

Research paper

Biodiversity in Deciduous Hardwood and Conifer Plantations of the Upper Liukuei (Shanping) Area

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【 Summary 】

This study presents data from vegetation plots of managed deciduous hardwood and conifer plantations in the Upper Liukuei area of southern Taiwan to test the responses of understory and ground vegetation communities to clear cuts. A pooled quadrat method was used to determine sample size. Rank abundance plots and diversity indices such as species richness, Simpson index, Shannon index, and Shannon evenness index were used to elucidate differences in diversity of the plantations. Preliminary analysis of bird survey data was used to determine the effect of forest types on bird diversity. Diversity analysis suggested that for both understory and ground vegetation, deciduous hardwood plantations are higher in diversity. Differences in levels of available sunlight and rates of re-establishment/growth during plantation development may have driven these trends. Bird analysis also showed significantly higher diversity in deciduous hardwood plantations. Specific food or nesting requirements of bird species may be the cause.

Key words: biological diversity, Shannon index, plantation, forest management.

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研究報告

六龜試驗林扇平地區人工闊葉林與人工針葉林 生物多樣性之比較

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摘 要

過去一個世紀以來，資源經營與生物多樣性保育之間常有許多衝突。人類長期經營與利用森林資源的結果，造成地景的破碎與天然林的大量減少，此一現象，使長久以來習用之森林經營方

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式與政策受到大眾的質疑，現有森林經營方式也必須因應此一變化而有所調整。因此，研究森林經營對生物多樣性的影響成為今日重要的課題之一。本研究針對六龜試驗林扇平地區之人工針葉林與人工闊葉林，分別就其所有木本植物、林下灌層、及地被植物層加以分析討論，應用如豐富度指數、Simpson 優勢度指數、Shannon 多樣性指數、及 Shannon 均勻度指數等生物多樣性指數，探討皆伐對人工林林下灌木層與地被植物層生物多樣性之影響，並利用初步之鳥類調查資料，驗證鳥類多樣性於人工針葉林與人工闊葉林之差異，以了解皆伐及其後之育林作業對長期生物多樣性變化與物種之出現所造成之影響。

生物多樣性之分析結果顯示落葉之人工闊葉林，不論在林下灌層或草本植物層，皆有較高之生物多樣性。人工針葉林之林下灌層並無顯著之優勢種產生。光線的可及性、造林的成敗與方式、造林地與周圍環境之空間變異情形、以及造林樹種與入侵樹種的生長速度等都可能是造成這兩種造林地林下灌層與地被植物層生物多樣性不同的原因。

鳥類的豐度排序圖及生物多樣性分析亦顯示與植被相同的現象。落葉的人工闊葉林明顯地有較多的鳥種出現，可能是因為人工闊葉林較多的林下灌木樹種與草本植物種，有較大的機率符合某些鳥類特殊的食性與築巢需求。其詳細之分布差異及差異之驅動機制上有待深入探討。

關鍵詞：生物多樣性指數、人工林、森林經營。

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INTRODUCTION

Biodiversity is the subject matter of conservation biology (Noss 1983). It is of interest because measures of diversity are frequently seen as indicators of the well-being of ecological systems (Maguran 1988). Motivated by widespread loss of species and natural habitats, national and global forestry organizations have recognized the need to manage for biodiversity and ecological research has focused increasingly on the consequences of exploitive and long-term management activities for species diversity (Burton et al. 1992, Halpern and Spies 1995). Consideration of biological diversity has guided the design, implementation, and critique of existing policy on natural resource management (Roberts and Gilliam 1995). Since management objectives are often directed toward a limited number of tree species, it may seem reasonable to hypothesize that forest management inevitably decreases plant diversity.

However, the effects of forest management on the patterns of diversity may vary considerably among ecosystem types and management techniques. Therefore, examining empirically the relationship between forest management and plant diversity in a variety of forest ecosystem types is necessary.

A variety of indices such as species richness, statistic indices, and dominance measures are used to evaluate diversity. Species richness, abundance, and species density are often used as indications of diversity for both vegetation and wildlife research (Robertson and Hackwell 1995, Donald et al. 1998, Hill 1998, Allen and O'Connor 2000, Howell et al. 2000, Poague et al. 2000, Rodewald and Yahner 2000). Heterogeneity indices such as the Shannon index and Shannon evenness index are usually used to provide heterogeneity information other than species richness for wildlife studies (Steele et al. 1984, Rosenstock

1998, Blair 1999, Poague et al. 2000). Dominance indices such as the Simpson's index integrate the number and relative abundance of a species and are sometimes used in ecological studies as measures of dominance coupled with evenness indices (Whittaker 1972, Magurran 1988, Cheng 1999). Among these indices, the statistical nature of the Shannon index makes it possible to use parametric statistics to compare sets of samples for which the diversity has been calculated (Whittaker 1972) and a Shannon *t*-test proposed by Hutchison (1970) can be used to identify significant differences between two communities.

