not important to birds with high moving ability.

Generalized linear regression analyses suggested BSR of buildings, fields, plantations, and ponds were majorly affected by patch area and landscape configuration. The neighboring patches with complex vegetation structure provides additional habitat for species and attracts the movement of bird individuals between habitat patches (Haynes *et al.*, 2006). Lindenmayer *et al.* (2010) suggested the total amount of native vegetation in neighboring patches is important to sustain BSR, rather than the effect of patch area. In

the mosaic landscape, BSR of the patch with simple vegetation structure was dominantly increased by the neighboring patches with complex vegetation structure. Birds, a taxon with high ability of movement, are easy to move among patches (Block and Brennan 1993). In the patches with simple vegetation structure, these bird individuals might just pass or stay for a short period time, or get an obvious place for territory guarding from neighboring patches (Block and Brennan, 1993). The composition of nearby habitats affected BSR of the patches with simple vegetation structure stronger, making the distance to nearest native forest patch negatively correlated with BSR. Therefore, species richness can be affected by the individuals from neighboring habitats, especially in taxa with better ability of movement.

Path analysis revealed patch area was still an important factor to BSR in native forests and plantations. This result supported area is the major factor to affect species richness of any taxa. However, the vegetation structure was also the very important factor to increase BSR, especially in very small patches. Evans *et al.* (2009) reported the urban avian community responds positively to complexity of vegetation structure, and negatively to artificial patch. The authors concluded local variables are more important than regional ones to BSR, especially in the region with lower habitat quality (Evans *et al.*, 2009). I concluded that patch area is still a major factor to sustain native biodiversity in fragmented landscapes. The large area and complex vegetation structure habitat are the best for native avian community. In small patches, local vegetation structure is the key factor to sustain higher native biodiversity, to both local patch and neighboring patches.

Tables

Table 2-1a. The forward variable selection in generalized linear regression analysis examining the effects of attributes of landscape structure and vegetation structure to bird species richness in the study site. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	0.596	<0.001
1	Total Plant Family Richness	1453.96	--	0.317	<0.001
2	Patch Area	1407.05	46.91	-0.371	<0.001
3	Total Foliage Volumes	1386.99	20.06	0.475	<0.001
4	The Number of Adjacent Habitat Type	1384.70	2.29	0.072	<0.05

Table 2-1b. The forward variable selection of generalized linear regression analysis examining the effects of patch area and six habitat types to bird species richness in the study site. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	2.016	<0.001
1	Patch Area	1704.19	--	-0.536	<0.001
2	Native Forests	1639.88	64.31	0.484	<0.001
3	Plantations	1572.17	67.71	0.332	<0.001

Table 2-2. The forward variable selection of generalized linear regression analysis examining the effects of attributes of landscape structure and vegetation structure to bird species richness in buildings. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	0.536	<0.001
1	Adjacent Plantations	115.34	--	0.605	<0.001

Table 2-3. The forward variable selection of generalized linear regression analysis examining the effects of attributes of landscape structure and vegetation structure to bird species richness in fields. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	2.232	<0.001
1	Adjacent Native Forests	231.374	--	0.430	<0.010
2	Foliage Volumes of Shrub	226.043	5.331	0.295	<0.010
3	Patch Area	218.174	7.869	0.363	<0.010

Table 2-4. The forward variable selection of generalized linear regression analysis examining the effects of attributes of landscape structure and vegetation structure to bird species richness in native forests. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	4.035	<0.001
1	Sub-canopy Plant Family Richness	593.970	--	0.221	<0.001
2	Adjacent Native Forests	587.096	6.874	0.266	<0.010
3	Foliage Volumes of Canopy	582.512	4.584	0.179	<0.010
4	Distance to Native Forest	578.052	4.460	-0.162	<0.050

Table 2-5. The forward variable selection of generalized linear regression analysis examining the effects of attributes of landscape structure and vegetation structure to bird species richness in orchards. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	4.863	<0.01
1	Total Plant Family Richness	81.604	--	0.534	<0.05

Table 2-6. The forward variable selection of generalized linear regression analysis examining the effects of attributes of landscape structure and vegetation structure to bird species richness in plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value	R ²
	Constant	--	--	5.169	<0.001	--
1	Patch Area	278.079	--	0.358	<0.001	0.542
2	Adjacent Native Forests	264.757	13.322	0.254	<0.001	0.657
3	Distance to Native Forest	256.312	8.445	-0.381	<0.010	0.718

Table 2-7. The forward variable selection of generalized linear regression analysis examining the effects of attributes of landscape structure and vegetation structure to bird species richness in ponds. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value	R ²
	Constant	--	--	-0.049	0.681	--
1	Adjacent Native Forests	15.023	--	0.366	<0.05	0.822
2	Adjacent Fields	11.192	3.831	0.574	<0.01	0.901
3	Distance to Plantation	0.738	10.454	-0.320	<0.01	0.971

Figures

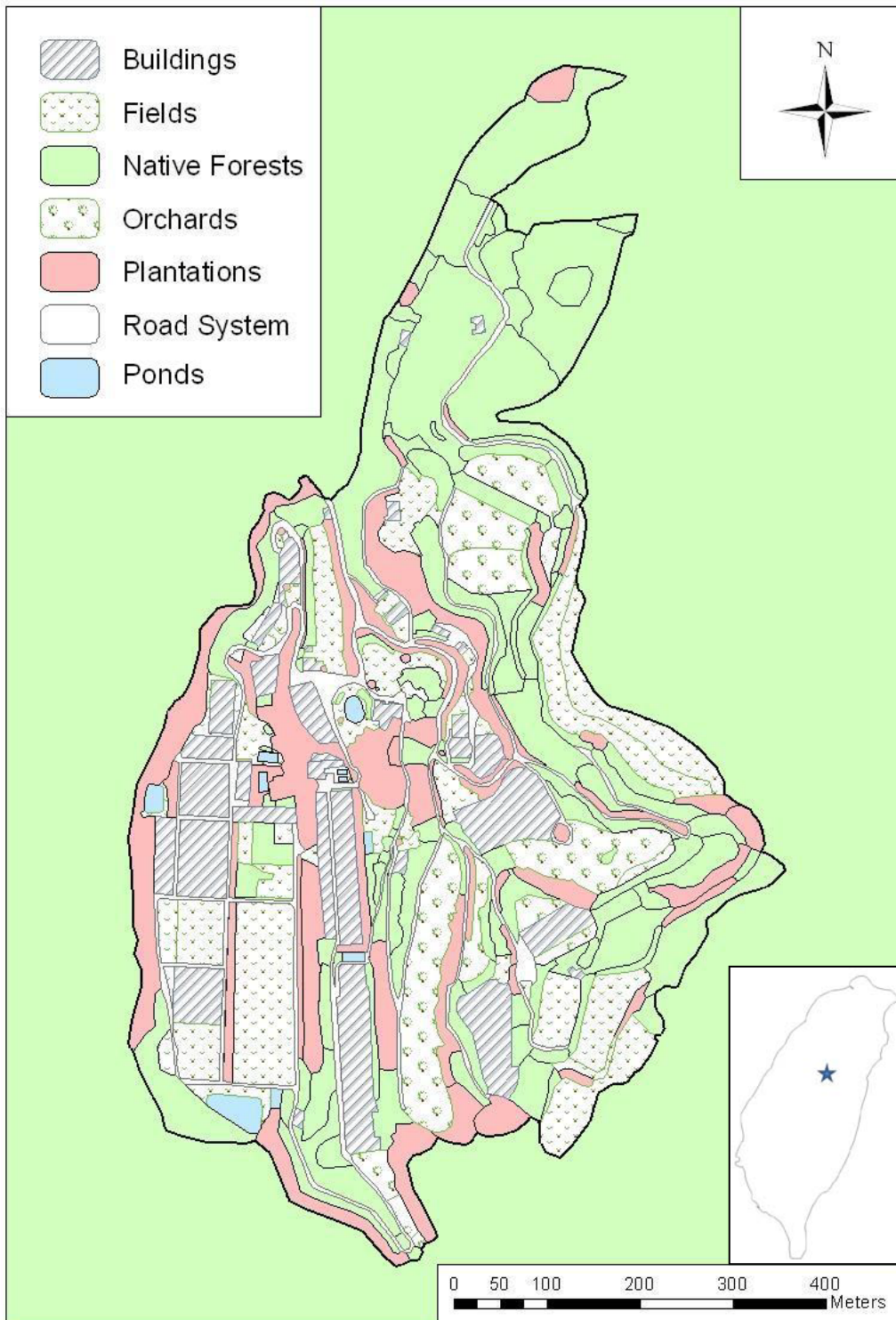


Figure 2-1. Map of the location and six habitat types of the study site.

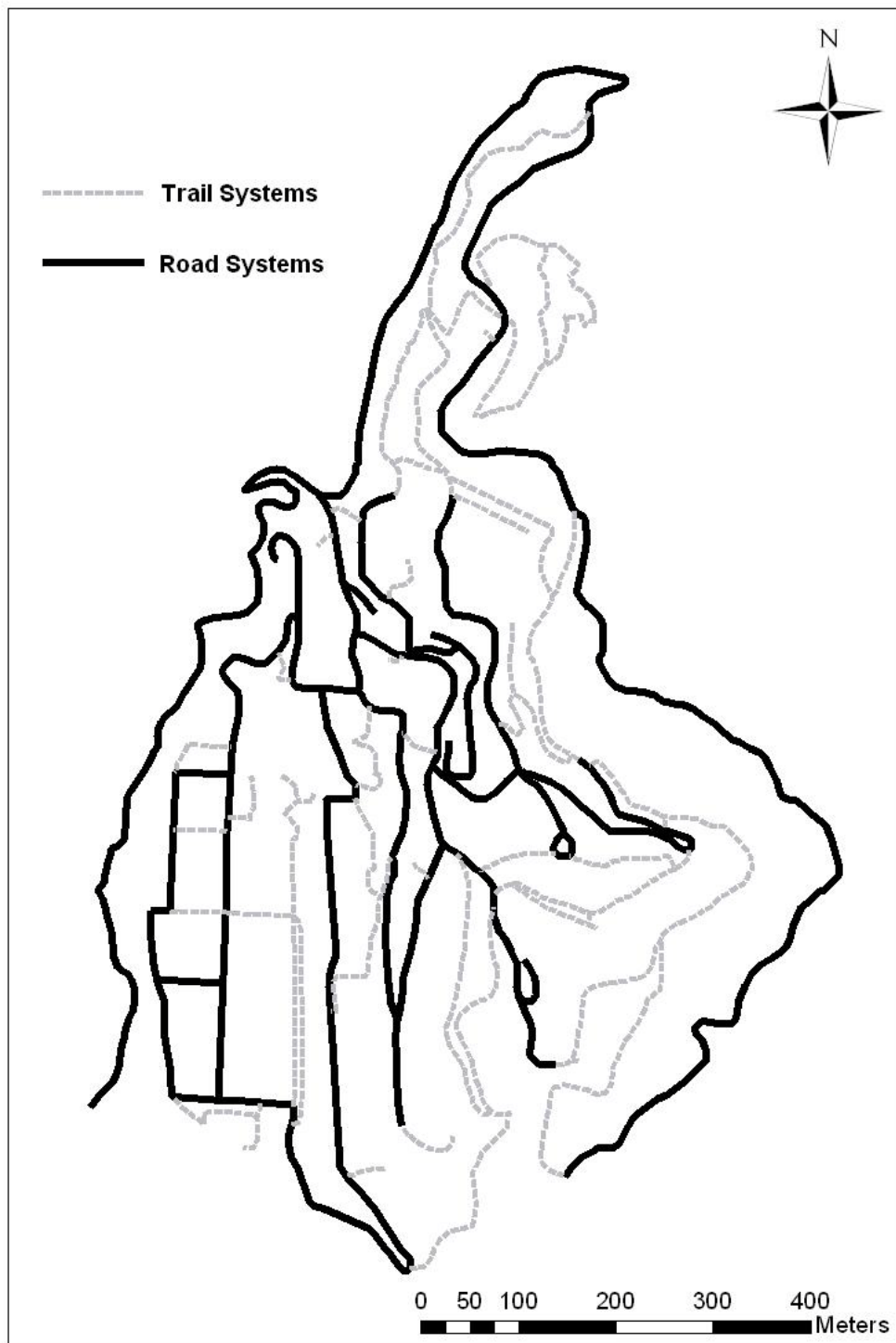


Figure 2-2. The road and trail systems in the study site.

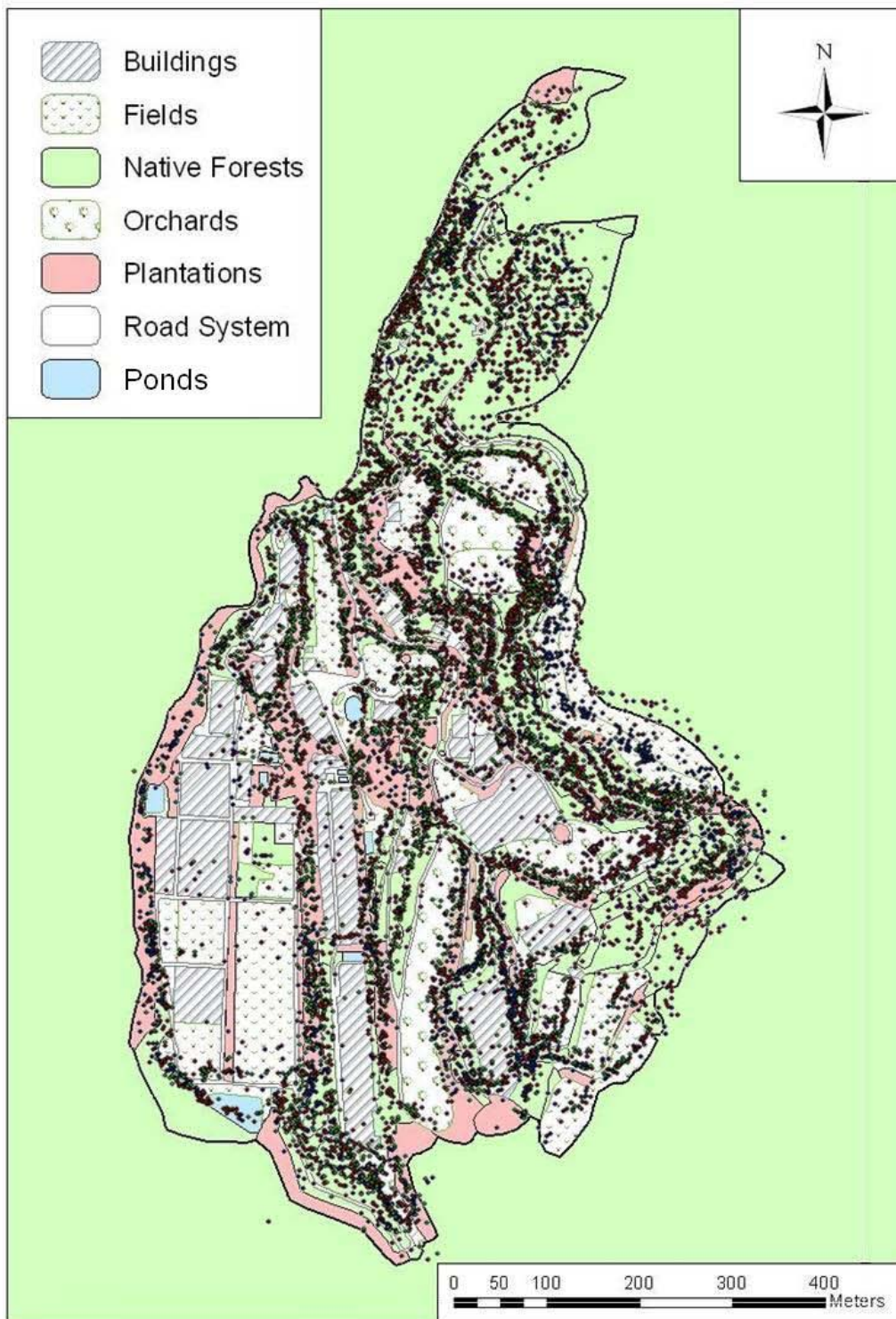


Figure 2-3. The map of the study site with six habitat types and all registration spots of bird individuals.

