Research paper

Microhabitat Partitioning of Frugivorous Birds: Exploration by a Multiple Correspondence Analysis

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【Summary】

Resource partitioning is one of the important strategies of niche differentiation for species that utilize similar resources, especially within a guild. We used a multiple correspondence analysis (MCA) to explore relationships in habitat use by 3 commonly seen fruit-eating birds (Taiwan Barbet *Megalaima nuchalis*, Black Bulbul *Hypsipetes leucocephalus*, and Grey-cheeked Fulvetta *Alcippe morrisonia*) at the Fushan Experimental Forest in northeastern Taiwan. From June 1997 to May 1998, the fruit type and vegetation level usage of these 3 bird species were recorded monthly. An MCA bi-plot graphically illustrated that the Taiwan Barbet and Black Bulbul mainly took drupes in the canopy, whereas the Grey-cheeked Fulvetta largely consumed fruit other than drupes and berries in the understory. In particular, the MCA could distinguish subtle differences between the former 2 frugivores. The bi-plot showed that the Black Bulbul used berries in the subcanopy more frequently than the Taiwan Barbet. These results support differentiated use of microhabitat by these 3 bird species. We recommend application of the MCA for its capability to clearly illustrate subtle associations among categorical variables in behavioral and habitat studies of wildlife.

Key words: Black Bulbul, fruit type, Grey-cheeked Fulvetta, Taiwan Barbet, vegetation level.

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研究報告

以Multiple Correspondence Analysis探索食果性鳥類的微棲地區隔

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摘　要

資源區隔為生態同功群物種之間區位分化的一種重要機制。本研究利用multiple correspondence analysis (MCA)探討福山試驗林內3種常見食果性鳥類(五色鳥*Megalaima nuchalis*、紅嘴黑鵯*Hypsipetes leucocephalus*及繡眼畫眉*Alcippe morrisonia*)在棲地利用上的差異。從1997年6月到1998年5月，每月定期至福山從事攝食生態觀察，記錄鳥種、取食果實類別及利用森林植層等資料。MCA分析顯示五色鳥及紅嘴黑鵯主要在樹冠層取食核果，而繡眼畫眉則較常出現在底層利用其他類別的果實。MCA可更進一步區分出紅嘴黑鵯與五色鳥在果實類別及植層使用上的細微差異，顯示紅嘴黑鵯比五色鳥較常出現在亞冠層取食漿果。本研究結果支持五色鳥、紅嘴黑鵯及繡眼畫眉三者透過對果實類別及植層利用的差異，達成資源區隔的現象。我們建議用MCA來發掘野生動物研究中有關行為及棲地利用等類別資料間的細微關係。

關鍵詞：紅嘴黑鵯、果實類別、繡眼畫眉、五色鳥、森林植層。

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INTRODUCTION

Niche differentiation is an important mechanism for different species sharing similar resources to reduce potential competition and thus to coexist sympatrically (Schoener 1974, Jablonski and Lee 1999). Ecological theories, including limiting similarity (MacArthur and Levins 1967) and character displacement (Bulmer 1974), predict a reduction in niche overlap among competing species by various strategies of niche differentiation. Among them, resource partitioning is one of the most common strategies, which can be achieved by 3 principal dimensions, including diets, microhabitats, and temporal activities (Pianka 1973, Schoener 1974, Alatalo 1981, Jablonski and Lee 2002). Species coexisting in the same habitat tend to forage in different locations and/or on different diets (Schoener 1974, Alatalo 1981, Jablonski and Lee 2002). Such resource partitioning usually results from competition among different species within an ecological guild (Morse 1980, Wallace and Temple 1987).