Although 4 or more repetitions of transects were tested to be sufficient for estimates of species richness and diversity, to avoid the bias of diversity measures caused by species-area relationships, different sampling techniques such as pooled quadrat were recommended to determine adequate sample size (Peilou 1975, Steele et al. 1984, Magurran 1988, Gaston and Spic 1998). When an adequate number of quadrats are pooled together, the organism aggregation effect can usually be limited and a more accurate estimation of biodiversity can be acquired.

The general trends for changes in species richness and community diversity through forest succession show an increase in both measures early in succession and then a decline in more mature forests. Species richness attains a maximum shortly after disturbance, remains relatively stable for the early successional stages, declines at the period of aggradation, and then rises again to a lower maximum than the one occurring shortly after disturbance for both natural forest and secondary coniferous forest (Whittaker 1972, Hibbs 1983, Schoonmaker and McKee 1988, Reiners 1992,

Bormann et al. 1995). It is also suggested that changes in understory diversity are fairly short-lived following clear-cut logging (Boring and Monk 1981, Barik et al. 1992, Halpern and Spies 1995, Beese and Bryant 1999). This study followed this model and assumed that 15-20 yrs after disturbance, species richness and diversity would become relatively stable. Some changes in species composition may still occur, but number of species is unlikely to increase in the near future.

Differences in habitat composition and structure influence bird species composition, and hence bird diversity, in different landscapes and along successional stages (Morrison 1992, Dickson et al. 1993, Hansen et al. 1995, Ding et al. 1997, Calvo and Blake 1998, Pei and Sun 1998, Yuan and Tsai 2000). In this study, bird species richness in different conifer plantations of the same age but different thinning intensities in the past showed no significant differences (Chung et al. 2000). Many reasons may contribute to this result such as the thinning intensities not being distinctive enough to create different habitats, the years after thinning were long enough to cancel the effects, or the spatial distribution of these conifer plantations made it possible for species to travel among them. Therefore, it is assumed that all selected conifer plantations are in relatively uniform structural condition and their thinning intensities in the past have no effects on bird diversity in this study. Hence, bird abundance can be used to reflect differences in different forest types, i.e., deciduous hardwood plantations and conifer plantations in the upper Liukuei area without the concern of different thinning methods among conifer plantations.

In this study, diversities of 2 different types of plantations are compared to under-

stand the possible effects of different management practices. Hardwood and conifer plantations usually undergo the same nursing procedures. Yet, the spatial variability of resources and environment (adjacent to natural hardwood forest), and rates of reestablishment and growth may drive different trends during plantation development.

MATERIALS AND METHODS

The study area was located in the Shanping area of Liukuei, 1 of 6 experimental forests of the Taiwan Forestry Research Institute. Elevation ranges from 700 to 1,800 m. Average annual rainfall is 3,800 mm concentrating from May to September. Annual temperature is 17.5 °C. Most of the areas are covered by natural hardwood forests or secondary hardwood forests. The conifer plantations form a continuous patch of 500 ha, about 20% of the area. The

hardwood plantations, on the other hand, are more scattered on the landscape forming less continuous patches with total area of 90 ha, about 4% of the area (Fig. 1).

For all plantations, the original species growing on the site were predominantly clear-cut prior to the establishment of the plantations. During the initial 6 yr of silvicultural practices, cutting of vines and cleaning of after-growth were performed annually. The main species planted in the conifer plantations in upper Liukuei is *Taiwania* (*Taiwania cryptomerioides*). Various degrees of thinning have been performed on a few stands to increase productivity. The primary planting tree species in the deciduous hardwood plantations in the upper Liukuei are zelkova (*Zelkova serrata*) and large-leaved nanmu (*Machilus kusanoi*). No thinning was performed on the plantations. Attempts to seed and plant a few of the deciduous hardwood plantations were un-