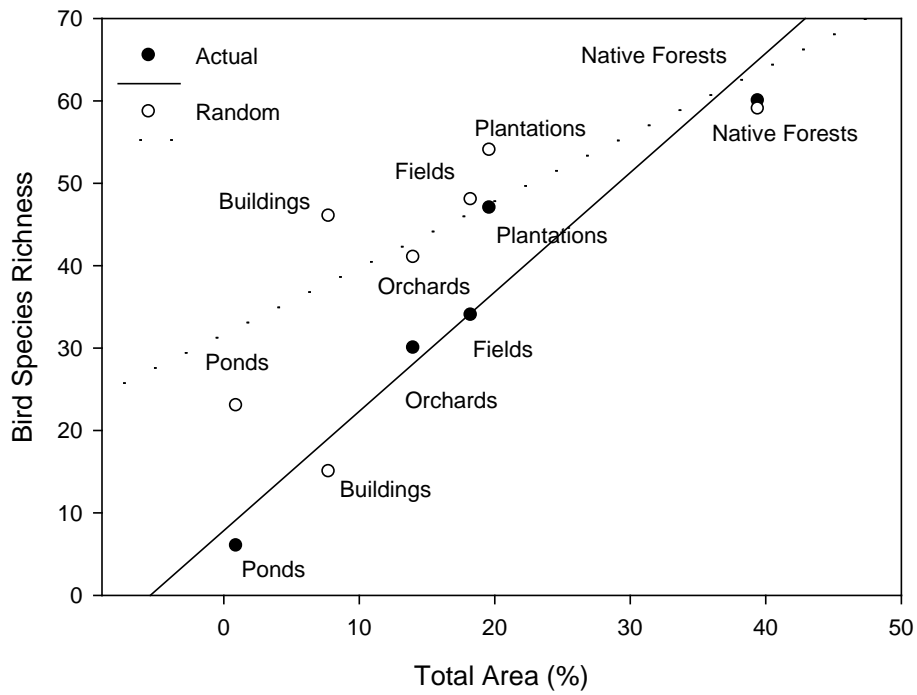


Figure 2-4. The comparison of actual and randomized bird species richness of six habitat types. Actual and randomized bird species richness distribution were significantly different (Paired t-test, $p < 0.05$).

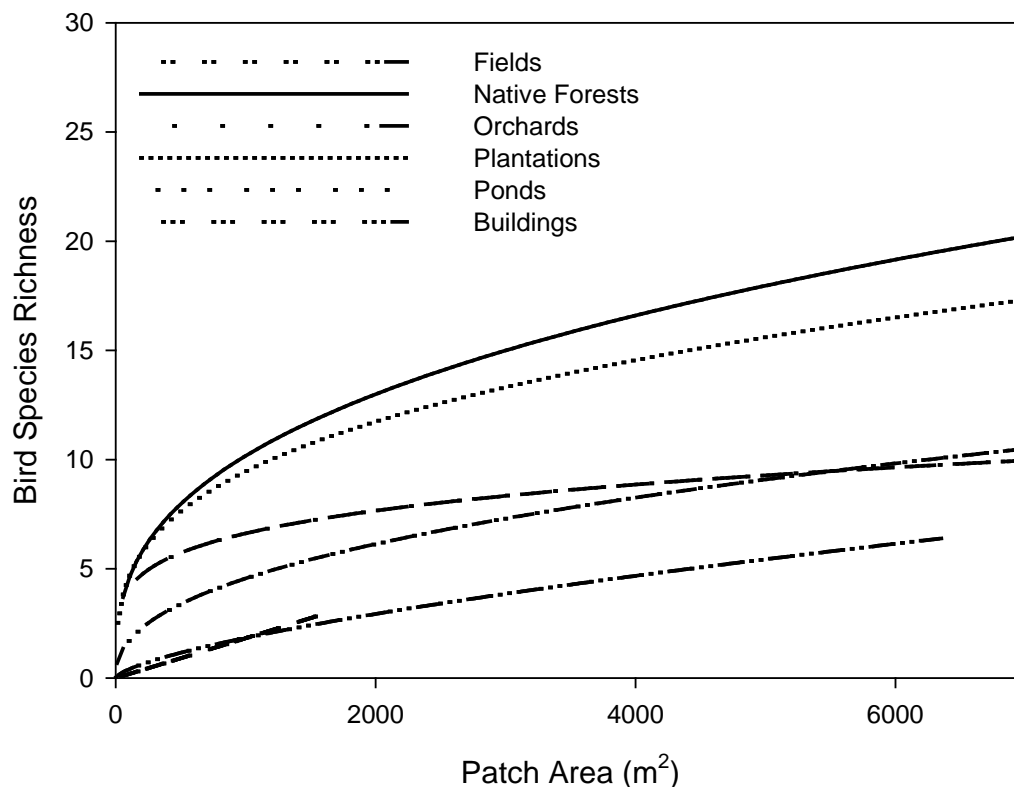


Figure 2-5. The comparison of species-area relationship (SAR) functions of bird species richness of each habitat type (Buildings: $S = 0.018 A^{0.674}$, $R^2 = 0.452$; Fields: $S = 0.235 A^{0.429}$, $R^2 = 0.572$; Native Forests: $S = 0.885 A^{0.354}$, $R^2 = 0.631$; Orchards: $S = 1.554 A^{0.210}$, $R^2 = 0.236$; Plantations: $S = 1.109 A^{0.310}$, $R^2 = 0.668$; Ponds: $S = 0.002 A^{1.013}$, $R^2 = 0.730$). The SAR functions of native forests and plantations were significantly different from buildings (both $p < 0.001$), fields (both $p < 0.001$), orchards (both $p < 0.001$) and ponds (both $p < 0.001$). However, there were no significant difference between the SAR functions of native forests and plantations ($p = 0.859$). The SAR functions of orchards and fields had significant difference with buildings (both $p < 0.001$) and ponds (both $p < 0.01$), but no significant difference between orchards and fields ($p = 0.947$). There was also no significant difference between the SAR functions of buildings and ponds ($p = 0.923$).

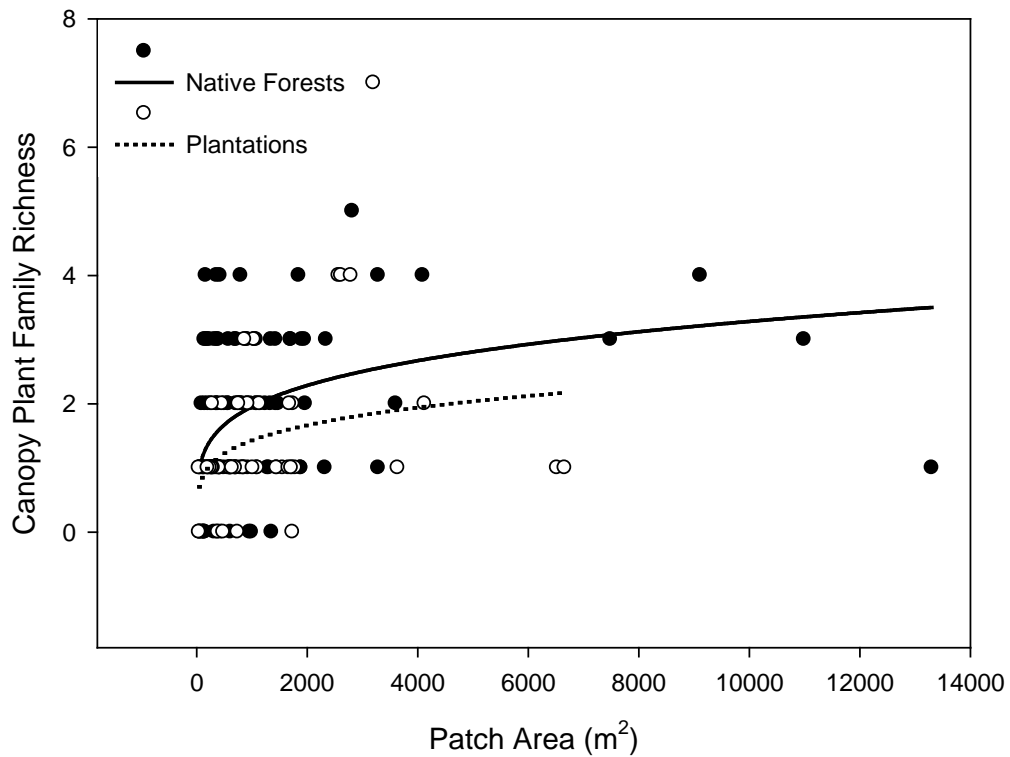


Figure 2-6. The comparison of species-area relationship functions of canopy plants family richness between native forests and plantations (Native Forests: $S = 0.414 A^{0.225}$, $R^2 = 0.153$; Plantations: $S = 0.314 A^{0.220}$, $R^2 = 0.125$). The canopy plant family richness of native forests and plantations was significantly different ($p < 0.05$).

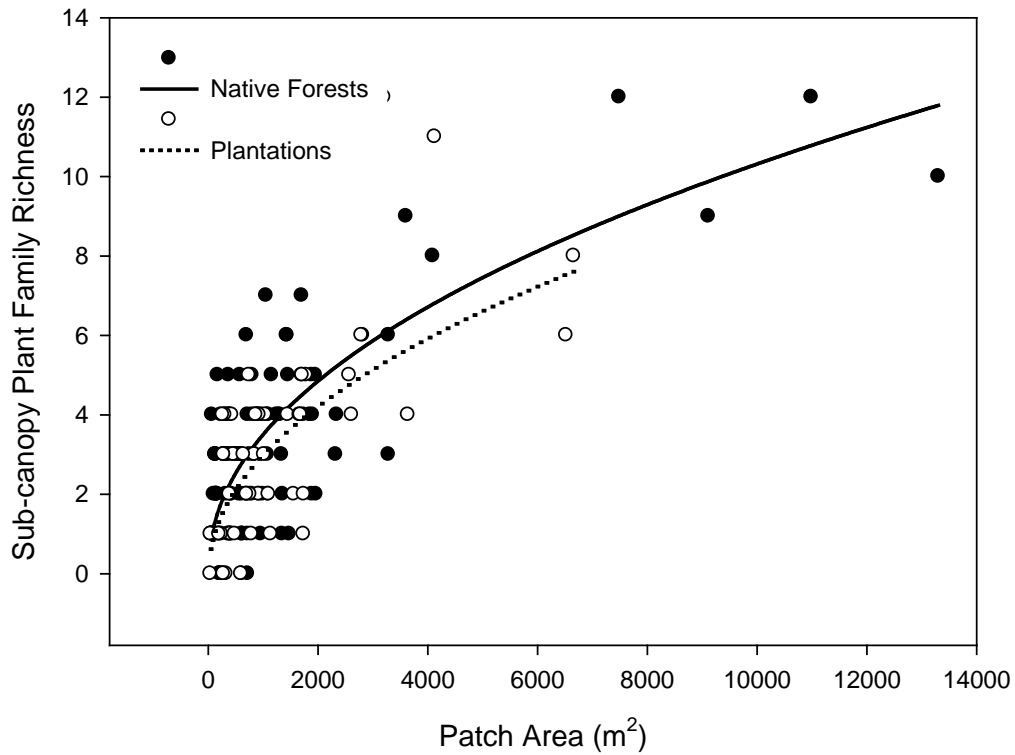


Figure 2-7. The comparison of species-area relationship functions of sub-canopy plants family richness between native forests and plantations (Native Forests: $S = 0.138 A^{0.469}$, $R^2 = 0.566$; Plantations: $S = 0.101 A^{0.491}$, $R^2 = 0.500$). The sub-canopy plant family richness of native forests and plantations was not significantly different ($p = 0.38$).

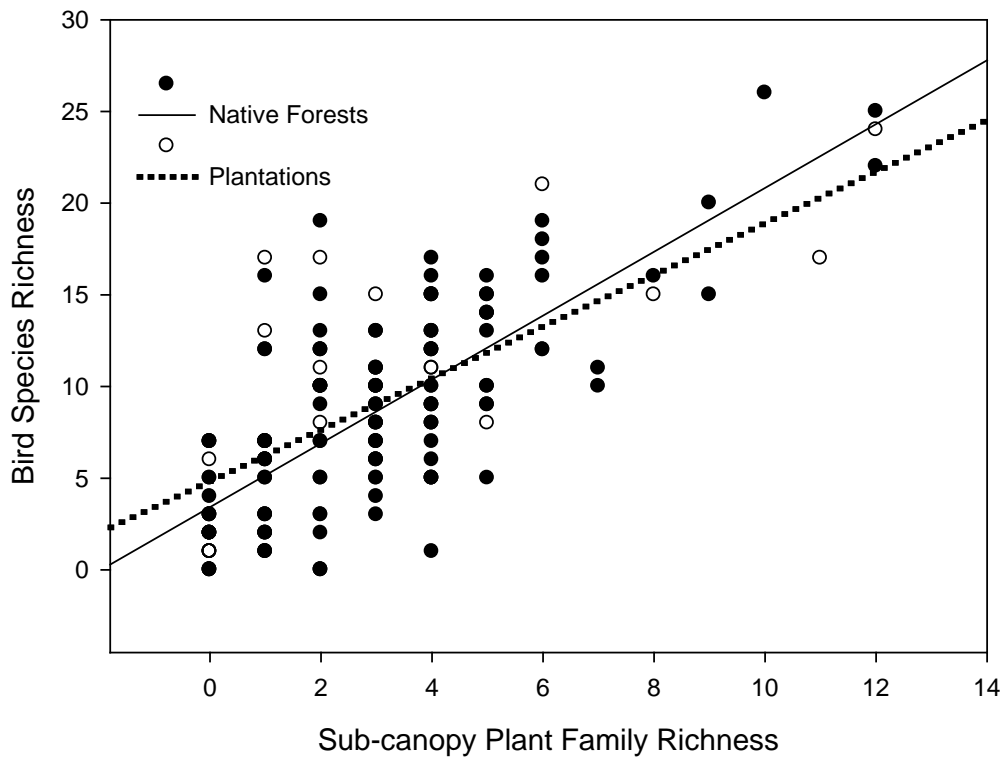


Figure 2-8. The comparison of correlation relationships between bird species richness and sub-canopy plant family richness of native forests and plantations (Native Forests: $y = 1.740x + 3.429$, $R^2 = 0.557$; Plantations: $y = 1.407x + 4.847$, $R^2 = 0.462$). The correlation coefficient of sub-canopy plant family richness and bird species richness in native forests and plantations were not significantly different ($p = 0.408$).

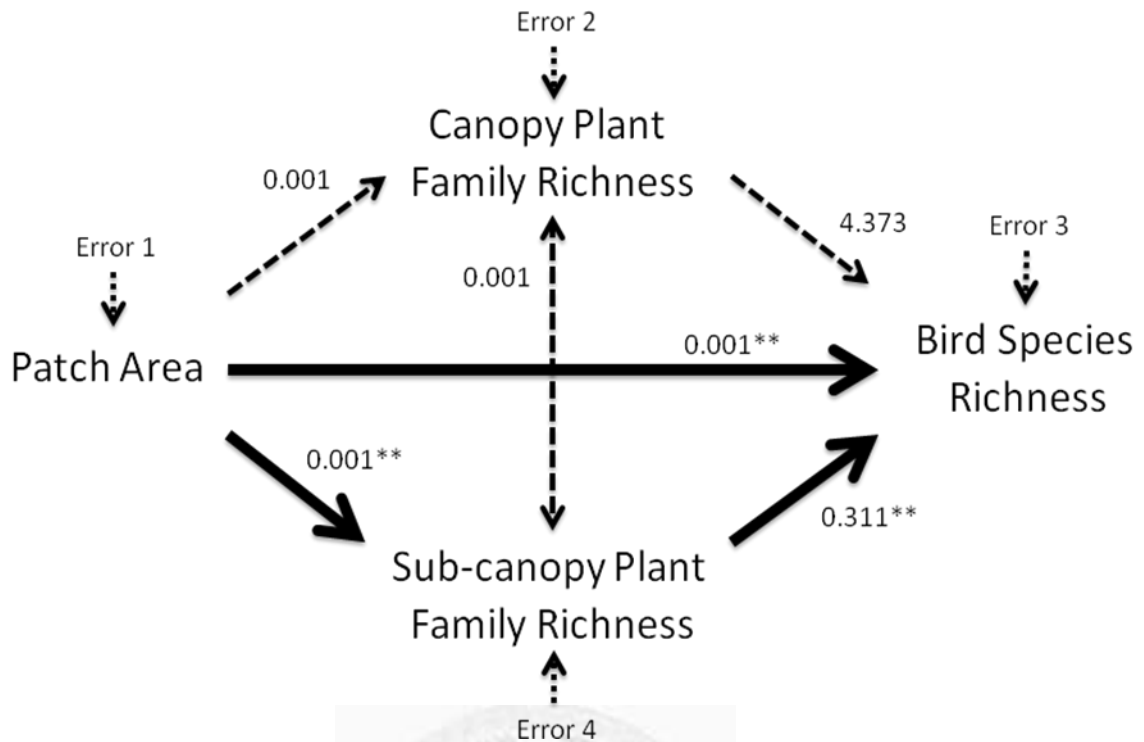


Figure 2-9. The model of path analysis: patch area was exogenous variable, canopy and sub-canopy plant family richness were intervening causal variables of endogenous variable, and the bird species richness was dependent variable of endogenous variable. Patch analysis suggest that patch area and sub-canopy plant family richness affected bird species richness significantly. The point estimates were marked besides the arrows, ** $p < 0.01$.