Frugivorous birds play an important role in forest communities, and they are the main agents of seed dispersal for many plant species (Morton 1973, Thompson and Willson 1979, Herrera 1998, Lozada et al. 2007). Chen and Chou (1999) reported the diet composition of 14 species of birds at Fushan Experimental Forest, northeastern Taiwan, by foraging observations, and found the most commonly seen fruit-eating birds at this forest were the Black Bulbul *Hypsipetes leucoceph-*

alus (Pycnonotidae), Taiwan Barbet *Megalaima nuchalis* (Capitonidae) (Feinstein et al. 2008), and Grey-cheeked Fulvetta *Alcippe morrisonia* (Timaliidae). Together, these 3 species accounted for 78% of fruit consumption (Chen and Chou 1999). Furthermore, they identified that these 3 frugivorous birds consumed very different assemblages of fruits (Chen and Chou 2008). The Black Bulbul and Taiwan Barbet concentrate their foraging of drupes and berries on trees, whereas the Grey-cheeked Fulvetta often takes other types of fruit from shrubs.

A multiple correspondence analysis (MCA) is less often used by wildlife researchers than are other multivariate methods such as principal component analysis, factor analysis, cluster analysis, and discriminant function analysis (Miles 1990, Moser et al. 1990). However, it is a very helpful technique in exploratory probing of datasets with many categorical variables (Hoffman and de Leeuw 1992, Beh 2005). Greenacre and Vrba (1984) first used a correspondence analysis to graphically display the association between antelopes and wildlife areas in Africa. Moser et al. (1990) used an MCA to show relationships among bird species, their foraging attributes, and habitat characteristics in an easily interpretable manner. In this paper, we use an MCA to distinguish subtle differences in habitat use among these 3 frugivores. The MCA was applied here because it enabled us to clarify associations among variables containing categorical data that may have been difficult to detect with traditional statistical illustrations (Moser et al. 1990). Despite the MCA and similar techniques having been widely used in incidence and abundance datasets of bird communities within environmental gradients (ter Braak 1985, 1986, Rottenborn 1999, Shiu 2003), it is seldom used in behavioral ecology studies of birds (Moser et al. 1990). The paper attempted to promote this multivariate approach in illustrating sophisticated relationships in foraging and habitat studies of wildlife.

MATERIALS AND METHODS

Study site

This study was conducted in the Fushan Experimental Forest (24°34'N, 121°34'E), at an elevation of about 600~800 m, in northeastern Taiwan. The Fushan Experimental Forest is a research site of the Taiwan Forestry Research Institute. It is a humid, subtropical forest. The canopy is dominated by trees of the Lauraceae and Fagaceae families, especially *Castanopsis carlesii*, *Machilus thunbergii*, *Engelhardtia roxburghiana*, *Meliosma squimulata*, and *Litsea acuminate* (Lin et al. 1997). The understory contains plants of the Myrsinaceae (e.g., *Maesa tenera*), Melastomataceae (e.g., *Melastoma candidum*), and Rubiaceae (*Lasianthus fordii*) families. Epiphytes are also common, e.g., *Asplenium antiquum*, *Pseudodrynaria coronans*, and *Aeschynanthus acuminatus*. A detailed description of the long-term ecological study site can be found in King and Hsia (1997).

Field investigation

We conducted fieldwork for 3~10 d per month from June 1997 to May 1998. Foraging data were collected mainly during the morning hours, between 06:00 and 10:00, and for another 2 h before dusk; both were periods of high foraging activity. Foraging birds were observed with binoculars from a system of 5 trails, about 15 km in total length, which run through 3 major parts of the study site: botanical garden, administration area, and natural forests. Each trail was surveyed approximately twice per month. When any individual of the target species was detected, we followed it closely with binoculars until a foraging behavior was clearly observed. The fruiting plant and vegetation level used by the foraging bird were recorded. The fruit type of the plant was determined later using the *Flora of Taiwan* (Li et al. 1975~1979) or by consulting botanists familiar with Fushan plants. Fruit types can be classified into drupes, berries, achenes, caryopses, capsules, and aggregate fruits. We divided the vegetation into 3 levels: the canopy, subcanopy, and understory. The understory level contained shrubbery and herbaceous plants and was usually up to 3 or 4 m in height depending on the location in the woods. Tree crowns above the understory were equally divided into subcanopy and canopy levels.