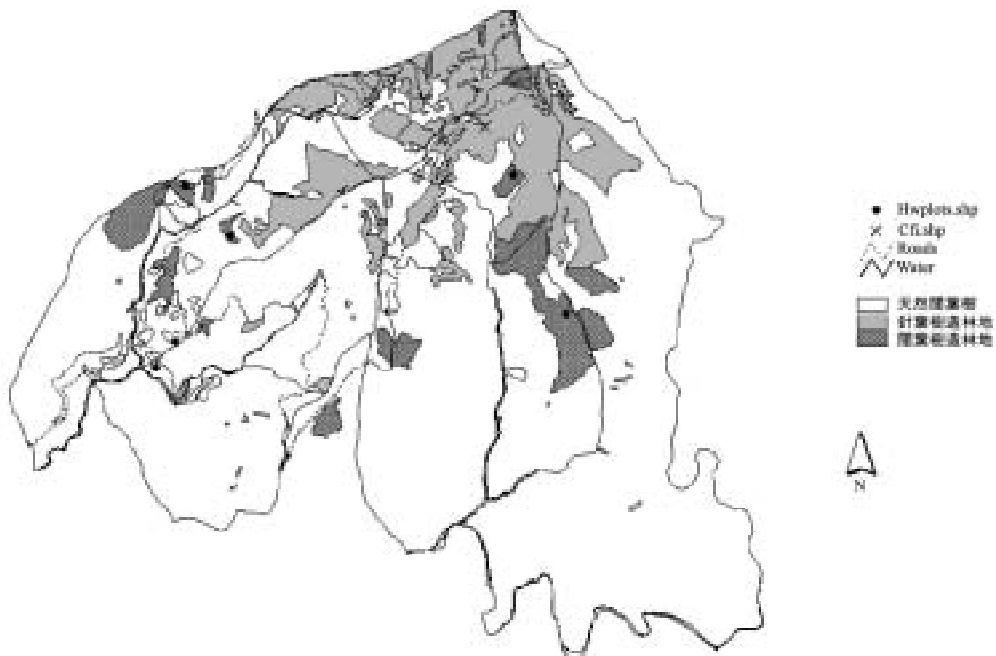


Fig. 1. Forest types and sample plots of the upper Liukuei (Shanping) area.

successful. Poor germination and/or survival of deciduous hardwood tree species in these plantations necessitated repeated planting in the years following the original planting, consequently, this has resulted in stands containing components of natural regeneration. In this study, conifer and deciduous hardwood plantations were chosen based on similarities of age (having reached the canopy closure stage), silvicultural management practices, and history. However, due to the limited planting area and age classes of the deciduous hardwood plantations, some variations were inevitable.

We carefully selected the study sites to minimize differences in site history by limiting sampling to plantations 15 to 20 yr old in the year 2000 and under similar planting contracts. Variation in site environment was also reduced by selecting plantations with similar levels and ranges of site characteristics such as elevation among forest types.

Sampling methods for deciduous hardwood and conifer plantations were identical. Twelve transects with a total of 120 sample plots of 5×5 m were established systematically (with a random start) (Fig. 1). Each transect contained 10 subplots with a total of 60 subplots and 6 transects on each plantation. Within each sample plot, inventories were taken for all vascular plant species. For woody vegetation taller than 1 m, species name, height, DBH, and canopy coverage were recorded. Crown coverage was inventoried for ground vegetation since it was impossible to distinguish each individual. A GRS densitometer with line-point transects was used to estimate canopy coverage at each vertical stratum (> 5 m, $1 - 5$ m, and < 1 m). Cover estimates generated using the GRS densitometer were based on an evaluation of cover data collected at

sample points evenly spaced along transects.

Bird surveys were conducted in variable circular-plots (Reynolds et al. 1980) on each sample plot and transect location from September 2000 to January 2001. During the survey period, each sample plot was surveyed once a month. Bird species, the number of individuals of each species, and the distance between the observer and the observed bird were recorded 2 times a day, from 05:00 to 07:00 and from 16:00 to 18:00, for 15 min per visit for each transect.

In this study, we used the pooled quadrat method to determine a valid sample size. Quadrats were pooled in a random sequence and the diversity index was calculated. A Shannon-Weaver cumulative diversity curve was generated to show the diversity of woody vegetation and to decide the appropriate sample size. The flattened portion of the curve was used to calculate diversity. To encounter the dependence of species richness of a sample, the same sample size was used in both deciduous hardwood and conifer plantations.

Rank abundance plots for all woody, understory, and ground vegetation were made to determine the abundance trends. The same method was applied to the bird data to understand the diversity trend of birds species in deciduous hardwood and conifer plantations.

We examined differences in diversity with data from 2 direct counts, species richness and number of individuals, and 4 indices: species density (N_0), the reciprocal Simpson index (N_2), the Shannon evenness index, and the Shannon index (H). Species richness is defined as a complete catalog of species in the community. The dominance measure of species heterogeneity, the reciprocal of Simpson's index ($1 - \sum P_i^2$), where P_i represents the proportional abun-

dance of the *i*th species in the sample, was used to examine abundances of the most common species. The Shannon index ($-\sum P_i \ln P_i$) and the Shannon evenness index, the ratio of observed diversity to maximum diversity, were calculated for diversity of both deciduous hardwood and conifer plantations. Diversities of the deciduous hardwood and conifer plantations were compared using the Shannon *t*-test following the method which Hustcheson (1970) proposed:

$$VarH = \frac{\sum P_i (\ln P_i)^2 - (\sum p_i \ln P_i)^2}{N} + \frac{S-1}{2N^2};$$

..... (1)

and

$$t = \frac{H_1 - H_2}{(VarH_1 + VarH_2)^{1/2}}$$

..... (2)

RESULTS

The diversity curves produced by the

Shannon index leveled off at about 50 quadrats indicating that this was the minimum sample size on which a diversity estimate should be based (Fig. 2). The diversity curve rose steeply at the beginning and increased continuously with sample size, confirming the dependence of diversity on sample size. This trend in species diversity peaked and declined several times prior to when most of the species were included, and, then the diversity curve flattened off. To ensure all species were presented in the sample, all 60 quadrats were used throughout the study. The sample size that was chosen was assumed to be the best fit for the study, however there is always an element of subjectivity in deciding the point at which a curve flattens off.