CHAPTER 3

Habitat Preferences of Bird Individuals in Fragmented Landscape

Abstract

Habitat fragmentation has been seriously threatening biodiversity, but recent studies show its effects are not universal to all species. To understand effects of habitat fragmentation to biodiversity clearly, it is necessary to examine habitat preference of individuals of a species in a fragmented landscape at finer scale. The study site, Meifeng Highlands Experimental Farm of National Taiwan University, was classified into 286 patches and six habitat types (buildings, fields, native forests, orchards, plantations, and ponds). The locations of all observed bird individuals (66 species, 11,740 registration spots) were mapped during three breeding seasons from 2005 to 2007. The vegetation structures of the 286 patches were measured in 2007.

Almost 90% of the registration spots were located within native forests and plantations. Among the six habitat types, only native forests and plantations positively correlated with the presences of bird individuals. For the habitat preferences of different reproductive statuses and ecological guilds, the variables of foliage volume were usually forwarded first than the variables of floristic composition. Foliage volume of sub-canopy was forwarded first in the analysis of local breeders; and foliage volume of canopy was forwarded

first for neighboring breeders. For omnivores, the variables of floristic composition were forwarded; but not forwarded for insectivores. In the analyses by species, foliage volume of sub-canopy was forwarded frequently. Within the landscape mosaic of the study site, the effects of habitat type were stronger than patch area to attract bird individuals; and the effects of vertical foliage structure was stronger than floristic composition to bird individuals. At finer scale of habitat preferences, vertical foliage structure and floristic composition of canopy and sub-canopy layers played different roles to different reproductive statuses, ecological guilds, and species. Omnivores preferred habitats with higher floristic composition; and insectivores preferred habitats with more complex vertical foliage structure. The habitats with complex vertical foliage structure in sub-canopy layer may attract omnivores, insectivores, and the bird species dwelling in other vertical foliage layers. These results explain the high correlation between vegetation structure and bird species richness. It is difficult to attract bird individuals in a large-area patch with inappropriate habitat type and vegetation structure. I conclude that increasing the complexity and diversity of vegetation structure is important to sustain more bird individuals and species, especially within small patches. At the same time, it is also an important management strategy to increase biodiversity in fragmented environments.

Keywords: bird individuals, floristic composition, habitat fragmentation, patch area, Taiwan, vertical foliage structure

摘要

棲地破碎化已經嚴重地威脅生物多樣性，但是近期研究顯示其對物種的影響並不一致。為了清楚瞭解棲地破碎化對生物多樣性的效應，必須從個體層級與細尺度下檢驗該效應對各物種棲地偏好的影響。研究地點（國立臺灣大學梅峰山地實驗農場）區分成 286 個區塊以及六種棲地類型（建築、耕地、天然林、果園、人工林、及水池）。2005 到 2007 年的三個繁殖季中，所有被觀察到的鳥類個體（共 66 種、11,740 個紀錄點）的位置皆記錄於地圖上，這 286 區塊的植群結構則在 2007 年測量。

將近 90% 的紀錄點位於天然林及人工林中。六種棲地類型中，僅有天然林及人工林與鳥類個體的存在呈正相關。在不同繁殖狀態及覓食同功群的分析中，與枝葉量有關的變量通常比與植群組成有關的變量先被篩選。在地繁殖者的分析中，次冠層的枝葉量先被篩選；鄰地繁殖者的分析中，則是冠層的枝葉量先被篩選。與植物組成有關的變量在雜食者的分析中被篩選，但是並未在食蟲者的分析中被篩選。在各鳥種的分析中，次冠層的枝葉量被篩選的頻率相當高。在地景鑲嵌體中，棲地類型吸引鳥類個體的效應比區塊面積還要來的強烈；而垂直枝葉結構對鳥類個體的吸引力可能比植物種類組成強烈。在細尺度中，冠層與次冠層的植群結構與植物種類組成的重疊程度分別因不同繁殖狀態、生態同功群及物種的個體而異。雜食者可能較偏好植物種類組成較多樣的棲地，而蟲食者則可能較偏好垂直枝葉結構較複雜的棲地。於次冠層具有複雜垂直枝葉結構的棲地應該能吸引雜食者、蟲食者，以及活動在冠層、次冠層、灌木層與地面層的鳥種。這些結果支持植群結構與鳥類群聚有高度相關的解釋。對鳥類個體而言，不適當的棲地類型和植群結構，即使面積再大也無法吸引鳥類個體。我的結論是：即使在面積較小的區塊中，植群結構的複雜度與種類多樣性對維持較高鳥類個體數與較高鳥種豐富度相當重要。同時，這也是在破碎化的環境中提高生物多樣性的經營策略。

關鍵詞：鳥類個體、植群組成、棲地破碎化、區塊面積、臺灣、垂直枝葉結構

Introduction

Habitat fragmentation has been a serious threat to biodiversity (Margules and Pressey, 2000; reviewed by Fahrig, 2003; Balmford, 2005), but the effects are not always universal to all species (Andrén, 1994). To make sound management and conservation strategies for native biodiversity, it is important to understand the wildlife-habitat relationships at a perspective of individual in fragmented environments (reviewed by Fahrig, 2003).

In general, habitat is a space where wildlife live. The individuals get resources for their survival and reproduction, and against their competitors, predators, and bad weathers (Block and Brennan, 1993; Morrison *et al.*, 2006). Therefore, the presence and absence of an individual among habitats reflect the physical and biological resources of their requirements (Morrison *et al.*, 2006).

Habitat selection is the process that an individual based on its innate and learned behavior, responses to distinguish different habitats among various landscape components and exhibits certain preferences of habitats (Block and Brennan, 1993). Therefore, habitat selection indicates the results of complex interactions among the effects of environmental responses, behavioral strategies and morphological constrains (Cody, 1985; McCollin, 1998) to enable survival and ultimate fitness (Johnson, 1980; Hutto, 1985; Block and Brennan, 1993; Jones, 2001). Johnson (1980) suggested that habitat selection is a hierarchical framework: first-order selection as landscape range; second-order selection as home range within landscape

range; third-order selection as the specific site within home range; and fourth-order selection as the site to get resources. This is not only a key index for understanding the life history of wildlife, but also a fundamental theory of wildlife management and conservation (Cody, 1985; Block and Brenna, 1993; Schooley, 1994; Morrison *et al.*, 2006; Deppe and Rotenberry, 2008).

Lack (1933) referred that the characters of habitat are the triggers to attract individuals to select a habitat. This idea is the basic concept of habitat selection and induces numerous studies on wildlife-habitat relationships. Svårdson (1949) and Hildén (1965) developed habitat selection as two process: the selection based on the characters of habitat and/or vegetation structure among environmental components at first, and then influenced by biotic interactions, such as intraspecific (Butler, 1980) and interspecific competitors (Werner and Hall, 1979), and predators (Werner *et al.*, 1983). Fretwell and Lucas (1970) assumed that an individual would use the habitat of highest suitability at first, and then expand to second habitat. This model is based on three assumptions: (1) suitability of habitat decreases with increasing intra-species competition by denser population density; (2) the best selective strategies maximize fitness of the individual; (3) the individual is free to enter any habitats (Fretwell and Lucas, 1970). When the suitability of the first habitat equals to the highest suitability of the second habitat, parts individuals will expand to other habitats (Fretwell and Lucas, 1970).

Bird is a suitable taxon to study habitat selection. The major reasons include: (1) high flying ability make birds can change habitat rapidly; (2) habitat preference between different birds species are obvious; (3) comparing to other taxa of wildlife, it is easier to identifying and observing different bird

species (Brown, 1984; Konishi *et al.*, 1989). Therefore, ornithologists had been played the key role in the development of the habitat concept in ecology and habitat selection studies.

In terrestrial ecosystems, habitats are usually determined by vegetation structure; habitat type is often defined by vegetation type (Hutto, 1985), plant community types (Ricklefs, 1979). Vegetation structure, an important factor to approach wildlife-habitat relationship (Wiens and Rotenberry, 1981; Law and Chidel, 2002), usually greatly determines the distribution of bird individuals (MacArthur and MacArthur, 1961; Cody, 1985; Rotenberry, 1985; Block and Brennan, 1993; Morrison *et al.*, 2006). The relationship of vegetation structure and avian community has been developed to the vegetation-habitat concept (Wiens, 1989), an important part of theory in avian ecology (Block and Brennan, 1993).

Vegetation structure can be distinguished as two basic and obvious aspects: vertical foliage structure (or physiognomy) and floristic composition (the composition of plant taxa) (Hildén, 1965; Wiens, 1969; Rotenberry, 1985; Block and Brennan, 1993). For vertical foliage structure, MacArthur and MacArthur (1961) constructed foliage height diversity-bird species richness hypothesis: bird species richness (BSR) increases with complex foliage height diversity (FHD). They reported that the more complex vertical foliage structure provides more micro-habitats and ecological niches to contain more bird individuals and species. The shelters increase the efficiency of individuals move through the habitats to forage, against biotic and abiotic threats (Hildén, 1965; Robinson and Holmes, 1982; 1984). Floristic composition is also the key to construct the distribution of bird individuals; different plant species

directly and indirectly affect the distribution of ecological resources (especially food resources) (Holmes and Robinson, 1981; Rotenberry, 1985). Each bird species may have different preference to various resources and exhibit the pattern of habitat use (MacArthur and MacArthur, 1961).

Rotenberry (1985) observed that vertical foliage structure is more important at broader scale, whereas floristic composition is more important at finer scales. This means these two aspects of vegetation structure convey different information about the distribution of resources, and different functions to bird individuals (Deppe and Rotenberry, 2008). This also reflects the hierarchical decision-making process in habitat selection (Johnson, 1980; Hutto, 1985): the bird individuals select the habitat according to vertical foliage structure (physiognomy) first, and then find the locations of resources to fit their requirements of foraging, nesting and *etc.* Above of all, these examinations explains why many bird individuals present in forests, the habitat type with most complex vegetation structure (MacArthur and MacArthur, 1961; Carey *et al.*, 1999; Hunter, 1999). It is reasonable to expect that habitats with certain combinations of vertical foliage structure and floristic composition would attract many bird individuals.

Rotenberry (1985) argued that the vertical foliage structure and floristic composition play different roles to the hierarchical decision-making process in habitat selection in different scales. However, it is difficult to clearly conduct census or investigation works of wildlife communities and vegetation structure at broader scale. These two aspects may also convey different functions of different species at finer scale. Rotenberry (1985) also referred that the finer scale (within-habitat type) investigations are better to untangle the

mechanisms of wildlife-habitat relationships. To increase the efficiency of management and conservation strategies, it is important to understand the details of habitat preferences of bird species respectively at finer scale.

This study was aimed to understand the effects of habitat types and vegetation structures to attract bird individuals at a finer scale. This study was conducted in a 50 ha study site with fragmented landscape. The locations of all observed bird individuals were mapped during three breeding seasons from 2005 to 2007. The landscape of study site was classified into 286 patches of six major habitat types (buildings, fields, native forests, orchards, plantations, and ponds). Vertical foliage structure and floristic composition of the 286 patch were measured in 2007. To understand the habitat preference of different statuses (local breeders, neighboring breeders, and wintering species), ecological guilds (omnivores and insectivores), and the species with enough number of registration spots for analyses, the effects of habitat type, vertical foliage structure, and floristic composition to the presence / absence of bird individuals were examined.

Methods

Descriptions of the study site and field works (attributes of landscape structure, vegetation structure, and avian community census) are specified in the Methods of Chapter 2.

Statistical analysis

The bird species were classified into three reproductive statuses in the study site: local breeders (LB, the species bred in study site; 15 species), neighboring breeders (NB, the species bred in the primary broad-leaved forests near the study site but not in the study site; 29 species) and wintering species (W, the species never bred in study site or neighboring region, either latitudinal and altitudinal migrants, 22 species) (Appendix 2). Several common species with distinct diet were also grouped by ecological guilds, Taiwan Yuhina (*Yuhina brunneiceps*), Steere's Liocichla (*Liocichla steerii*), and Taiwan Sibia (*Heterophasia auricularis*) were grouped into omnivores; Ferruginous Flycatcher (*Muscicapa ferruginea*), Thicket Flycatcher (*Ficedula hyperythra*), and Vivid Niltava (*Niltava vivida*) were grouped to insectivores (Family Muscicapidae).

To test the effects and interactions of patch area and six habitat types (buildings, fields, native forests, orchards, plantations, and ponds) on the habitat preferences of all bird individuals, forward variable selection of binary logistic regression analysis was done by SPSS 17.0 (SPSS, 2007) for all registration spots and null spots in the whole study site. To test the effects and interactions of attributes of vegetation structure (listed in the Methods of

Chapter 2) on the habitat preferences of bird individuals in native forests and plantations, forward variable selection of binary logistic regression analysis was done for each reproductive status, ecological guild, and common species (the number of registration spots of the species enough for analyses) of birds.

In the binary logistic regression analysis, the dependent variable must be either 0 or 1. The actual registration spots were assigned as 1 and the null spots were assigned as 0 in the dependent variable. The null spots were generated regularly on the map of the study site (Figure 3-1). The total amount of null spots was approximately equaled to the total amount of the actual registration spots in each examination. The amount of null spots in certain patch was proportional to patch area. Therefore, the amounts of null spots of each patch were perfectly proportional to patch area. To follow the assumption of binary logistic regression, the independent variables must be numerical. The categorical data (habitat types) were transformed into numerical variables by indicator variables (Neter *et al.*, 1996). All independent variables were standardized ($-1 \leq X \leq 1$, mean = 0) respectively before binary logistic regression analyses. In the examination to all bird individuals, the attributes of patch area and six habitat types were the independent variables. In the examination of different reproductive statuses, ecological guilds, and common species, the attributes of vegetation structure in native forests and plantations were the independent variables.

Results

There were 11,740 registration spots recorded in total. 88.09 % distributed in native forests and plantations, 0.81 % in buildings, 6.94 % in fields, 4.10 % in orchards, and 0.06 % in ponds. In the binary logistic regression analyses (forward selection) to examine the effects and interactions of patch area and six habitat types on bird individuals, buildings were forwarded first, followed by orchards, fields, patch area, ponds, native forests, and plantations (Table 3-1). Only native forests and plantations had positive standard coefficients; buildings, orchards, fields, patch area, and ponds had negative standard coefficients.

Binary logistic regression analyses were used to examine the effects of vegetation structure on different reproductive statuses and ecological guilds of birds. For local breeders, foliage volume of sub-canopy was forwarded first, followed by canopy plant family richness, and sub-canopy plant family richness (Table 3-2). For neighboring breeders, foliage volume of canopy was forwarded first, followed by sub-canopy plant family richness (Table 3-3). For wintering species, foliage volume of sub-canopy was forwarded first, followed by foliage volume of canopy, and canopy plant family richness (Table 3-4). For omnivores, foliage volume of sub-canopy was forwarded first, followed by canopy plant family richness, and sub-canopy plant family richness (Table 3-5). For insectivores, foliage volume of canopy was forwarded first, followed by foliage volume of sub-canopy (Table 3-6).

Binary logistic regression analyses were used to examine the effects of

vegetation on 12 common local breeding bird species. For Taiwan Yuhina, foliage volume of sub-canopy was forwarded first, followed by canopy plant family richness, foliage volume of shrub, sub-canopy plant family richness, and foliage volume of canopy (Table 3-7). For Steere's Liocichla, foliage volume of sub-canopy was forwarded first, followed by canopy plant family richness, sub-canopy plant family richness, and foliage volume of shrub (Table 3-8). For Taiwan Sibia, canopy plant family richness was forwarded first, followed by foliage volume of sub-canopy, sub-canopy plant family richness, foliage volume of shrub, and foliage volume of canopy (Table 3-9). For Gray-cheeked Fulvetta (*Alcippe morrisonia*), foliage volume of canopy was forwarded first, followed by canopy plant family richness, foliage volume of sub-canopy, foliage volume of shrub, and sub-canopy plant family richness (Table 3-10). For Red-headed Tree Babbler (*Stachyris ruficeps*), foliage volume of sub-canopy was forwarded first, followed by canopy plant family richness, foliage volume of shrub, and sub-canopy plant family richness (Table 3-11). For Bamboo Partridge (*Bambusicola thoracicus*), foliage volume of sub-canopy was forwarded first, followed by foliage volume of canopy, and canopy plant family richness (Table 3-12). For White-tailed Blue Robin (*Myiomela leucura*), foliage volume of sub-canopy was forwarded first, followed by canopy plant family richness (Table 3-13). For White-throated Flycatcher Warbler (*Abroscopus albogularis*), foliage volume of canopy was forwarded first, followed by sub-canopy plant family richness, foliage volume of sub-canopy (Table 3-14). For Brown Bullfinch (*Pyrrhula nipalensis*), foliage volume of sub-canopy was forwarded first, followed by sub-canopy plant family richness (Table 3-15). For Strong-footed Bush Warbler (*Cettia fortipes*),

foliage volume of shrub was forwarded first, followed by foliage volume of canopy, and sub-canopy plant family richness (Table 3-16). For Vivid Niltava, foliage volume of canopy was forwarded first, followed by foliage volume of sub-canopy, and sub-canopy plant family richness (Table 3-17). For Red-headed Tit (*Aegithalos concinnus*), foliage volume of sub-canopy was forwarded first, followed by canopy plant family richness, foliage volume of shrub, foliage volume of canopy, and sub-canopy plant family richness (Table 3-18). The results of binary logistic regression analyses of reproductive statuses, ecological guilds, and species were summed in Table 3-19.