Statistical analysis

The MCA is applied to analyze data in a multidimensional contingency table to explore associations among levels of several variables (Greenacre 1984, SAS 1989, Moser et al. 1990). The example in this paper is a 3-way contingency table with bird species, fruit type, and vegetation level, and the joint frequency of observations in each cell (Table 1). Results of the MCA can be further graphically displayed in a bi-plot (Greenacre 1984, Moser et al. 1990). In the bi-plot, levels of different variables are positively associated when they lie in the same direction from the origin, but are negatively associated when they lie in opposite directions (Greenacre and Hastie 1987). Furthermore, the intensity of the association of levels from different variables increases as the angle from the origin to these 2 levels decreases.

RESULTS

The Taiwan Barbet and Black Bulbul were more similar to each other in fruit type and vegetation level use than to the Grey-cheeked Fulvetta (Table 1). The former 2 species mainly took drupes (73.9 and 63.8%, respectively) and berries (21.7 and 36.2%, respectively), but the Grey-cheeked Fulvetta ate more other fruit types (43.9%), e.g., achenes, caryopses, capsules, and aggregate fruits than drupes (26.6%) and berries (29.5%). In terms of vegetation level, the Taiwan Barbet and

Table 1. Foraging events on fruit types and in vegetation levels of 3 frugivorous bird species in the Fushan Experimental Forest, Taiwan, from June 1997 to May 1998

Bird species	Vegetation level	Fruit-type			
		Drupe	Berry	Others	Total
Taiwan Barbet	Canopy	31	5		36
	Subcanopy	2	5		7
	Understory	1		2	3
	Total	34	10	2	46
Black Bulbul	Canopy	83	9		92
	Subcanopy		35		35
	Understory		3		3
	Total	83	47		130
Grey-cheeked Fulvetta	Canopy	33	11	5	49
	Subcanopy	21	24	19	64
	Understory	9	35	80	124
	Total	63	70	104	237

Black Bulbul predominantly took fruit from the canopy (78.3 and 70.8%, respectively), while the Grey-cheeked Fulvetta often ate fruit in the understory (52.3%).

The Taiwan Barbet was located close to the drupe and canopy on the bi-plot (Fig. 1), and this implies that the Taiwan Barbet predominantly took drupes in the canopy. With similar dietary habits, the Black Bulbul was located somewhere between drupe/canopy and berry/subcanopy. Originating from the intersection, the angle between the Black Bulbul and the drupe/canopy was smaller than that between the Black Bulbul and the berry/subcanopy. This indicates that the Black Bulbul ate more drupes than berries and did so more often in the canopy than in the subcanopy. In contrast, the Grey-cheeked Fulvetta mainly consumed other types of fruit and stayed in the understory, and its position on the bi-plot was located on the opposite side from the Taiwan Barbet and Black Bulbul (Fig. 1). This clearly shows that the Grey-cheeked Fulvetta used very different niches from the other 2 frugivores. In addition, a strong association was found between fruit type and vegetation level; drupes were located close to the canopy, berries to the subcanopy, and other fruits to the understory in the bi-plot (Fig. 1).

DISCUSSION

Application of the MCA enabled us to graphically detect differences in fruit type and vegetation level use among the 3 bird species. The bi-plot supported the 3 bird species not using fruit types or vegetation levels randomly because the Taiwan Barbet, drupe, and canopy were very close to one another, as were the Grey-cheeked Fulvetta, other fruit types, and understory. Our results support the