Rank abundance plots of the woody flora showed that the deciduous hardwood plantations had more species and less dominance than did the conifer plantations (Fig. 3). The selection of diversity indices listed in table 1 confirms that in all cases, the deciduous hardwood plantations were considered more

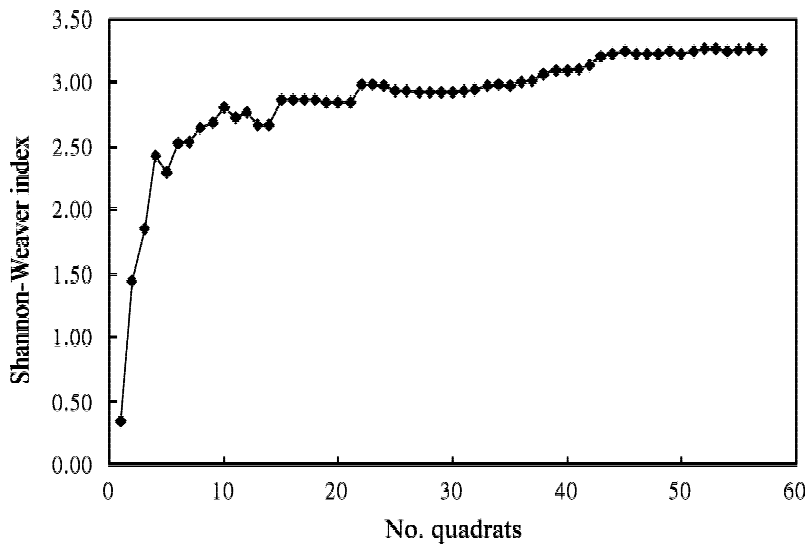


Fig. 2. Shannon cumulative diversity curve of sample quadrats in the upper Liukuei (Shanping) area.

diverse than the conifer plantations. One or 2 species were dominant while the remainders were equally common. Although the trends found in the deciduous hardwood plantations showed greater diversity for the vegetation stratum, the understory and ground vegetation strata showed somewhat different characteristic patterns of species abundance. The understory stratum in the deciduous hardwood plantations showed a pattern where few species were dominant, some had medium abundance, and most were represented by only a few individuals, which

is closer to the situation in a natural deciduous hardwood forest. In contrast, the pattern of conifer plantations showed all species to be almost equally rare and represented by only a few individuals throughout the plantations. The herbaceous vegetation, however, showed a similar characteristic pattern of species abundance: a few species were dominant, a few species had medium abundance but a lot less individuals compared to the dominant species, and most were represented by only a few individuals.