Discussion

Almost 90% of the registration spots were located within native forests and plantations. In binary logistic regression analysis, native forests and plantations positively correlated with the presence of bird individuals; buildings, orchards, and ponds negatively correlated with the presence of bird individuals. The results suggested that the habitat types with complex vegetation structure (native forests and plantations) were the key to attract bird individuals (MacArthur and MacArthur, 1961; Rotenberry, 1985). The buildings and ponds were difficult to attract bird individuals without any shelters and food resources from vegetation, the risk of predation and starvation might be higher over there. The vegetation structure of fields sometimes covered in ground layer then attracted some bird species, such as Oriental Tree-pipit (*Anthus hodgsoni*) and White Wagtail (*Motacilla alba*). If some shrubs or tall grass presented in fields, some bird species active in shrub layer may be attracted in, such as Steere's Liocichla, Strong-footed Bush Warbler, and Vinous-throated Parrotbill (*Paradoxornis webbianus*). The vegetation structure in orchards were composed by simple vegetation structure and low floristic composition, because there were almost only single fruit tree species planted in an orchard. Other foraging plants will be the key to attract bird individuals in orchards. The fields and orchards were tightly under agricultural and horticultural management: removing non-economical plants, using insecticide and herbicide, and tents covering. These management methods decreased the complexity of vegetation structure and subsequently biodiversity (Rands, 1986); the tents in orchards isolated bird individuals from

plants. Patch area also was negatively correlated with the presence of bird individuals, because the patch area of buildings, fields, orchards, and ponds usually larger than native forests and plantations in this study site. This result suggests that the effects of habitat type are sometimes stronger than the effects of patch area at within-habitat scale.

In binary logistic regression analyses of different reproductive statuses and ecological guilds, the variables of foliage volume were usually forwarded earlier than the variables of plant family richness. These results implied that the attraction of vertical foliage structure was stronger than floristic composition to bird individuals. Complex vertical foliage structure provides the shelters for bird individuals to avoid predators and bad weathers, and contains diverse micro-habitats and high foliage volumes for more arthropods. Highly floristic composition provides diverse food resources to insectivores, frugivores, nectivores, and granivores. At the aspect of fitness of bird individual, the fatal risk of predation was usually higher than the risk of starvation. Birds tend to stay in the habitat with complex vertical foliage structure to avoid predators at first, and then forage within the habitat with high floristic composition. In the binary logistic regression analyses of bird species, the variables of foliage volume were usually forwarded first, and followed by the variables of plant family richness. Therefore, these results probably supported the hypothesis (Rotenberry, 1985) that the physiognomy is more important in the hierarchical decision-making process of habitat selection at within-habitat scale. Müller *et al.* (2010) used airborne laser scanning (LiDAR: light detection and ranging) to measure the vegetation structure, and showed that the vegetation physiognomy was more powerful

predictor of the bird community than floristic composition. Henning and Remsburg (2009) suggested that the vegetation of understory contains more bird species. Besides, the complex vertical foliage structure or high foliage volumes are also important to nest site selection of birds (Martin *et al.*, 2000; Forstmeier and Weiss, 2004).

The variables of floristic composition were forwarded in the analyses of omnivores; but not forwarded in the analyses of insectivores. The habitats with high foliage volumes should contain high leaf amounts. The high leaf amounts support high abundance of arthropods, because most of arthropods are found on the surface of leaf (Robinson and Holmes, 1984), especially Lepidoptera larvae, Homoptera, and Hemiptera. High foliage volumes may contains some fruits and flowers (but not always) to attract insects, such as Lepidoptera and Hymenoptera. The habitats with higher foliage volumes might provide more insect food resources than botanical food resources. Therefore, the habitats with higher foliage volumes were easier to attract insectivores than omnivores, frugivores, nectivores, and granivores. The habitats with higher plant richness should contain more fruits and flowers of different plant species, and also attracts more Lepidoptera and Hymenoptera. High plant richness may contains high foliage volumes (but not always), and supports some arthropods. The habitat with high plant richness might provide more diverse botanical food resources than insect food resources. Therefore, the habitats with higher plant richness were easier to attract omnivores, frugivores, nectivores, and granivores than insectivores (Figure 3-2). Besides, Steere's Liocichla, Taiwan Yuhina, and Taiwan Sibia were classified to omnivores, but botanical food resources are the major foods of Taiwan

Yuhina and Taiwan Sibia (Yen, 1990; Yuan *et al.*, 2004; Lee *et al.*, 2005; Severinghaus *et al.*, 2010b). According to optimal foraging theory (MacArthur and Pianka, 1966; Schoener, 1969; Stephens and Krebs, 1986), omnivores might forage efficiently in the habitats with higher plant richness; insectivores might forage efficiently in the habitats with higher foliage volumes. Therefore, omnivores probably prefer the habitats with high floristic composition; and insectivores probably prefer the habitats with complex vertical foliage structure.

The foliage volume of sub-canopy was forwarded in the analysis of local breeders; the foliage volume of canopy was forwarded in the analysis of neighboring breeders. High foliage volume of canopy sometimes constructed the corridor among native forests and plantations, increasing the connectivity of tree canopy. The local breeders excelled survival and reproduction in the fragmented environment, so the connectivity of tree canopy might not be important to their habitat preferences. The neighboring breeders bred in the nearby primary broadleaved forest, they just stayed in fragmented environment for a short period time. The habitat with high connectivity of tree canopy was similar to the continuous canopy layer in the primary broad-leaved forest. Therefore, the neighboring breeders might prefer the habitat with high foliage volumes in canopy layer in fragmented environment. The wintering species were mostly recorded in March, the preparing period for migration, the food resources might be more important to those bird individuals. Therefore, the frequency of foraging from vegetation would be increased, and the importance of shelters might be lower than food resources.

In the habitat preferences analyses of species, the results probably

reflected habitat preferences of each species respectively. Foliage volume of sub-canopy was forwarded frequently. As the function of vertical foliage structure discussed above, this character of habitat may attract omnivores, insectivores, and the species dwell in canopy, sub-canopy, shrub, and ground layers. These results implied that the habitats with complex vertical foliage structure in sub-canopy layer might contain high bird species richness. For the understory-dwelling species (Severinghaus *et al.*, 2010a; 2010b; Yen, 1990), such as Steere's Liocichla, Red-headed Tree Babbler, Bamboo Partridge, White-tailed Blue Robin, Strong-footed Bush Warbler, and Red-headed Tit, foliage volume of canopy were forwarded negatively or not be forwarded, the results might reflect that foliage volume of canopy was not very important to these species. The canopy plant family richness was forwarded in the analyses of Bamboo Partridge, because this species forages the seeds of canopy trees, and nesting in ground layer (Severinghaus *et al.*, 2010a). For Strong-footed Bush Warbler, foliage volume of shrub was forwarded first, and foliage volume of canopy and the sub-canopy plant family richness were negatively correlated with. The results conform to the preferred habitat of this species – tall grasslands (Severinghaus *et al.*, 2010b). Vivid Niltava and White-throated Flycatcher Warbler are insectivores foraging in canopy and sub-canopy layers (Severinghaus *et al.*, 2010b), so foliage volume of canopy and sub-canopy were forwarded first. Taiwan Yuhina is an omnivore foraging in canopy and sub-canopy layers (Yen, 1990; Yuan *et al.*, 2004; Lee *et al.*, 2005; Severinghaus *et al.*, 2010b); Taiwan Sibia is also an omnivore mainly foraging in canopy layers. Therefore, in the analyses, foliage volume in sub-canopy was forwarded first to Taiwan Yuhina; the canopy plant family

richness was forwarded first to Taiwan Sibia. For Grey-cheeked Fulvetta, variables of foliage volumes and plant family richness were forwarded. This species is an insectivore in breeding season, frugivore or nectivore in non-breeding season; foraging and nesting in shrub and sub-canopy layers (Yen, 1990, Chou *et al.*, 1998; Chen and Hsieh, 2002; Severinghaus *et al.*, 2010b), so both vertical foliage structure and floristic composition were important factors to its habitat preference. For Brown Bullfinch, foliage volume and plant family richness of sub-canopy were forwarded. Brown Bullfinch usually stay on the top of tree canopy (Severinghaus *et al.*, 2010b), in this study site, the highest tree canopy usually composed by Japanese cryptomeria (*Cryptomeria japonica*) with less botanical food resources for Brown Bullfinch. Therefore, Brown Bullfinch foraged the botanical food resources in sub-canopy layer.

As detailed earlier, the effects of habitat type were stronger than the effects of patch area to attract bird individuals at within-habitat scale. At within-habitat scale, vertical foliage structure and floristic composition in canopy and sub-canopy layers attract different reproductive statues, ecological guilds, and species of bird individuals. In Chapter 2, the complexity of vegetation structure is highly correlated with bird species richness, this result is also supported by the results of this chapter. These results also solidify the explanation of the relationship between vegetation structure and bird community. I conclude that increasing the complexity of vegetation structure is important to sustain more bird individuals and species, even within the small patches. At the same time, it is also an important management strategy to increase biodiversity in fragmented landscapes.

Tables

Table 3-1. The forward variable selection of binary logistic regression analysis examining the effects of patch area and six habitat types on the habitat preferences of all bird individuals in the whole study site. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	1.417	<0.001
1	Buildings	19658.55	--	-0.242	<0.001
2	Orchards	19125.80	532.75	-0.090	<0.001
3	Field	18479.52	646.27	-0.050	<0.001
4	Patch Area	18160.76	318.76	-0.278	<0.001
5	Ponds	18141.25	19.51	-0.122	<0.001
6	Native Forests	18123.28	17.97	0.641	<0.001
7	Plantations	18123.12	0.16	0.494	<0.001

Table 3-2. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of local breeders in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	-0.085	<0.001
1	Foliage Volume of Sub-canopy	35501.698	--	0.198	<0.001
2	Canopy Plant Family Richness	35186.730	314.968	0.123	<0.010
3	Sub-canopy Plant Family Richness	35127.038	59.692	0.521	<0.001

Table 3-3. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of neighboring breeders in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	-2.179	<0.001
1	Foliage Volume of Canopy	2726.056	--	0.416	<0.001
2	Sub-canopy Plant Family Richness	2715.865	10.191	0.191	<0.010

Table 3-4. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of wintering species in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	-1.605	<0.001
1	Foliage Volume of Sub-canopy	3939.620	--	0.379	<0.001
2	Foliage Volume of Canopy	3919.236	20.384	-0.380	<0.001
3	Canopy Plant Family Richness	3912.742	6.494	0.144	<0.010

Table 3-5. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of omnivores in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	0.150	<0.001
1	Foliage Volume of Sub-canopy	19206.059	--	0.614	<0.001
2	Canopy Plant Family Richness	18956.444	249.615	0.250	<0.001
3	Sub-canopy Plant Family Richness	18920.721	35.723	0.129	<0.001

Table 3-6. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of insectivores in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	-2.966	<0.001
1	Foliage Volume of Canopy	1707.488	--	0.561	<0.001
2	Foliage Volume of Sub-canopy	1691.171	16.317	0.321	<0.001

Table 3-7. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of Taiwan Yuhina (*Yuhina brunneiceps*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	-0.139	<0.001
1	Foliage Volume of Sub-canopy	8437.168	--	0.668	<0.001
2	Canopy Plant Family Richness	8367.055	70.113	0.210	<0.001
3	Foliage Volume of Shrub	8348.715	18.340	-0.202	<0.001
4	Sub-canopy Plant Family Richness	8332.211	16.504	0.137	<0.001
5	Foliage Volume of Canopy	8327.535	4.676	0.097	<0.050

Table 3-8. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of Steere's Liocichla (*Liocichla steerii*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	0.183	<0.001
1	Foliage Volume of Sub-canopy	9824.780	--	0.567	<0.001
2	Canopy Plant Family Richness	9705.345	119.435	0.215	<0.001
3	Sub-canopy Plant Family Richness	9681.284	24.061	0.127	<0.001
4	Foliage Volume of Shrub	9675.370	5.914	0.071	<0.050

Table 3-9. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of Taiwan Sibia (*Heterophasia auricularis*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	ΔAIC	St. Coeff.	P-value
	Constant	--	--	-1.814	<0.001
1	Canopy Plant Family Richness	3762.139	--	0.367	<0.001
2	Foliage Volume of Sub-canopy	3601.195	160.944	0.513	<0.010
3	Sub-canopy Plant Family Richness	3590.815	10.380	0.238	<0.001
4	Foliage Volume of Shrub	3580.095	10.720	-0.227	<0.050
5	Foliage Volume of Canopy	3569.448	10.647	0.216	<0.050

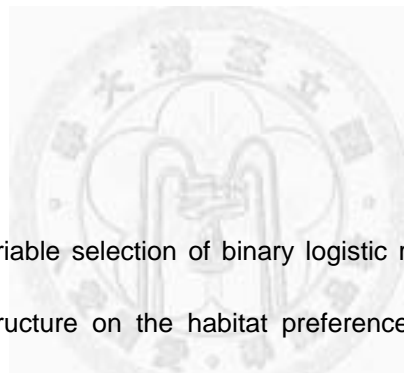


Table 3-10. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of Gray-cheeked Fulvetta (*Alcippe morrisonia*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	ΔAIC	St. Coeff.	P-value
	Constant	--	--	-3.581	<0.001
1	Foliage Volume of Canopy	1431.537	--	0.471	<0.001
2	Canopy Plant Family Richness	1391.019	40.518	0.526	<0.001
3	Foliage Volume of Sub-canopy	1369.551	21.468	0.401	<0.001
4	Foliage Volume of Shrub	1363.595	5.956	0.368	<0.010
5	Sub-canopy Plant Family Richness	1357.975	5.620	-0.367	<0.050

Table 3-11. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of Red-headed Tree Babbler (*Stachyris ruficeps*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	-1.474	<0.001
1	Foliage Volume of Sub-canopy	4431.002	--	0.407	<0.001
2	Canopy Plant Family Richness	4336.523	94.479	0.384	<0.001
3	Foliage Volume of Shrub	4314.520	22.003	0.294	<0.001
4	Sub-canopy Plant Family Richness	4299.739	14.781	-0.201	<0.001

Table 3-12. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of Bamboo Partridge (*Bambusicola thoracicus*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	-2.656	<0.001
1	Foliage Volume of Sub-canopy	2013.861	--	0.680	<0.001
2	Foliage Volume of Canopy	1989.019	24.842	-0.798	<0.001
3	Canopy Plant Family Richness	1967.699	21.320	0.373	<0.001

Table 3-13. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of White-tailed Blue Robin (*Myiomela leucura*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	Δ AIC	St. Coeff.	P-value
	Constant	--	--	-1.373	<0.001
1	Foliage Volume of Sub-canopy	4577.441	--	0.737	<0.001
2	Canopy Plant Family Richness	4527.647	49.794	0.271	<0.001

Table 3-14. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of White-throated Flycatcher Warbler (*Abroscopus albogularis*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	ΔAIC	St. Coeff.	P-value
	Constant	--	--	-3.789	<0.001
1	Foliage Volume of Canopy	1009.747	--	0.567	<0.001
2	Sub-canopy Plant Family Richness	1002.357	7.390	0.296	<0.010
3	Foliage Volume of Sub-canopy	998.639	3.718	0.219	<0.050

Table 3-15. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of Brown Bullfinch (*Pyrrhula nipalensis*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	ΔAIC	St. Coeff.	P-value
	Constant	--	--	-1.849	<0.001
1	Foliage Volume of Sub-canopy	3394.352	--	0.583	<0.001
2	Sub-canopy Plant Family Richness	3353.950	40.402	-0.353	<0.001

Table 3-16. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of Strong-footed Bush Warbler (*Cettia fortipes*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	ΔAIC	St. Coeff.	P-value
	Constant	--	--	-2.279	<0.001
1	Foliage Volume of Shrub	2858.916	--	1.233	<0.001
2	Foliage Volume of Canopy	2675.708	183.208	-0.556	<0.001
3	Sub-canopy Plant Family Richness	2632.179	43.529	-0.536	<0.001

Table 3-17. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of Vivid Niltava (*Niltava vivida*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	ΔAIC	St. Coeff.	P-value
	Constant	--	--	-3.701	<0.001
1	Foliage Volume of Canopy	1065.808	--	0.243	<0.050
2	Foliage Volume of Sub-canopy	1043.933	21.875	0.481	<0.001
3	Sub-canopy Plant Family Richness	1036.224	7.709	0.303	<0.010

Table 3-18. The forward variable selection of binary logistic regression analysis examining the effects of vegetation structure on the habitat preferences of Red-headed Tit (*Aegithalos concinnus*) in native forests and plantations. AIC: Akaike's information criterion; St. Coeff.: standard coefficient.