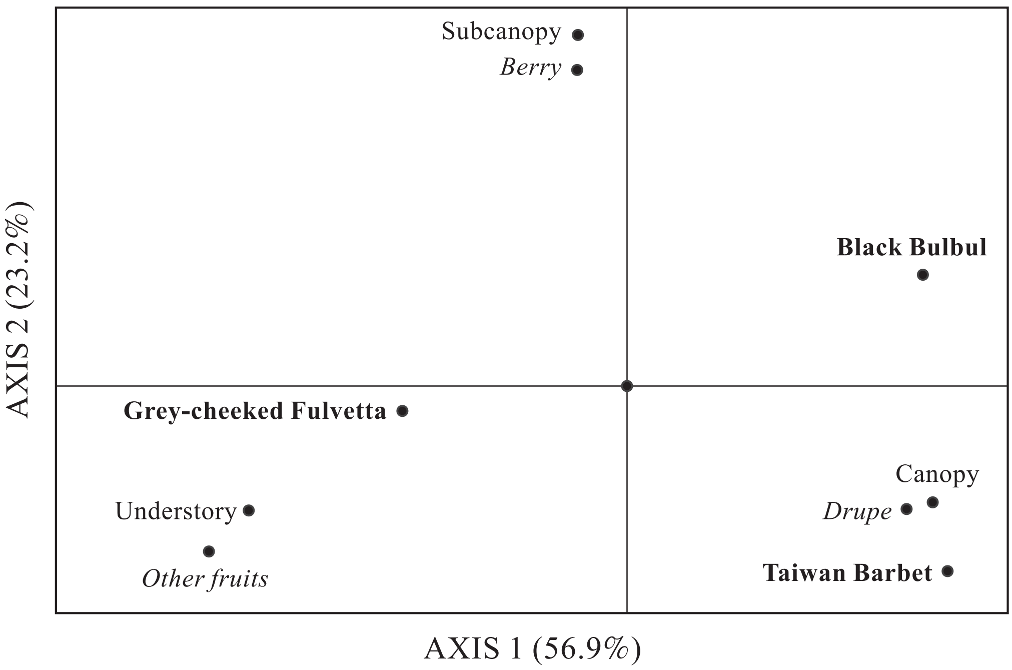

Fig. 1. A multiple correspondence analysis bi-plot of fruit types and vegetation levels used by the Taiwan Barbet, Black Bulbul, and Grey-cheeked Fulvetta in the Fushan Experimental Forest (generated from data in Table 1). Bird species are in bold type, fruit types are italicized, and the origin is located at the intersection of the axes.

existence of resource partitioning among the 3 fruigivores, and such a divergence in habitat use may result from differences in morphology and foraging habits (Chen and Chou 2008). Bill lengths of the Taiwan Barbet (23.9±2.1 [SD] cm, n = 64; data from Shiu et al. 2005), Black Bulbul (22.8±1.5 cm, n = 58), and Grey-cheeked Fulvetta (11.6±1.0 cm, n = 471) greatly differ. The former 2 are obligatory frugivores that have larger bills and are adapted to foraging on fruits of large trees that may depend on them as seed dispersers (Snow 1971, McKey 1975). In contrast, the Grey-cheeked Fulvetta, an omnivore, has a smaller bill and eats fruits other than drupes and berries in the understory level (Chen and Chou 2008).

In addition, subtle differences between the Black Bulbul and Taiwan Barbet were also clearly revealed, and such distinctions are difficult to perceive based on univariate statistical charts (Chen and Chou 2008). The Black Bulbul and Taiwan Barbet are both obligatory friguvores and thus tend to be more competitive for drupes and berries at the Fushan Experimental Forest (McKey 1975, Howe and Estabrook 1977). The MCA biplot illustrates that the Black Bulbul foraged somewhere between the drupe/canopy and berry/subcanopy, whereas the Taiwan Barbet mainly took drupes from the canopy. This implies that the Black Bulbul has a broader foraging niche than the Taiwan Barbet. In contrast, the Taiwan Barbet is more specialized in feeding on drupes in large trees.

Furthermore, the Taiwan Barbet spent on average 1~3 min on a foraging bout in fruiting trees (Chang 2010), but the Black Bulbul usually finished 1 bout within 1 min (Chen CC, pers. observ.). These observations indicate that the Taiwan Barbet appears to be dominant over the Black Bulbul regarding frugivory. However, whether resource partitioning has resulted from competition among species or different feeding preferences may be difficult to distinguish at this stage (Morse 1980, 1989), and further investigation should be conducted in the future.

Moser et al. (1990) used an MCA to illustrate relationships among bird species, their foraging techniques, and habitat characteristics. They showed that the ecological niche of bird species can easily be distinguished in a bi-plot based on behavior and habitat use. A secondary result revealing an association between foraging technique and the habitat character was detected. A strong association between fruit type and vegetation level was also found through the MCA in this study. These results showed that the MCA can find extra relationships between variables outside the target species and such outcomes are usually neglected by researchers when applying other statistical methods.