The characteristic pattern of abundance

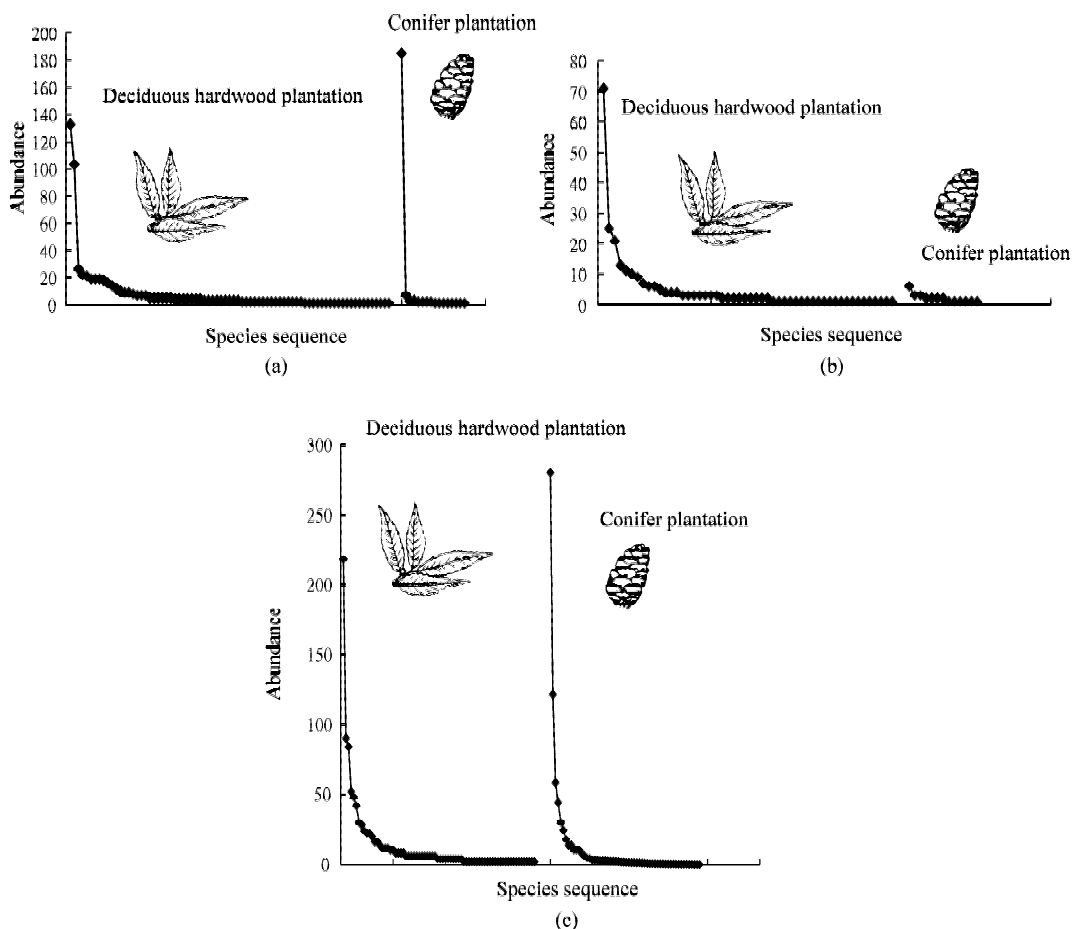


Fig. 3. Rank abundance plots of vegetation of different strata in the upper Liukuei (Shanping) area. (a) All woody vegetation. (b) Mid-canopy vegetation. (c) Ground vegetation.

Table 1. Diversity indices of different vegetation strata of the deciduous hardwood plantation and conifer plantation in the upper Liukuei (Shanping) area

Strata	Diversity index	Deciduous	
		Hardwood Plantation	Conifer Plantation
All woody vegetation	Species richness (S)	77	16
	Species density	0.051	0.011
	Individuals (N)	615	214
	Simpson (1 - D)	0.9148	0.2519
	Shannon index*	3.2784	0.7327
	Shannon evenness	0.7547	0.2643
Understory vegetation	Species richness (S)	53	13
	Species density	0.035	0.009
	Individuals (N)	257	26
	Simpson (1 - D)	0.8991	0.9231
	Shannon index*	3.0396	2.3778
	Shannon evenness	0.7656	0.9270
Ground vegetation	Species richness (S)	74	58
	Species density	0.049	0.039
	Total coverage	980	708.767
	Simpson (1 - D)	0.9215	0.7983
	Shannon index*	3.3120	2.3157
	Shannon evenness	0.7695	0.5703

*Shows a significant difference at a 99% confidence level.

reflects 2 underlying successional processes of plantations following logging and planting: rapid colonization by nearby woody species and the gradual re-establishment or recovery of a characteristic understory stratum. On deciduous hardwood plantations, invasion was rapid after logging and planting resulting in a higher abundance for the understory stratum. This higher abundance and greater diversity for the understory stratum imply the colonization success of shade tolerant species such as *Beilschmiedia erythrophloia*, *Neolitsea aciculata*, *Machilus japonica*, *Machilus thunbergii*, *Michelia compressa*, *Pasania hance*, and *Pasania harlandii*, which invaded rapidly during the first few growing seasons after the establishment of the plantations. These understory woody and herbaceous plants, includ-

ing trees that can exist as advance regeneration species such as *Celtis sinensis*, *Mallotus paniculatus*, *Oreocnide pedunculata*, *Morus australis*, *Ficus fistulosa*, *Litsea cubeba*, *Acer albopurpurascens*, *Elaeocarpus sylvestris*, *Clerodendrum trichotomum*, and *Sapindus mukorossii*, may remain in the understory for a very long time.

The rank abundance plots showed that conifer plantations have fewer abundant and rare species than did deciduous hardwood plantations (Fig. 3). When species richness was examined alone, the vegetation of all strata of deciduous hardwood plantations had more species and individuals/coverage than those of conifer plantations, especially for understory vegetation. This observation was confirmed by the indices tested. The Shannon index of heterogeneity, which incorpo-

rates information on the proportional abundances of species, showed significant differences.

The results showed a significant difference in heterogeneity for all strata between deciduous hardwood plantations and conifer plantations at a 99% confidence level (Table 1). It was very interesting that the Shannon evenness index showed that for understory vegetation of the conifer plantations, all species were almost equally abundant, 0.93 (Table 1). No species dominated the community. However ground vegetation showed a reverse trend. The lower evenness value indicated higher species dominance structure in the deciduous hardwood plantations (Table 1). The reciprocal Simpson's index showed a forest composition of greater dominance in the overall woody vegetation and ground vegetation of deciduous hardwood plantations while having less diverse understory vegetation.

When comparing the understory stratum with the herbaceous stratum of the deciduous hardwood plantations, herbaceous vegetation in the Shanping area was signifi-

cantly higher in heterogeneity at a 99% confidence level ($t(H_{\text{herb}} - H_{\text{under}}) = 2.8348$ and $df = 408$).