Order	Factors	AIC	ΔAIC	St. Coeff.	P-value
	Constant	--	--	-2.076	<0.001
1	Foliage Volume of Sub-canopy	3025.987	--	0.658	<0.001
2	Canopy Plant Family Richness	3007.340	18.647	0.237	<0.010
3	Foliage Volume of Canopy	2995.775	11.565	-0.281	<0.001
4	Sub-canopy Plant Family Richness	2986.005	9.770	0.187	<0.010

Table 3-19. The summary table of binary logistic regression analyses of reproductive statuses, ecological guilds, and species. FVC: Foliage Volume of Canopy, FVS: Foliage Volume of Sub-canopy, FVSh: Foliage Volume of Shrub, CPFR: Canopy Plant Family Richness, SPFR: Sub-canopy Plant Family Richness, “-”: indicating the standard coefficient of the variable was significantly negative.

Forwarded Sequence	1	2	3	4	5
Reproductive Statuses					
Local Breeders	FVS	CPFR	SPFR	--	--
Neighboring Breeders	FVC	SPFR	--	--	--
Wintering Species	FVS	- FVC	CPFR	--	--
Ecological Guilds					
Omnivores	FVS	CPFR	SPFR	--	--
Insectivores	FVC	FVS	--	--	--
Bird Species					
<i>Yuhina brunneiceps</i>	FVS	CPFR	- FVSh	SPFR	FVC
<i>Liocichla steerii</i>	FVS	CPFR	SPFR	FVSh	--
<i>Heterophasia auricularis</i>	CPFR	FVS	SPFR	- FVSh	FVC
<i>Alcippe morrisonia</i>	FVC	CPFR	FVS	FVSh	- SPFR
<i>Stachyris ruficeps</i>	FVS	CPFR	FVSh	- SPFR	--
<i>Bambusicola thoracicus</i>	FVS	- FVC	CPFR	--	--
<i>Myiomela leucura</i>	FVS	CPFR	--	--	--
<i>Abroscopus albogularis</i>	FVC	SPFR	FVS	--	--
<i>Pyrrhula nipalensis</i>	FVS	- SPFR	--	--	--
<i>Cettia fortipes</i>	FVS	- FVC	- SPFR	--	--
<i>Niltava vivida</i>	FVC	FVS	SPFR	--	--
<i>Aecogithalos concinnus</i>	FVS	CPFR	- FVC	SPFR	--

Figures

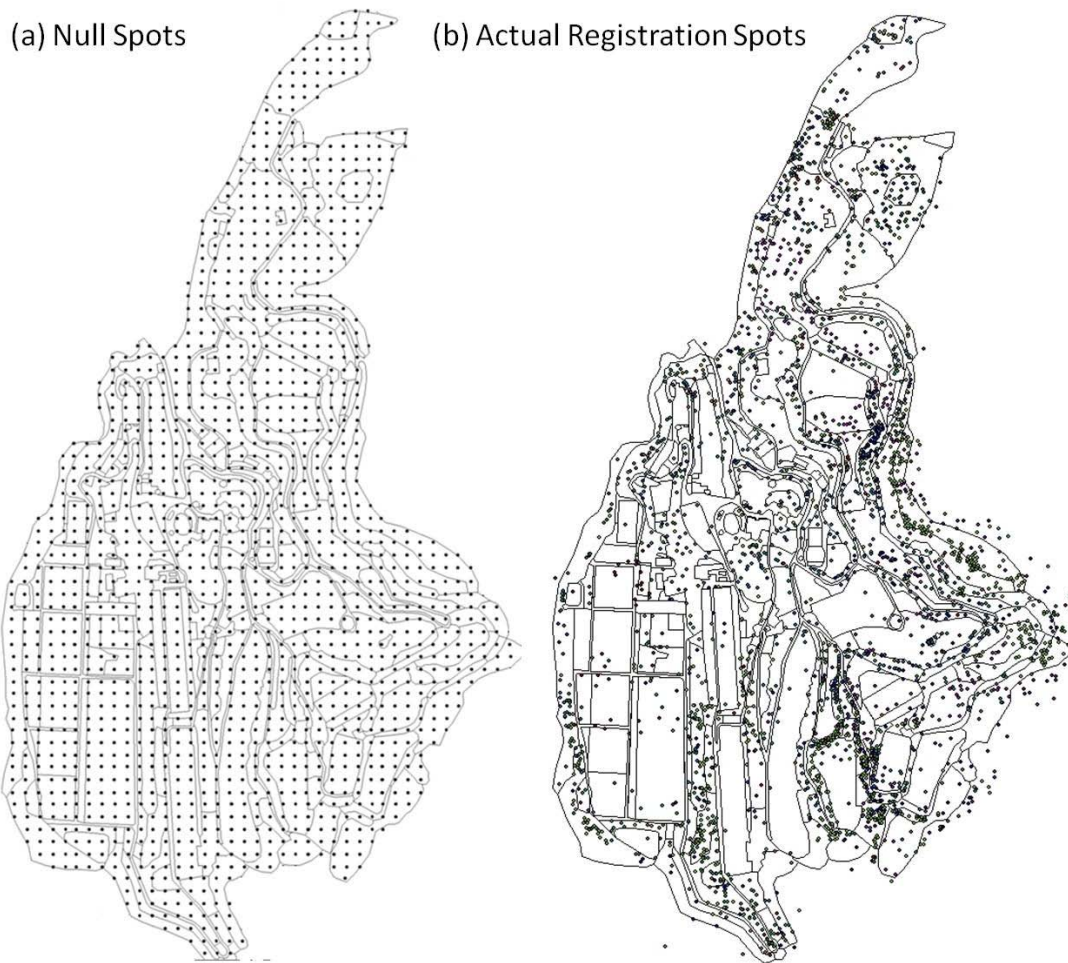


Figure 3-1. The distribution of the regular null spots. The null spots were generated regularly on the map of the study site. The total amount of null spots(a) was approximately equaled to the total amount of the actual registration spots(b) in each examination. The amount of null spots in certain patch was proportional to patch area. Therefore, the amounts of null spots of each patch were perfectly proportional to patch area.

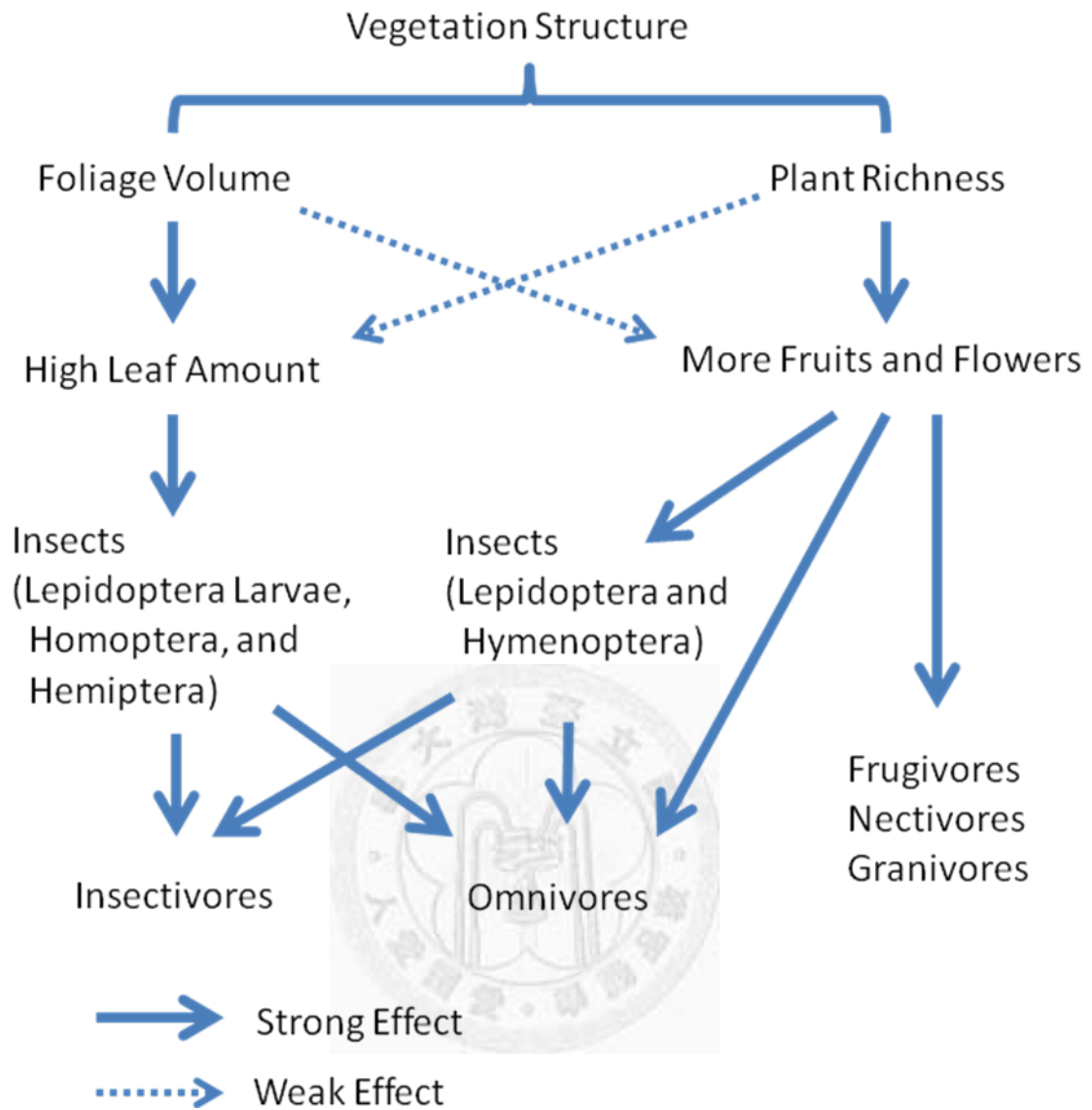


Figure 3-2. The effects of vegetation structure to different ecological guilds of birds.

CHAPTER 4

Edge Effects on Different Bird Reproductive Statuses in Fragmented Landscape

Abstract

Habitat fragmentation has been threatening biodiversity seriously, but recent studies show its effects are not universal to all species. “Edge effects” is often referred as one major cause that why habitat fragmentation does not have universal effect on all species. To understand edge effects on biodiversity clearly, it is important to examine the responses of different species, reproductive statuses, or ecological guilds to edges of different habitat types at individual perspective and finer scale. The study site, Meifeng Highlands Experimental Farm of National Taiwan University, was classified into 286 patches and 661 buffer zones of five major habitat types (buildings, fields, native forests, orchards, and plantations). The locations of all observed bird individuals (66 species, 11,740 registration spots) were mapped during three breeding seasons from 2005 to 2007. The vegetation structures of the 286 patches were measured in 2007.

The registration spot densities of local breeders were significantly higher than neighboring breeders (bred in neighboring primary broadleaved forests but not in the study site) and wintering species, but there were no significant difference between neighboring species and wintering species. For local

breeders, the registration spot densities in edge buffer zones were significantly higher than interior ones in orchards, native forests, and plantations; but no significant differences in buildings and fields. For neighboring breeders, the registration spot densities among different ranks of buffer zones were not significantly different in every habitat types. For wintering species, the registration spot densities in edge buffer zones were significantly higher than interior ones in native forests, but no significant differences in buildings, fields, orchards, and plantations.

These results support that edge effects are not universal to different species. Local breeders may be attracted to native forests and plantations edges for foraging or nesting. Neighboring breeders and wintering species probably do not prefer this fragmented landscape, so lower registration spot densities make no obvious edge effects. There were higher biodiversity along edges in native forests and plantations, but mostly composed by local breeders, only few neighboring breeders and wintering species. There were some species had been observed in the neighboring primary forests, but seldom observed in the study site. If only examine edge effects on community level, some species which seldom present near edges would be neglected. Therefore, to examine edge effects on biodiversity clearly, it is very important to conduct the researches at the perspective of individuals by species, reproductive statuses, or ecological guilds at finer scale and include large, intact native habitat patches.

Keywords: edge effects, habitat fragmentation, habitat type, reproductive status, Taiwan

摘要

棲地破碎化已經嚴重地威脅生物多樣性，但是近期研究顯示其對物種的影響並不一致。邊緣效應被認為是造成棲地破碎化對物種的影響不一致的主要原因之一。為了清楚瞭解邊緣效應對生物多樣性的影響，從個體層級檢驗邊緣效应在細尺度、不同棲地類型中，對於各物種、繁殖狀態或生態同功群的影響相當重要。研究地點（國立臺灣大學梅峰山地實驗農場）區分成 286 個區塊、661 個距離帶以及五種主要的棲地類型（建築、耕地、天然林、果園、及人工林）。2005 到 2007 年的三個繁殖季中，所有被觀察到的鳥類個體（共 66 種、11,740 個紀錄點）的位置皆記錄於地圖上，這 286 區塊的植群結構則於 2007 年測量。在地繁殖者的紀錄點密度顯著地高於鄰地繁殖者（不在研究地內繁殖，但在鄰近原始林繁殖）與冬候鳥種，但是鄰地繁殖者與冬候鳥種的紀錄點密度之間則沒有顯著的差異。在地繁殖者於果園、天然林、和人工林中，邊緣距離帶的紀錄點密度顯著地高於內部棲地；但是在建築與耕地中則沒有顯著的差異。在所有的棲地類型中，鄰地繁殖者的紀錄點密度於不同層級的距離帶之間沒有顯著的差異。冬候鳥種在天然林邊緣距離帶的紀錄點密度顯著地高於內部棲地；但是在建築、耕地、果園與人工林中則沒有顯著的差異。這些結果支持邊緣效應對不同物種不一致的論述。在地繁殖者可能為覓食或築巢而被吸引到天然林或人工林的邊緣。鄰地繁殖者與冬候鳥種則可能因為不偏好破碎地景，因此紀錄點過少而沒有顯示明顯的邊緣效應。在天然林與人工林中，邊緣附近有較高的物種多樣性，但是大多數由在地繁殖者組成，僅有少部份的鄰地繁殖者與冬候鳥種。有些物種曾經在鄰近的原始闊葉林被觀察到，但是很少在研究地被觀察到。如果僅在群聚的層級檢驗邊緣效應，有些甚少出現在邊緣的物種則可能被忽略。因此，為清楚瞭解邊緣效應對生物多樣性的影響，在細尺度與個體的層級分別依物種、繁殖狀態或生態同功群探討便相當重要，而且也應納入大塊的原生棲地區塊。

關鍵詞：邊緣效應、棲地破碎化、棲地類型、繁殖狀態、臺灣

Introduction

Habitat fragmentation is one of the important issues in conservation biology (Tilman *et al.*, 1994; Margules and Pressey, 2000; Dirzo and Raven, 2003; Balmford *et al.*, 2005; Zipkin *et al.*, 2009). It has been threatening the distribution and abundance of biodiversity seriously (Wilcove *et al.*, 1986; Forman, 1995; Collinge, 1996; Turner, 1996; Debinski and Holt, 2000), but recent studies show its effects are not universal to all species (Andr n, 1994; reviewed by Fahrig, 2003). Habitat fragmentation not only decreases patch area but also increases the edges of patches (reviewed by Fahrig, 2003), and then increases edge effects (Leopold, 1933; Lovejoy *et al.*, 1986). “Edge effects” is one of the causes that why habitat fragmentation do not have universal effect to all species (reviewed by Fahrig, 2003; Ries *et al.*, 2004).

Clements (1907) introduced the term “ecotone”, the zone between two different ecosystems. It is the earliest reference which related to habitat edges in ecology. Edges are generally defined as boundaries between two distinctly habitat types, such as the edge between a meadow and a forest. In game management, Leopold (1933) used “edge effects” to describe edges provide diverse resources from both adjacent habitat types, and then sustain higher diversity of game species in fragmented landscapes. Other early articles (*e.g.*, Lay, 1938; Johnston, 1947) solidified this general concept into the paradigm as “edges are good” to wildlife management (Harris, 1988; Yahner, 1988). During the late 1970s, with observing higher risks of nest predation and parasitism of some birds near edges (Gates and Gysel, 1978; Chasko and

Gates, 1982), the negative effects of edges on biodiversity began to attract more attention. Most studies concern with anthropogenic edges (Lovejoy *et al.*, 1986), such as the edge between an agricultural field and a forest, especially in fragmented landscapes. As many anthropogenic edges have been produced, edge effects have been found to strongly decrease the population size of habitat specialists (Wilcove, 1985; Saunders *et al.*, 1991; Mills, 1995). However, on the contrary, population size of some other generalist species increased or unaffected by these anthropogenic edges (reviewed by Paton, 1994; Murica, 1995; Ries *et al.*, 2004; Collinge, 2009). Therefore, these anthropogenic edges are often viewed as undesirable landscape components (Harris, 1988; Saunders *et al.*, 1991).

Depending on the habitat preferences of different species, edge effects might be positive, negative, neutral or mixed (Ambuel and Temple, 1983; Donovan *et al.*, 1997; reviewed by Ries *et al.*, 2004). Edge effects increase the population size of edge species (Carlson and Hartman, 2001), and decrease the population size of interior species (Donovan *et al.*, 1997). For edge species, edges contain ecological resources and micro-habitats from both habitat types (McCollin, 1998; Fagan *et al.*, 1999). Leopold (1933) suggested that the population density of Bobwhite Quail (*Colinus virginianus*) is higher in landscape contained forests, brushlands, grasslands and agricultural fields. It is important to species whose life cycle needs different ecological resources from many habitat types, such as amphibians (Ponsero and Joly, 1998). In addition, the biodiversity of edges sometimes are enhanced by high immigration rate of edge species (Hilty *et al.*, 2006). For interior species, they are only adapted to the interior zones of habitat patches

and not tolerant to edges. Highly fragmented landscapes would create great amount of unsuitable habitats for interior species and increase the mortality rate and decrease breeding success of interior species by various processes (Fahrig, 2002), such as nest predation (Gates and Gysel, 1978; Donovan *et al.*, 1997) and parasitism (Kurki *et al.*, 2000). As habitat gets more fragments and edges, there will be fewer individuals of interior species could exist. As edge species and interior species responds differently to habitat edges, effects of habitat fragmentation on biodiversity are not universal. That is, the response of species to edges is based on its habitat preferences, reproductive status, and ecological guild.

To understand effects of habitat fragmentation on biodiversity, it is important to examine the responses of different species to edges at a perspective of individual (Johnson, 1980; Hutto, 1985; Cody, 1985; Block and Brennan, 1993; Fahrig, 2003; Ries *et al.*, 2004) in fragmented landscapes. Besides, Rotenberry (1985) also referred that the finer scale (within-habitat type) investigations are better to untangle the mechanisms of wildlife-habitat relationships. To increase the efficiency of management and conservation strategies, it is important to understand the details of habitat preferences of birds at finer scale.

Birds are a suitable taxon to study the responses of individuals to edges for following reasons: (1) high flying ability make birds can change habitat rapidly; (2) habitat preferences among different birds species are obvious; (3) comparing to other taxa of wildlife, it is easier to identify and observe different bird species (Brown, 1984; Konishi *et al.*, 1989). In addition, the high flying ability of birds may weaken the isolation effects of habitat fragmentation

(Block and Brennan, 1993). Therefore, the occurrence of bird individuals should reflect the response to edges clearly.

This chapter was aimed to understand the responses of different reproductive statuses (local breeders, neighboring breeders, and wintering species) of birds to habitat edges at a bird individual perspective. In Chapter 3, the habitat preferences of different reproductive statuses of birds significantly differed. Therefore, the responses to edges should be different in different habitat types. This study was conducted in a 50 ha study site with fragmented landscape. The locations of all observed bird individuals were mapped during three breeding seasons from 2005 to 2007. The landscape of study site was classified into 286 patches and 661 buffer zones of five major habitat types (buildings, fields, native forests, orchards, and plantations). To understand the responses to edges of different reproductive statuses of birds in each habitat type, the registration spot densities of different ranks of buffer zones in each habitat type were examined respectively.

Methods

The study site and field works (attributes of landscape structure and avian community) were specified in the Methods of Chapter 2.

All patches were divided to inward buffer zones per 5 m (Figure 4-1), then generated eight ranks of buffer zones.

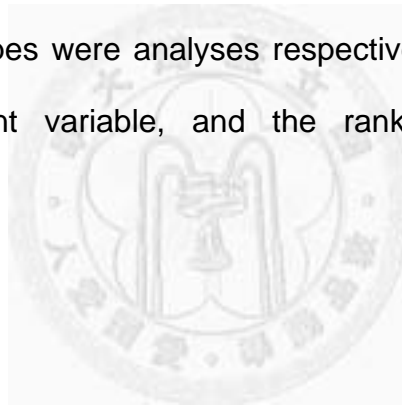
1. 0 –5 m (n = 31 in buildings, 43 in fields, 125 in native forests, 15 in orchards, 64 in plantations),
2. 6 –10 m (n = 21 in buildings, 35 in fields, 94 in native forests, 14 in orchards, 35 in plantations),
3. 11 –15 m (n = 11 in buildings, 17 in fields, 38 in native forests, 11 in orchards, 17 in plantations),
4. 16 –20 m (n = 5 in buildings, 9 in fields, 15 in native forests, 9 in orchards, 7 in plantations),
5. 21 –25 m (n = 3 in buildings, 6 in fields, 9 in native forests, 7 in orchards, 2 in plantations),
6. 26 –30 m (n = 3 in buildings, 1 in fields, 5 in native forests, 3 in orchards),
7. 31 –35 m (n = 1 in fields, 3 in native forests, 1 in orchards),
8. 36 –40 m (n = 1 in native forests).

The bird species recorded in the study site were classified into three reproductive statuses: local breeders (LB, the species bred in the study site; 15 species), neighboring breeders (NB, the species bred in the neighboring primary broad-leaved forests but not within the study site; 29 species) and wintering species (W, the species never bred in the study site or neighboring

region, either latitudinal or altitudinal migrants) (Appendix 2) To avoid the effects of area (the number of registration spots is positively correlated with the area), I calculated the registration spot densities of three reproductive statuses in each buffer zone, instead of the number of registration spots.

Statistical analysis

To compare the registration spot densities of three reproductive statuses, and different ranks of buffer zones, one-way ANOVA and Tukey's Test by SYSTAT 12.0 (SYSTAT, 2007) was done for each habitat type and each reproductive status. The registration spot densities of different reproductive statuses and habitat types were analysed respectively. The registration spot density was dependent variable, and the ranks of buffer zone was independent variable.



Results

There were 11,740 registration spots recorded in total. Among them, 88.09% were distributed in native forests and plantations, 0.81% in buildings, 6.94% in fields, and 4.10% in orchards. Combining different habitat types together, the registration spot densities were significantly different among three reproductive statuses (Figure 4-3, one-way ANOVA, $F = 443.541$, $p < 0.001$). The registration spot densities of local breeders were significantly higher than neighboring breeders (Figure 4-3, Tukey's test, $p < 0.001$) and wintering species (Figure 4-3, Tukey's test, $p < 0.001$). There were no significance difference between the registration spot densities of neighboring breeders and wintering species (Figure 4-3, Tukey's test, $p = 0.855$). For local breeders, the registration spot densities among different ranks of buffer zones were significantly different (Figure 4-3, one-way ANOVA, $F = 5.199$, $p < 0.001$). The registration spot densities of 0 –5 m buffer zones were significantly higher than 6 –10 m buffer zones (Figure 4-3, Tukey's Test, $p < 0.05$), 11 –15 m buffer zones (Figure 4-3, Tukey's Test, $p < 0.001$), and 16 –20 m buffer zones (Figure 4-3, Tukey's Test, $p < 0.05$). The registration spot densities among different ranks of buffer zones were not significantly different for neighboring breeders (Figure 4-3, one-way ANOVA, $F = 0.292$, $p = 0.940$) and for wintering species (Figure 4-3, one-way ANOVA, $F = 0.836$, $p = 0.545$).

For local breeders, the registration spot densities among different ranks of buffer zones were not significantly different in buildings (Figure 4-4a, one-way ANOVA, $F = 1.690$, $p = 0.149$) and fields (Figure 4-4b, one-way

ANOVA, $F = 2.733$, $p = 0.170$). The registration spot densities among different ranks of buffer zones were significantly different in orchards (Figure 4-4c, one-way ANOVA, $F = 6.126$, $p < 0.001$), native forests (Figure 4-4d, one-way ANOVA, $F = 2.858$, $p < 0.01$), and plantations (Figure 4-4e, one-way ANOVA, $F = 6.099$, $p < 0.001$). In orchards, the registration spot densities of 0 –5 m buffer zones were significantly higher than 6 –10 m buffer zones (Figure 4-4c, Tukey's Test, $p < 0.05$), 11 –15 m buffer zones (Figure 4-4c, Tukey's Test, $p < 0.01$), 16 –20 m buffer zones (Figure 4-4c, Tukey's Test, $p < 0.01$), and 21 –25 m buffer zones (Figure 4-4c, Tukey's Test, $p < 0.01$). In native forests, the registration spot densities of 0 –5 m buffer zones were significantly higher than 6 –10 m buffer zones (Figure 4-4d, Tukey's Test, $p < 0.05$), and 11 –15 m buffer zones (Figure 4-4d, Tukey's Test, $p < 0.01$). In plantations, the registration spot densities of 0 –5 m buffer zones were significantly higher than 11 –15 m buffer zones (Figure 4-4e, Tukey's Test, $p < 0.01$), and 16 –20 m buffer zones (Figure 4-4e, Tukey's Test, $p < 0.05$).

For neighboring breeders, the registration spot densities among different ranks of buffer zones were not significantly different in buildings (Figure 4-5a, one-way ANOVA, $F = 0.484$, $p = 0.787$), fields (Figure 4-5b, one-way ANOVA, $F = 0.292$, $p = 0.940$), orchards (Figure 4-5c, one-way ANOVA, $F = 0.736$, $p = 0.623$), native forests (Figure 4-5d, one-way ANOVA, $F = 0.689$, $p = 0.682$), and plantations (Figure 4-5e, one-way ANOVA, $F = 1.408$, $p = 0.235$).

For wintering species, the registration spot densities among different ranks of buffer zones were not significantly different in buildings (Figure 4-6a, one-way ANOVA, $F = 0.240$, $p = 0.944$), fields (Figure 4-6b, one-way ANOVA, $F = 0.836$, $p = 0.545$), orchards (Figure 4-6c, one-way ANOVA, $F = 2.101$, $p =$

0.137) and plantations (Figure 4-6e, one-way ANOVA, $F = 2.285$, $p = 0.064$). The registration spot densities in native forests were significantly different among different ranks of buffer zones (Figure 4-6d, one-way ANOVA, $F = 3.776$, $p < 0.01$). In native forests, the registration spot densities of 0 –5 m buffer zones were significantly higher than 6 –10 m buffer zones (Figure 4-6d, Tukey's Test, $p < 0.01$), and 11 –15 m buffer zones (Figure 4-6d, Tukey's Test, $p < 0.05$).



Discussion

In the whole study site, the registration spots densities of local breeders were significantly higher than neighboring breeders and wintering species. There were 88% of registration spots distributed within native forests and plantations. It implies that native forests and plantations were very important habitat types to this avian community. In this study, most of the registration spots were local breeders, instead of neighboring breeders and wintering species. The wintering species mainly presented in winter and early spring and were largely excluded from the field censuses focused on breeding species. Although neighboring species presented in the native forests and plantations, these forest patches might be too small and fragmented for these neighboring species to breed. Therefore, most of the individuals recorded in the study site were local breeders.

The registration spot densities of any reproductive statuses among different ranks of buffer zones were not significantly different in buildings and fields. In Chapter 2, buildings and fields were not important habitat types to bird species richness. In Chapter 3, buildings and fields had strongly negative effects to attract bird individuals. Both suggest buildings and fields were not preferred by most birds. Excluded some species preferred non-forest habitats, such as White Wagtail (*Motacilla alba*), Oriental Tree-pipit (*Anthus hodgsoni*), and Pacific Swallow (*Hirundo tahitica*), there were only few bird individuals presented in buildings and fields, and showed no significant differences among different ranks of buffer zones, especially neighboring breeders and wintering species. For local breeders, although did not reach the 0.05

significance level, there were still a trend that registration spot densities in buildings and fields decreased from edge to interior. In Chapter 2, the habitat types of adjacent patches were important to sustain bird species richness in buildings and fields. Therefore, this trend implies that the higher densities in edge buffer zones were mainly composed by bird individuals temporally moved in from adjacent habitats, especially native forests and plantations.

For local breeders in orchards, native forests, and plantations, the registration spot densities in the edge buffer zones were significantly higher than the interior ones. Forest edges usually have higher solar radiation, temperature, and lower humidity than forest interiors (reviewed by Murcia, 1995; Chen *et al.*, 1999, Rodewald and Yahner, 2001). The growth rate and germination rate of seedlings are higher near edges (Chen *et al.*, 1992; Matlack, 1994). The diversity of shade intolerant plants should be higher in edges than interiors (Saunders *et al.*, 1991), such as *Debregeasia edulis* and *Alnus formosana*. Therefore, forest edges usually contain more plant species than interiors (Harris, 1988). Higher plant species richness sustained higher insect species richness (Robinson and Holmes, 1984), so the insect diversity of forest edges are also often higher than interiors (Murica, 1995). Therefore, forest edges might provide more botanical and insect food resources to attract more bird individuals. The orchards in the study site were under intensive horticultural managements: removing non-economical plants, and using insecticide and herbicide. These managed methods enhance the differences of vegetation structure between orchard edges and interiors (Rands, 1986). In addition, in this study site, Taiwan cherry (*Prunus campanulata*) were usually planted along roadside for landscaping scenery, but coincidentally provided

important food resources for some nectivores, such as Taiwan Yuhina (*Yuhina brunneiceps*) (Yuan, *et al.*, 2004; Lee *et al.*, 2005).

For wintering species, the registration spot densities in edge buffer zones were higher than interior ones in native forests and in orchards and plantations (although both did not reach the significance level of 0.05). The wintering species were mostly recorded in March, the preparing period for migration, the food resources might be more important to those bird individuals. The frequency of foraging from vegetation would be increased, and the importance of shelters might be lower for them than food resources. Therefore, the bird individuals were attracted by the edges with more food resources. Even though did not reach the statistical significance due to limited sample size, registration spot densities in orchards and plantations were still higher in edges buffer zones than interior ones.

Bird individuals usually more frequently show up near their nest sites, so nest site selection may affect the edge preference of birds (*e.g.* Lee *et al.*, 2005). Nest sites selections are usually based on factors affecting reproductive success. As for abiotic factors, forest edges usually have higher temperature and solar radiation (reviewed by Murcia, 1995; Chen *et al.*, 1999, Rodewald and Yahner, 2001) and may decrease energetic costs of incubation, and sustain the micro-environments around the nest (Deeming, 2002). As for biotic factors, nest predation and parasitism are regarded as the major negative effects to reproductive success (Martin, 1998). The comparisons of nest predation rates between forest edges and interiors vary among species, habitats, and regions: some studies referred the nest predation rate in edges is higher than interiors (Gates and Gysel, 1978; Johnson and Temple, 1990;

Peak, 2007); some studies referred the risk of predation are not significantly different between edges and interiors (Yahner, 1991). Therefore, to understand edge effects, it is important to integrate the factors that affect the benefits and costs. For instance, Taiwan Yuhina nesting at the edges of native forests, plantations, and orchards in the same study site of this study (Lee *et al.*, 2005). They nested many times during one breeding season to adapt with the high risk of predation and bad weathers (Yuan, *et al.*, 2004).

The results support that edge effects are not universal to all species. Local breeders may be attracted by native forests and plantations edges for foraging and nesting. Neighboring breeders and wintering species did not prefer this fragmented landscape, so lower registration spot densities make no obvious edge effects. There were higher biodiversity near edges in native forests and plantations, but mostly composed by local breeders (well adapted to this fragmented study site). Neighboring breeders and wintering species had been observed in the neighboring primary forests, but seldom observed in the study site, such as White-throated Laughing-thrush (*Garrulax albogularis*), Island Thrush (*Turdus poliocephalus*) and Swinhoe's Pheasant (*Lophura swinhoii*). All of them might do not prefer fragmented landscape and edge habitats and therefore become rare in the study site. If only examining edge effects at community level, some species which seldom present near edges would be neglected. Therefore, these results support that edge effects are situation specific (Ries *et al.*, 2004). To examine edge effects on biodiversity clearly, it is very important to conduct researches on individual level at finer scale and include large, intact native habitat patches.