Differences between the deciduous hardwood and conifer plantations were also revealed by bird data. The rank abundance plot of birds showed that the deciduous hardwood plantations had a greater range in number of species (Fig. 4). The collected bird survey data recorded a total of 42 species in 20 families (Table 2). The common bird names followed the Wildlife Distribution Database in Taiwan (Lee et al. 1998). No migrant species were recorded during the survey period. There were 41 species recorded in deciduous hardwood plantations, 39 species if birds with large territories such as the serpent eagle (*Spilornis cheela*) and black eagle (*Ictinaetus malayensis*) were not included, while 24 were recorded in conifer plantations (Table 2). The 3 species that appeared in the conifer plantations but not in the deciduous hardwood plantations were jay (*Garrulus glandarius*), yellow-bellied bush warbler (*Cettia acanthizoides*), a bush insectivore, and nuthatch (*Sitta*

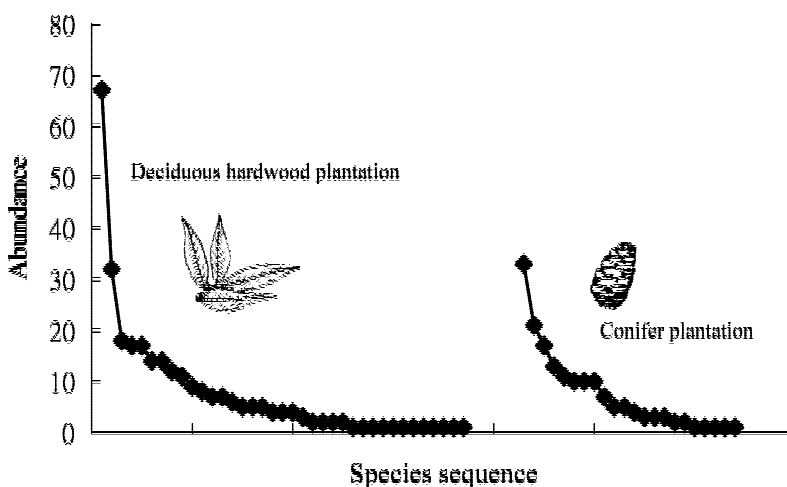


Fig. 4. Rank abundance plot of bird species recorded in the upper Liukuei (Shanping) area.

Table 2. Bird species name list and presence/absence data of the deciduous hardwood plantation and conifer plantation in the upper Liukuei (Shanping) area

Family	Common name ¹⁾	Scientific name	Presence/Absence	
			Deciduous hardwood plantation	Conifer plantation
Accipitridae	Serpent Eagle	<i>Spilornis cheela</i>	+	
	Black Eagle	<i>Ictinaetus malayensis</i>	+ ²⁾	
Phasianidae	Bamboo Partridge	<i>Bambusicola thoracica</i>	+	+
	Formosan Hill Partridge	<i>Arborophila crudigularis</i>	+	+
Strigidae	Mountain Scops Owl	<i>Otus spilocephalus</i>	+	+
	Collared Scops Owl	<i>Otus bakkamoena</i>	+	
	Collared Pigmy Owl	<i>Glaucidium brodiei</i>	+	
Capitonidae	Muller's Barbet	<i>Megalaima oorti</i>	+	
Picidae	Pigmy Woodpecker	<i>Picoides canicapillus</i>	+	
	Black-napped Green Woodpecker	<i>Picus canus</i>	+	+
Motacillidae	Red-throated Pipit	<i>Anthus cervinus</i>	+	
Campephagidae	Grey-throated Minivet	<i>Pericrocotus solaris</i>	+	
Pycnonotidae	Finch-billed Bulbul	<i>Spizixos semitorques</i>		
	Black Bulbul	<i>Hypsipetes madagascariensis</i>	+	
Oriolidae	Maroon Oriole	<i>Oriolus traillii</i>	+	
Dicruridae	Bronzed Drongo	<i>Dicrurus aeneus</i>	+	
Corvidae	Jay	<i>Garrulus glandarius</i>		+
	Formosan Blue Magpie	<i>Urocissa caerulea</i>	+ ²⁾	
	Gray Tree Pie	<i>Dendrocitta formosae</i>	+	
	Large-billed Crow	<i>Corvus macrorhynchos</i>	+	+
Turdidae	White-tailed Blue Robin	<i>Cinclidium leucurum</i>	+	+
	Blue Shortwing	<i>Brachypteryx montana</i>	+	+
	Brown Thrush	<i>Turdus chrysolaus</i>	+	
	White's Ground Thrush	<i>Zoothera dauma</i>	+	
	Formosan Whistling Thrush	<i>Myiophoneus insularis</i>	+	
Timaliidae	Rusty-cheeked Scimitar Babbler	<i>Pomatorhinus erythrogenys</i>	+	+
	Lesser Scimitar Babbler	<i>Pomatorhinus ruficollis</i>	+	+ ²⁾
	Scaly-breasted Wren Babbler	<i>Pnoepyga pusilla</i>	+	+
	Red-headed Babbler	<i>Stachyris ruficeps</i>	+	+
	Steere's Babbler	<i>Liocichla steerii</i>	+	+
	Gould's Nun Babbler	<i>Alcippe brunnea</i>	+	+
	White-eyed Nun Babbler	<i>Alcippe morrisonia</i>	+	+
	White-eared Sibia	<i>Heterophasia auricularis</i>	+	+
	Formosan Yuhina	<i>Yuhina brunneiceps</i>	+	+
	White-bellied Yuhina	<i>Yuhina zantholeuca</i>	+	+ ²⁾
Sylviidae	Yellow-bellied Bush Warbler	<i>Cettia acanthizoides</i>		+
	Brown Bush Warbler	<i>Bradypterus seebohmi</i>	+	
	Fulvous-faced Flycatcher Warbler	<i>Abroscopus albogularis</i>	+	+
Muscicapidae	Blace-naped Blue Monarch	<i>Hypothymis azurea</i>	+	
	Rufous-bellied Blue Flycatcher	<i>Niltava vivida</i>	+	+
Paridae	Breen-backed Tit	<i>Parus monticolus</i>	+	+
	Coal Tit	<i>Parus ater</i>	+ ²⁾	
Sittidae	Nuthatch	<i>Sitta europaea</i>		+
Dicaeidae	Plain Flowerpecker	<i>Dicaeum concolor</i>	+ ²⁾	
Zosteropidae	White Eye	<i>Zosterops japonica</i>	+	+
Estrildidae	Spotted Munia	<i>Lonchura punctulata</i>	+	
TOTAL			41	24