Figures

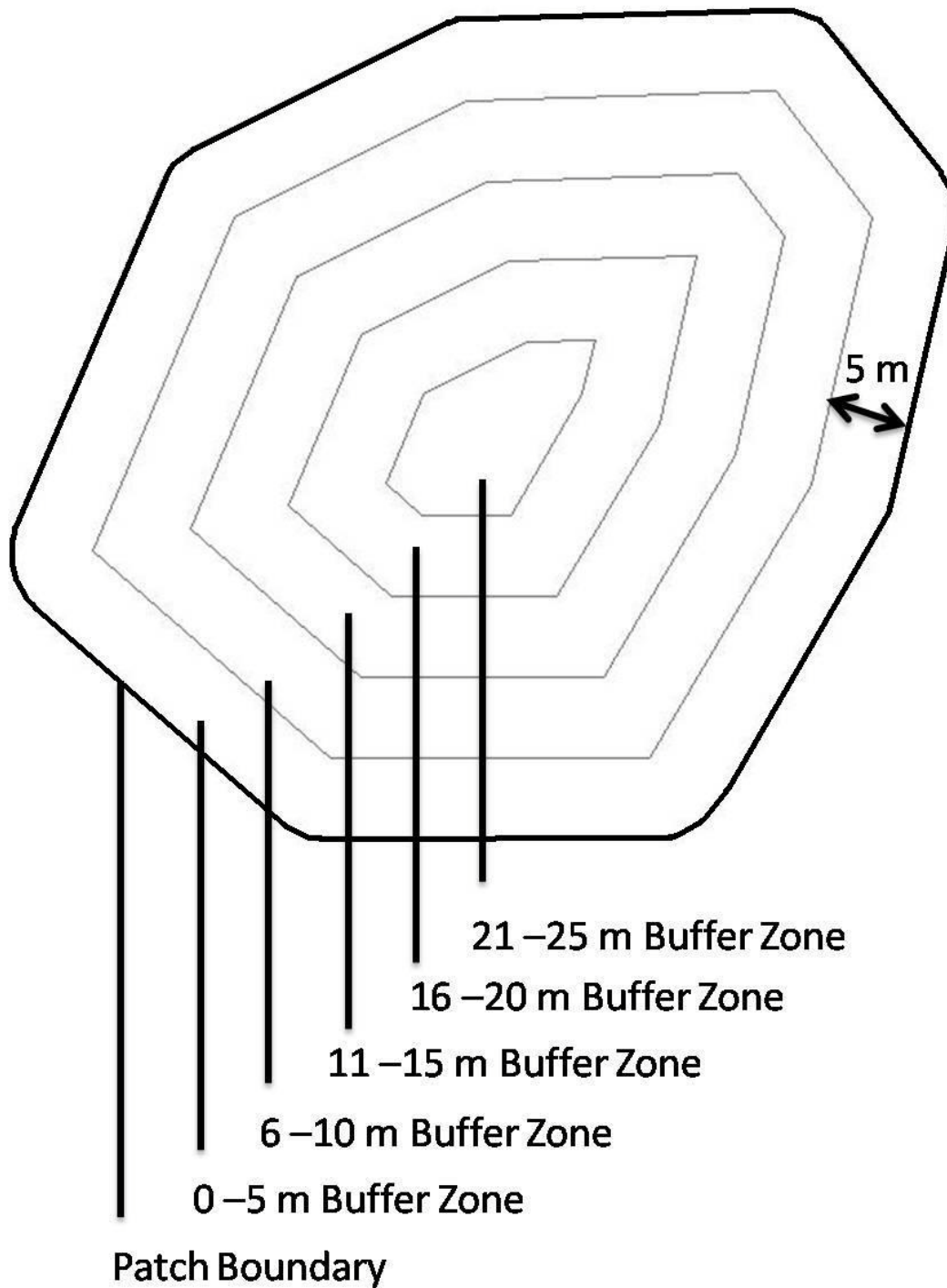


Figure 4-1. The ranks of buffer zones of a patch

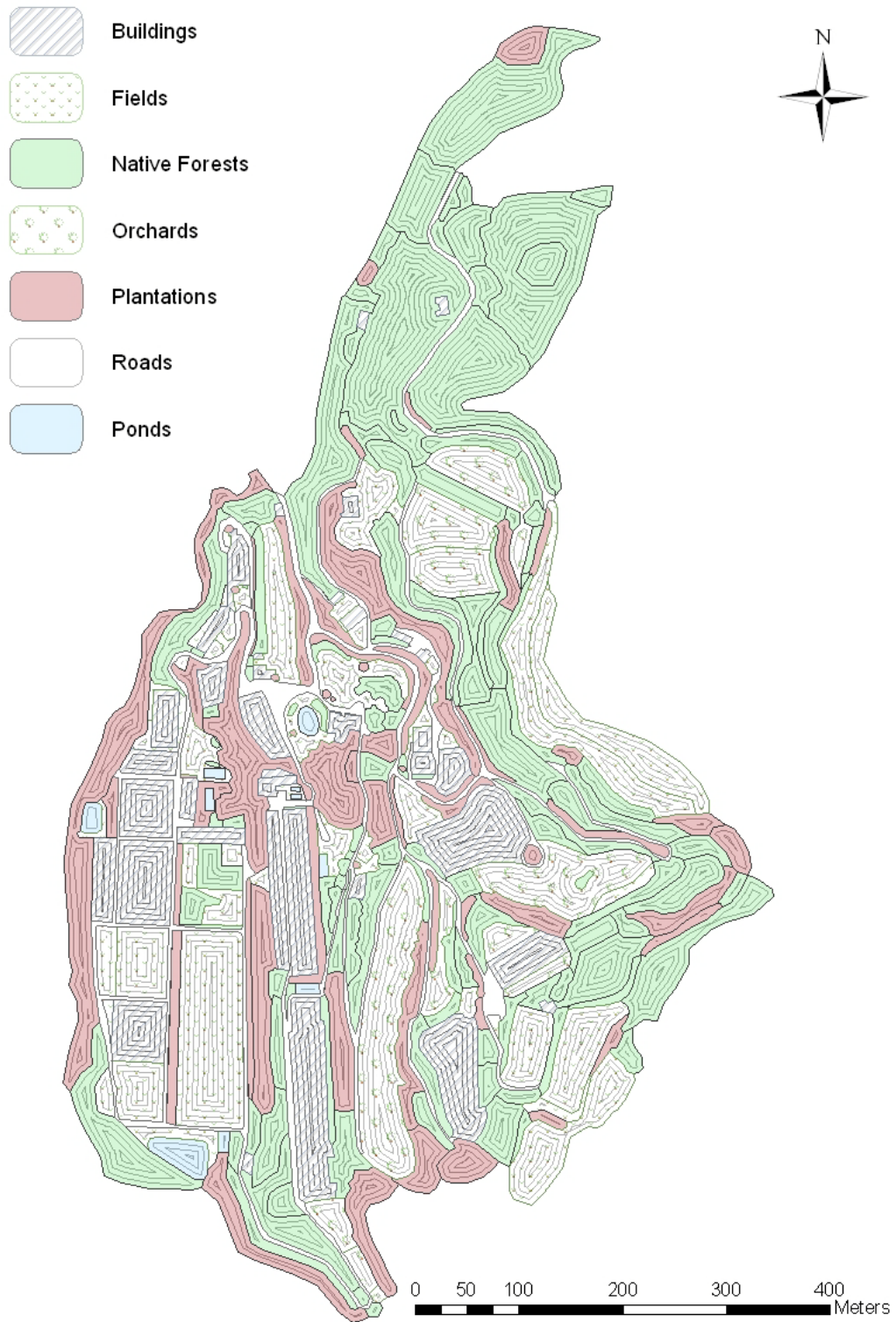


Figure 4-2. The classified patches with habitat types and the buffer zones

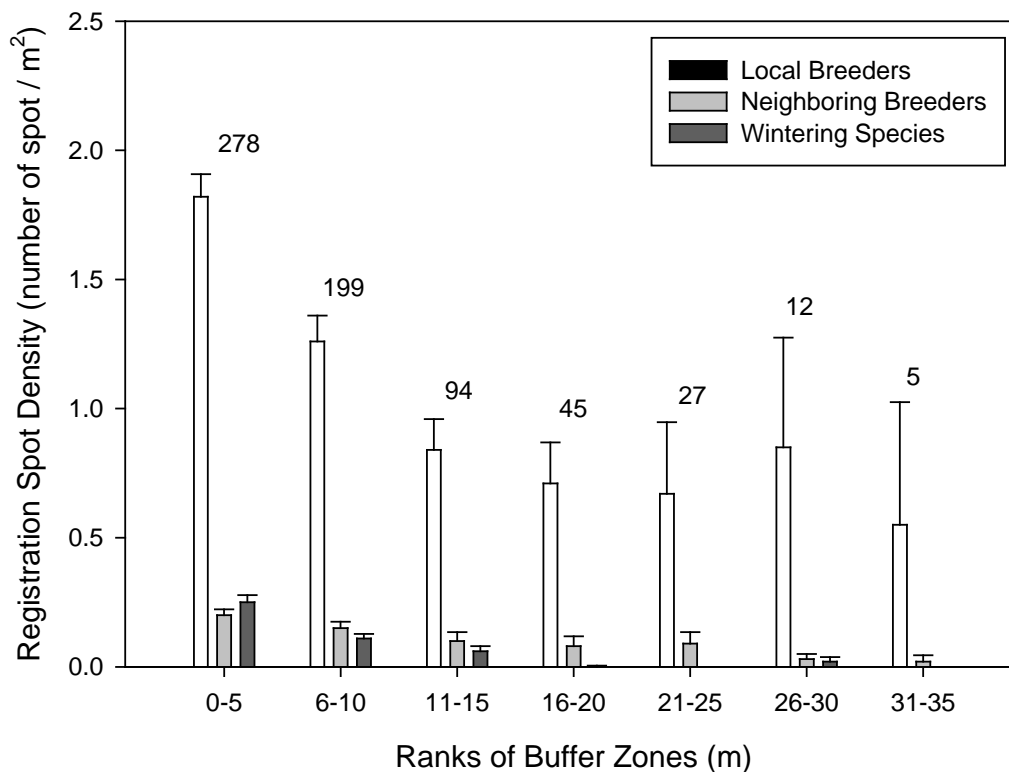


Figure 4-3. The registration spot densities among different ranks of buffer zones of local breeders, neighboring breeders and wintering species. Combining different habitat types together, the registration spot densities were significantly different among three reproductive statuses (one-way ANOVA, $F = 443.541$, $p < 0.001$). The registration spot densities of local breeders were significantly higher than neighboring breeders (Tukey's test, $p < 0.001$) and wintering species (Tukey's test, $p < 0.001$). There were no significance difference between the registration spot densities of neighboring breeders and wintering species (Tukey's test, $p = 0.855$). For local breeders, the registration spot densities among different ranks of buffer zones were significantly different (one-way ANOVA, $F = 5.199$, $p < 0.001$). The registration spot densities of 0 –5 m buffer zones were significantly higher than 6 –10 m buffer zones (Tukey's Test, $p < 0.05$), 11 –15 m buffer zones (Tukey's Test, $p < 0.001$), and 16 –20 m buffer zones (Tukey's Test, $p < 0.05$). The registration spot densities among different ranks of buffer zones were not significantly different for neighboring breeders (one-way ANOVA, $F = 0.292$, $p = 0.940$) and for wintering species (one-way ANOVA, $F = 0.836$, $p = 0.545$).

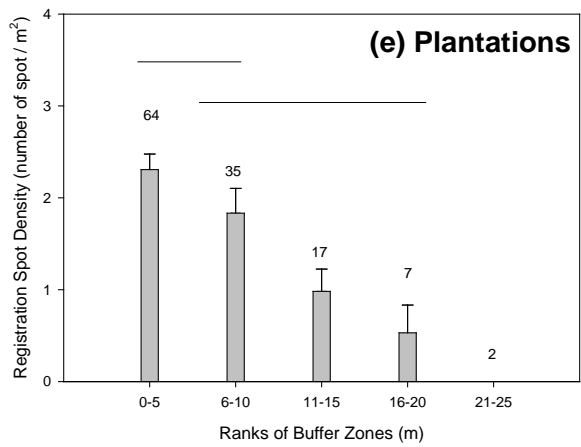
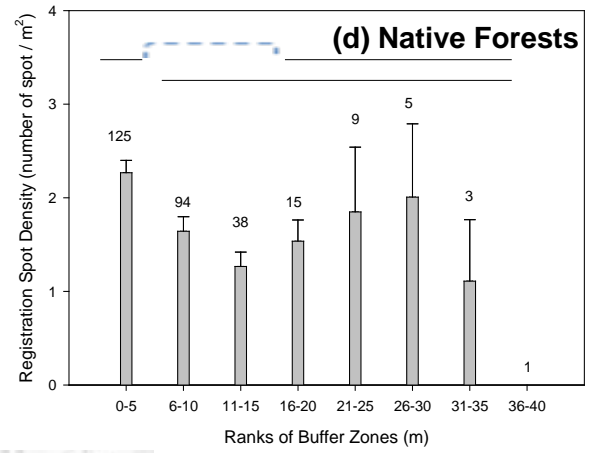
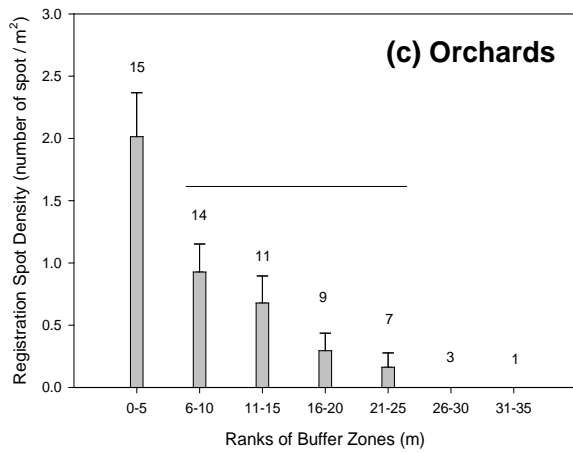
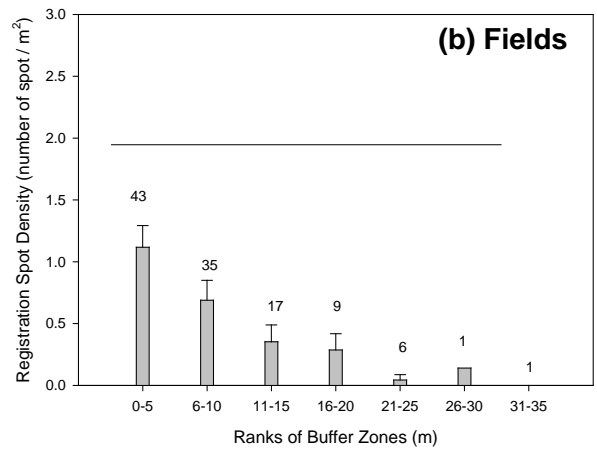
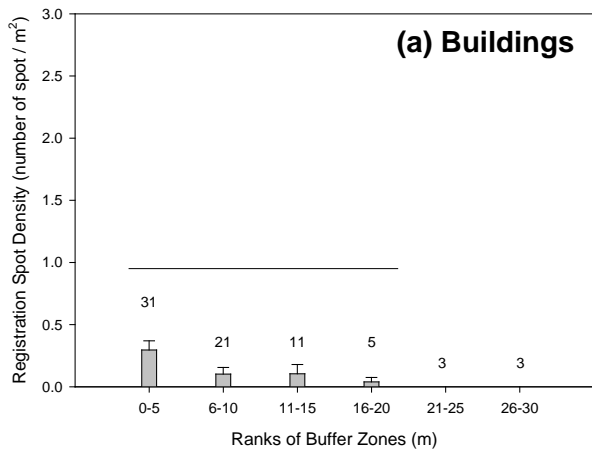


Figure 4-4. The registration spot densities among different ranks of buffer zones of local breeders in buildings, fields, orchards, native forests, and plantations. The bars under the same horizontal line indicate non-significant differences among them.

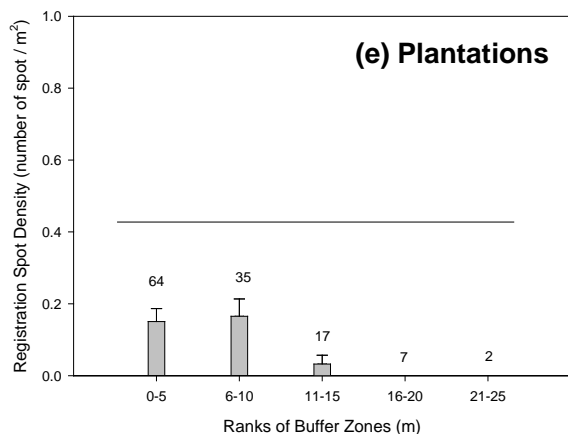
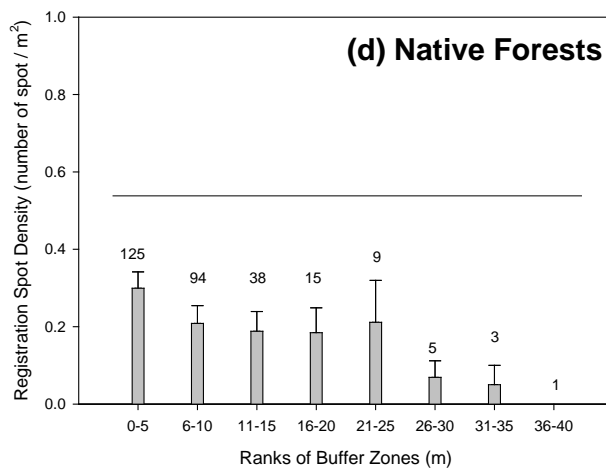
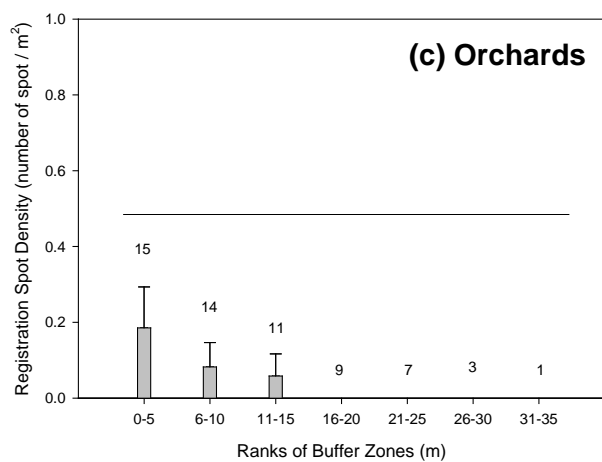
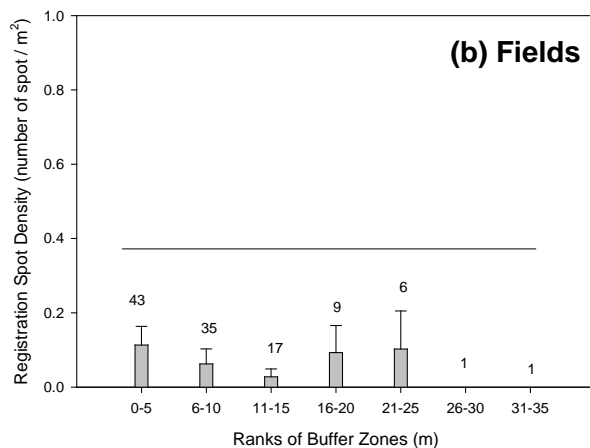
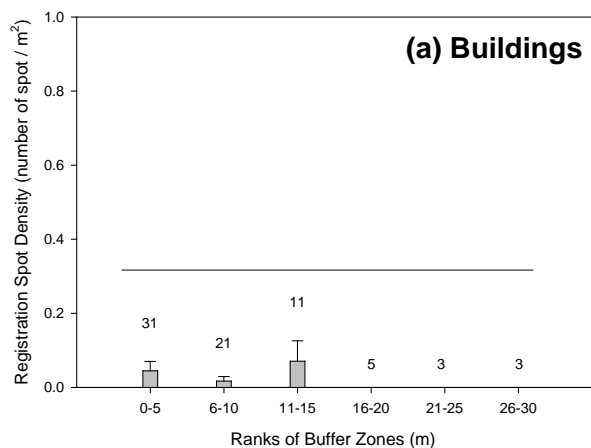


Figure 4-5. The registration spot densities among different ranks of buffer zones of neighboring breeders in buildings, fields, orchards, native forests, and plantations. The bars under the same horizontal line indicate non-significant differences among them.

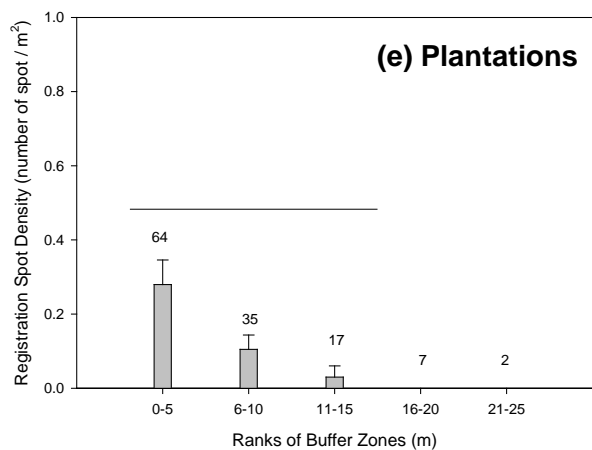
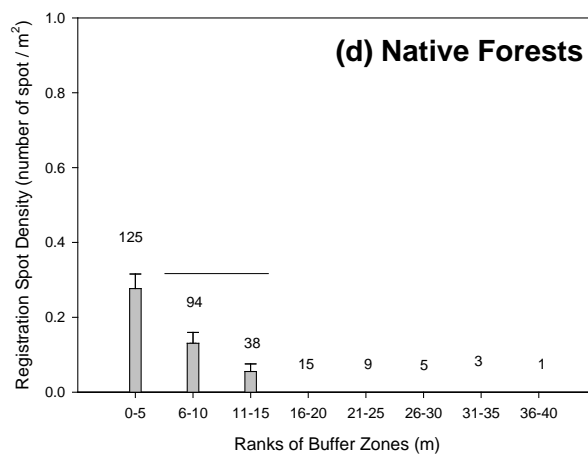
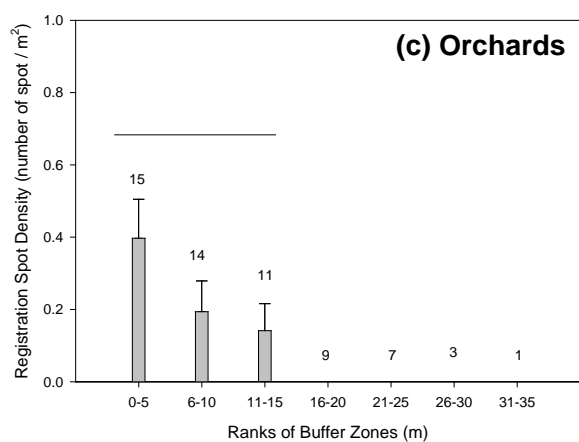
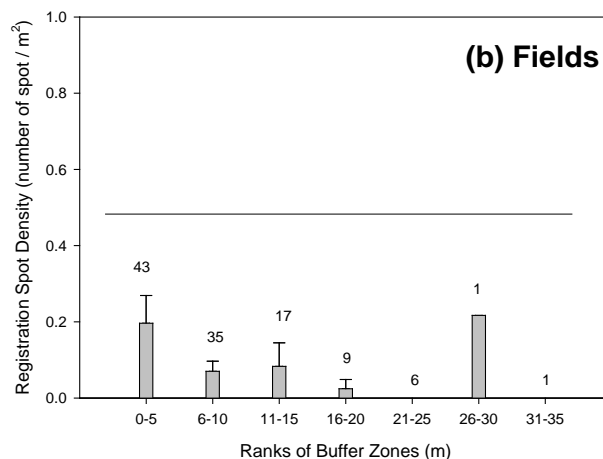
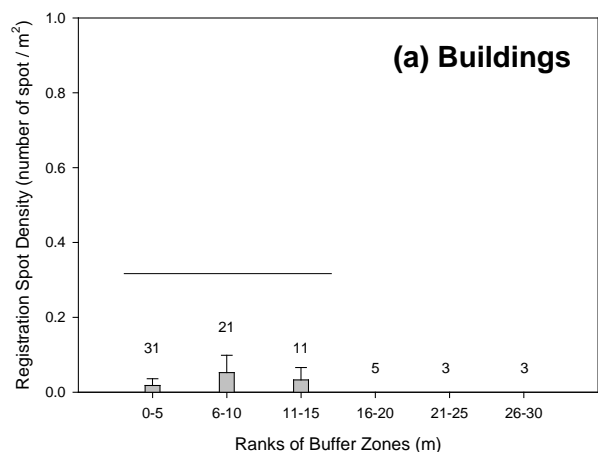


Figure 4-6. The registration spot densities among different ranks of buffer zones of wintering species in buildings, fields, orchards, native forests, and plantations. The bars under the same horizontal line indicate non-significant differences among them.

CHAPTER 5

Conclusions

To sustain higher biodiversity in fragmented environments, there are three important components: landscape structure, vertical foliage structure, and floristic composition. Diverse landscape structure attracts more individuals of different species (especially some species which need special ecological resources from different landscape components) and increases species richness. Patch area is still the fundamental factor to affect species richness, but its effects are sometimes weakened in inappropriate habitat types. Edge effects also increase species richness but only obviously in local breeders which adapt well to edges, but some interior species might avoid habitat patches which are too fragmented or small. Therefore, large patch area and diverse landscape components both are important to sustain higher species richness.

Complex vertical foliage structure provides more shelters and micro-habitats to contain more individuals, also provides more ecological niches for more species. High floristic richness provides diverse food resources to attract more individuals and more species of different ecological guilds. Different species, reproductive statuses, and ecological guilds preferred different situations of vertical foliage structure and floristic composition. Therefore, both diverse vertical foliage structure and floristic composition are important to attract individuals and sustain high species richness.

In fragmented landscape, patches can be classified by area (large and

small) and vegetation structure (simple and complex). For patches with simple vegetation structure (no matter large or small), in order to manage habitats for avian biodiversity, it is important to increase the complexity of vegetation structure. For small patch with complex vegetation structure, if located close to patches with simple vegetation structure, it will be the key feature to attract bird individuals. Large patches with complex vegetation structure are the best to sustain biodiversity and should be kept intact as much as possible, even though they are not able to attract some species which prefer non-forest habitats. Therefore, in the regional scale, let the landscape configuration of a fragmented landscape become a mosaic landscape that contain large native forest patches would be the better situation for more individual and higher biodiversity.

Effects of habitat fragmentation and edge effects are not universal to all species. Thus, to understand these effects clearly, it is very important to examine the wildlife-habitat relationships at a perspective of individual and at finer scale. The detailed examinations of wildlife-habitat relationships of this study should provide insightful guidelines for biodiversity conservation in Taiwan and the other parts of world.

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Appendixes

Appendix 1. List of plant families recorded in canopy (C) and sub-canopy (S) layers

Family Name	Chinese Name	C	S	Family Name	Chinese Name	C	S
Cephalotaxaceae	三尖杉科	○		Rutaceae	芸香科	○	○
Pinaceae	松科		○	Aceraceae	槭樹科	○	○
Taxodiaceae	杉科	○	○	Sabiaceae	清風藤科	○	○
Cupressaceae	柏科	○	○	Anacardiaceae	漆樹科	○	○
Myricaceae	楊梅科		○	Hippocastanaceae	七葉樹科		○
Juglandaceae	胡桃科	○	○	Aquifoliaceae	冬青科	○	○
Salicaceae	楊柳科	○	○	Celastraceae	衛矛科		○
Betulaceae	樺木科	○	○	Staphyleaceae	省沽油科		○
Fagaceae	殼斗科	○	○	Rhamnaceae	鼠李科		○
Ulmaceae	榆科	○	○	Flacourtiaceae	大風子科	○	○
Urticaceae	蕁麻科		○	Stachyuraceae	旌節花科		○
Magnoliaceae	木蘭科	○	○	Myrtaceae	桃金娘科		○
Lauraceae	樟科	○	○	Araliaceae	五加科	○	○
Actinidiaceae	獼猴桃科	○	○	Ericaceae	杜鵑科		○
Theaceae	茶科	○	○	Myrsinaceae	紫金牛科		○
Saxifragaceae	虎耳草科		○	Symplocaceae	灰木科		○
Pittosporaceae	海桐科		○	Oleaceae	木犀科	○	○
Rosaceae	薔薇科	○	○	Verbenaceae	馬鞭草科	○	○
Euphorbiaceae	大戟科	○	○	Caprifoliaceae	忍冬科		○

Appendix 2. List of bird species recorded; LB: local breeder; NB: neighboring Breeder; W: wintering species

Family Name	Scientific Name	Chinese Name	Status in Meifeng
Phasianidae	<i>Arborophila crudigularis</i>	深山竹雞	NB
	<i>Bambusicola thoracicus</i>	竹雞	LB
	<i>Lophura swinhoii</i>	藍腹鵓	NB
Accipitridae	<i>Butastur indicus</i>	灰面鵟鷹	W
	<i>Accipiter vigatus</i>	台灣松雀鷹	NB
Scolopacidae	<i>Scolopax rusticola</i>	山鵲	W
Columbidae	<i>Columba pulchricollis</i>	灰林鴿	NB
	<i>Streptopelia orientalis</i>	金背鳩	LB
	<i>Treon sieboldii</i>	綠鳩	NB
Cuculidae	<i>Cuculus sparverioides</i>	鷹鵒	NB
	<i>Cuculus saturatus</i>	中杜鵑	NB
Strigidae	<i>Strix aluco</i>	灰林鴞	NB
Apodidae	<i>Hirundapus cochinchinensis</i>	灰喉針尾雨燕	NB
	<i>Apus pacificus</i>	白腰雨燕	NB
Ramphastidae	<i>Megalaima nuchalis</i>	五色鳥	NB
Picidae	<i>Dendrocopos leucotos</i>	大赤啄木	NB
Campephagidae	<i>Pericrocotus solaris</i>	灰喉山椒	NB
Dicruridae	<i>Dicrurus aeneus</i>	小卷尾	W
Corvidae	<i>Garrulus glandarius</i>	檣鳥	NB
	<i>Dendrocitta formosae</i>	樹鵲	W
Paridae	<i>Parus monticolus</i>	青背山雀	LB
	<i>Parus holsti</i>	黃山雀	NB
Hirundinidae	<i>Hirundo tahitica</i>	洋燕	LB
Aegithalidae	<i>Aegithalos concinnus</i>	紅頭山雀	LB
Cisticolidae	<i>Prinia inornata</i>	褐頭鷓鴣	NB
Pycnonotidae	<i>Spizixos semitorques</i>	白環鸚嘴鵯	NB
	<i>Pycnonotus sinensis</i>	白頭翁	NB
	<i>Microscelis leucocephalus</i>	紅嘴黑鵯	W
Sylviidae	<i>Cettia fortipes</i>	小鶯	LB
	<i>Cettia acanthizoides</i>	深山鶯	W
	<i>Bradypterus alishanensis</i>	台灣叢樹鶯	W
	<i>Abroscopus albogularis</i>	棕面鶯	LB
Timalidae	<i>Pomatorhinus erythrogenys</i>	大彎嘴畫眉	NB
	<i>Pomatorhinus ruficollis</i>	小彎嘴畫眉	NB
	<i>Pnoepyga albiventer</i>	鱗胸鷓鴣	NB

Appendix 2 (continued). List of bird species recorded; LB: local breeder; NB: neighboring Breeder; W: wintering species

Family Name	Scientific Name	Chinese Name	Status in Meifeng
Timalidae	<i>Stachyris ruficeps</i>	山紅頭	LB
	<i>Garrulax poecilorhynchus</i>	竹鳥	NB
	<i>Garrulax morrisonianus</i>	金翼白眉	W
	<i>Liocichla steerii</i>	藪鳥	LB, omnivore
	<i>Actinodura morrisoniana</i>	紋翼畫眉	NB
	<i>Alcippe morrisonia</i>	繡眼畫眉	LB
	<i>Heterophasia auricularis</i>	白耳畫眉	LB, omnivore
	<i>Yuhina brunneiceps</i>	冠羽畫眉	LB, omnivore
	<i>Paradoxornis webbianus</i>	粉紅鸚嘴	LB
Reguliidae	<i>Regulus goodfellowi</i>	火冠戴菊	W
Sittidae	<i>Sitta europaea</i>	茶腹鳴	NB
Turdidae	<i>Turdus aurea</i>	虎鶇	W
	<i>Turdus poliocephalus</i>	白頭鶇	NB
	<i>Turdus pallidus</i>	白腹鶇	W
	<i>Turdus chrysolaus</i>	赤腹鶇	W
Muscicapidae	<i>Luscinia johnstoniae</i>	栗背林鶇	W
	<i>Luscinia cyanurus</i>	藍尾鶇	W
	<i>Phoenicurus aureus</i>	黃尾鶇	W
	<i>Myiomela leucura</i>	白尾鶇	LB
	<i>Muscicapa ferruginea</i>	紅尾鶇	NB, insectivore
	<i>Ficedula hyperythra</i>	黃胸青鶇	NB, insectivore
	<i>Niltava vivida</i>	黃腹琉璃	LB, insectivore
Dicaeidae	<i>Dicaeum ignipectum</i>	紅胸啄花	NB
Motacillidae	<i>Motacilla alba</i>	白鶇	W
	<i>Anthus hodgsoni</i>	樹鶇	W
	<i>Anthus rubescens</i>	黃腹鶇	W
Fringillidae	<i>Fringilla montifringilla</i>	花雀	W
	<i>Carpodacus vinaceus</i>	酒紅朱雀	W
	<i>Pyrrhula nipalensis</i>	褐鶇	NB
Emberizidae	<i>Emberiza pusilla</i>	小鶇	W
	<i>Emberiza spodocephala</i>	黑臉鶇	W