¹⁾ From Lin and Yang 1996²⁾ Sighting not recorded during inventory time period

Table 3. Bird diversity indices of the deciduous hardwood plantation and conifer plantation in the upper Liukuei (Shanping) area

Diversity index	Deciduous hardwood plantation	Conifer plantation
Species richness (S)	37	22
Individuals (N)	289	164
Simpson (1 - D)	0.9132	0.9102
Shannon index*	2.9153	2.6352
Shannon evenness	0.8073	0.8525

¹⁾*Shows a significant differences at a 99% confidence level.

europaea), a bole gleaner. Twenty species were recorded only in deciduous hardwood plantations. Four of them, i.e., Collared Pigmy Owl (*Glaucidium brodiei*), Maroon Oriole (*Oriolus traillii*), Formosan Blue Magpie (*Urocissa caerulea*), and Plain Flowerpecker (*Dicaeum concolor*), are considered uncommon or rare species in Taiwan. There were a total of 37 and 22 species recorded in the deciduous hardwood and conifer plantations, respectively, when sightings recorded other than survey time period were excluded. If records of 1 survey time were to use for diversity indices, the Shannon index showed significant higher bird diversity in deciduous hardwood plantations (Table 3). The Shannon evenness and Simpson indices showed no dominant species for either plantation types (Table 3). Overall, every index tested from measures of richness to those of evenness showed that the deciduous hardwood plantations were substantially more diverse than conifer plantations.

DISCUSSION

Higher bird species richness and/or overall abundance have been found in closed canopy temperate broadleaf forests when compared to their counterpart coniferous forests (James and Wamer 1982). In a long-term study of Polish forests, both species richness and overall bird abundance were

lower in coniferous than in broadleaf forests (Tomialojc and Wesolowski 1996). Similarly, in southern Finland, a higher bird species richness and abundance was found in broadleaf forests (Solonen 1996). Some other studies found no significant differences in bird species richness and overall abundance between broadleaf and coniferous forests in England and America (Adams and Edington 1973, Willson and Comet 1996, Donald et al. 1998). Apparently, forest structure has greater effect on bird species richness and abundance than age (clear-cut, young, or mature), forest type (managed or natural), or forest composition (Hansen et al. 1995, Beese and Bryant 1999, King and DeGraaf 2000). Broadleaf stands, especially deciduous hardwood stands, generally have a more open canopy than do coniferous stands and one can expect a relatively better-developed understory layer in the former, which was found to be the case in this study. Halpern and Spies (1995) suggested that the level of resources such as light may contribute to the trend of differences in vascular plant species diversity. Some species may have been present before harvesting and responded to increased light and moisture, others may have colonized the area by wind-blown seeds from surrounding clearcuts (Beese and Bryant 1999).

The general conclusion from published studies is that indices weighted towards

species richness are more useful for detecting differences between sites than indices that emphasize the dominance/evenness component of diversity. Such indices are usually good at their ability to discriminate yet highly sensitive to sample size (Whittaker 1972, Pielou 1975, Magurran 1988). The construction of a diversity curve in this study helped ensure that the sample size was adequate for the diversity index being used. It is also important to distinguish the indices that are most affected by rare species, such as species richness and the Shannon index, and indices that are sensitive to changes in the abundance of the most common species, such as the Simpson index and Shannon evenness.

The information gained from indices such as species richness, while giving valuable insights into diversity, can mask shifts in dominance/evenness. It sometimes fails to discriminate situations where species richness and the number of individuals are identical but evenness varies. On the other hand, indices such as the Simpson and evenness indices, while giving important information regarding the dominance/evenness phenomenon, sometimes fail to reveal the fact that there are too few individuals when species richness is very low. It would therefore appear important to couple estimates of species richness with abundance information such as rank abundance plots and a measure of either dominance or evenness wherever possible (Magurran 1988, Halpern and Spies 1995, Roberts and Gilliam 1995, Beese and Bryant 1999).

There is little consensus on the best diversity measure to use and no index has received the backing of the majority of researchers. Different studies support different theories; the selection of diversity indices has remained more a matter of fash-

ion or habit than of any rigorous appraisal of their relative qualities. Yet, despite these and other problems, on practical grounds, they do provide valuable insights into the ecological processes of an ecosystem.

Data sets that are derived by surveying current conditions of managed natural resources are likely to contain unknown components of variation. The study sites differ due to geographic locations and related environmental factors, the history of management, planning efforts or success, and so on. We carefully selected our study sites to minimize such differences. Even so, such factors undoubtedly contributed an unknown amount of variation to the results. For example, the pre-harvest condition of both vegetation community diversity and composition are unknown. Also, as mentioned in an earlier section, the conifer plantations in the Shanping area seem to form a more continuous patch than the deciduous hardwood plantations, which may have affected the colonization success of invaders. Finally, no single generalization prevails for all situations, therefore, the general theories for changes in species richness and community diversity through forest succession that were followed in this study may need to be carefully reviewed when long-term biodiversity trends along successional stages for deciduous hardwood plantations and conifer plantations in Taiwan are available.

The results of this study suggest that structural complexity in managed stands enhances diversity and provides habitat for many native bird species in the Shanping area. Some species, however, react differently to structural complexity. For example, ground-foraging insectivores and canopy gleaners may react differently to understory cover. Clearly, no single management strat-

egy will provide suitable habitat for all species. This individualistic approach emphasizes the importance of setting specific management objectives. Managing for "biodiversity" is a hollow goal. Any management action will benefit some species and hinder others. Managers should carefully evaluate which species or community attributes they are most concerned with and design silvicultural strategies accordingly.

Further work is needed to better understand the compositional differences in bird communities and the bird-habitat relationship. More study is also needed on the consequences of alternative silvicultural strategies as well as vegetational composition for other taxonomic groups and for socioeconomic considerations.

CONCLUSION

For model based index, species richness, and the Shannon index, all strata of deciduous hardwood plantations showed greater diversity than conifer plantations in the upper Liukuei (Shanping) area. However, the Shannon evenness index and Simpson index gave different but consistent results, higher in the understory canopy in conifer plantations in the upper Liukuei (Shanpin) area. This phenomenon of more evenly distributed understory species in the Shanping area was simply because conifer plantations in the Shanping area have only a few understory species with only a few individuals for each species.

The greater abundance in both understory and ground vegetation strata of deciduous plantations in the Shanping area may have been caused by the amount of penetrating light. When examined closely, the species occurring in the understory stratum of deciduous hardwood plantations include both shade tolerant species such as

Beilschmiedia erythrophloia, *Neolitsea aciculata*, *Machilus japonica*, and *Machilus thunbergii* and advance regenerations such as *Mallotus paniculatus*, *Oreocnide pedunculata*, *Morus australis*, and *Celtis sinensis*. In the conifer plantations, only shade tolerant species existed in the understory stratum such as *Pasania hancei*, *Machilus thunbergii*, *Pasania harlandii*, and *Michelia compressa*. Since the deciduous hardwood plantations permit greater penetration of sunlight during the seasons when no leaves are present, greater opportunities are provided for the growth and development of understory and herbaceous species. The replanting of certain deciduous hardwood plantations in the upper Liukuei (Shanping) area due to planting failure may have also contributed to the more abundant sunlight conditions. This trend in forest composition for both deciduous hardwood plantations and conifer plantations in the Shanping area confirms the stand initiation stage of the stand development model proposed by Bormann and Likens (1995) and by Whittaker (1972) where there is a steady increase of species after a major disturbance. Another factor that may have contributed to the differences in diversity is the chemical environment under different forest types. Needles of conifer plantations tend to be more acidic which may have made the conditions for growth favor species that are adapted to these environments.

The heterogeneity of the ground vegetation stratum and the understory stratum of the deciduous hardwood plantations were significantly higher than those of the conifer plantations, at a 99% confidence level, illustrating the differential effects of disturbance on these 2 important functional groups in the Shanping area. For understory shrub species, clear-cutting and thinning

and pruning afterward may enhance species heterogeneity by reducing the dominance of characteristic understory shrubs while releasing other subordinate shrub and ground-layer species. Subsequently, residual species heterogeneity declines with recovery of dominance (through re-sprouting and colonial spread) of the principal understory species.

The more abundant bird species observed in the Shanping area confirms the assertion that diversity indices provide a measure of the deleterious effect of conifer plantations in the Shanping area on wildlife. Many bird species have specific food and nest requirements and it may be that the low diversity of vegetation in the conifer plantations is limiting bird diversity. This relationship has been confirmed by many published articles (Steele et al. 1984, Donald et al. 1998, Rosenstock 1998).

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