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LITERATURE CITED

Alatalo RV. 1981. Interspecific competition in tits *Parus* spp. and the goldcrest *Regulus regulus*: foraging shifts in multispecific flocks. Oikos 37:335-44.

Beh EJ. 2005. S-PLUS code for simple and multiple correspondence analysis. Comput Stat 20:415-38.

Bulmer MG. 1974. Density-dependent selection and character displacement. Am Nat 108:45-58.

Chang SY. 2010. Food resource use of Taiwan Barbets (*Megalaima nuchalis*) and its effects on seed dispersal [thesis]. Tainan, Taiwan: National Cheng Kung Univ. 99 p. [in Chinese with English summary].

Chen CC, Chou LS. 1999. The diet of forest birds at Fushan Experimental Forest. Taiwan J For Sci 14(3):275-87.

Chen CC, Chou LS. 2008. Differences in foraging ecology between generalized and specialized frugivorous birds in Fushan Experimental Forest, Taiwan. Taiwan J For Sci 23:233-42.

Feinstein J, Yang X, Li SH. 2008. Molecular systematics and historical biogeography of the Black-browed Barbet species complex (*Megalaima oorti*). Ibis 150:40-9.

Githiru M, Lens L, Bennur LA, Ogol CPKO. 2002. Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. Oikos 96:320-30.

Greenacre M, Hastie T. 1987. The geometric interpretation of correspondence analysis. J Am Stat Assoc 82:437-47.

Greenacre MJ. 1984. Theory and applications of correspondence analysis. London: Academic Press. 364 p.

Greenacre MJ, Vrba ES. 1984. Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. Ecology 65:984-97.

Herrera CM. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. Ecol Monogr 68:511-38.

Hoffman DL, de Leeuw J. 1992. Interpreting multiple correspondence analysis as a multidimensional scaling method. Market Lett 3:259-72.

Howe HF, Estabrook FF. 1977. On interspecific competition for avian dispersers in tropical trees. Am Nat 111:817-32.

Jablonski PG, Lee SD. 1999. Foraging niche differences between species are correlated with body-size differences in mixed-species flocks near Seoul, Korea. Ornis Fennica 76:17-23.

Jablonski PG, Lee SD. 2002. Foraging niche shifts in mixed-species flocks of tits in Korea. J Field Ornithol 73:246-52.

King HB, Hsia YJ. 1997. Establishment, progress and performance of the Taiwan ecological research network program. In: King HB, Hamburg SP, Hsia YJ, editors. Long-term ecological research in East Asia-Pacific region. Taipei, Taiwan: Taiwan Forestry Research Institute. p 83-96.

Li HL, Liu TS, Huang TC, Koyama T, DeVol CE. 1975~1979. Flora of Taiwan. Vols. 1~6. Taipei, Taiwan: Epoch Publishing Company.

Lin KC, Hwanwu CB, Liu CC. 1997. Phenology of broadleaf tree species in the Fushan Experimental Forest of northeastern Taiwan. Taiwan J For Sci 12:347-53. [in Chinese with English summary].

Lozada TL, de Koning GHJ, Marché R, Klein A-M, Tscharntke T. 2007. Tree recovery and seed dispersal by birds: comparing forest, agroforestry, and abandoned agroforestry in coastal Ecuador. Persp Plant Ecol Evol Syst 8:131-40.

MacArthur RH, Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am Nat 101:377-85.

McKey D. 1975. The ecology of coevolved seed dispersal systems. In: Gilbert LE, Raven PH, editors. Coevolution of animals and plants. Austin, TX: Univ. of Texas Press. p 159-91.

Miles DB. 1990. A comparison of three multivariate statistical techniques for the analysis of avian foraging data. Stud Avian Biol 13:295-308.

Morse DH. 1980. Foraging and coexistence of spruce-woods warblers. Living Bird 18:7-25.
Morse DH. 1989. American warblers. Cambridge, MA: Harvard Univ. Press. 406 p.
Morton ES. 1973. On the evolutionary advantages and disadvantages of fruit eating in tropical birds. Am Nat 107:8-22.
Moser EB, Barrow WC Jr, Hamilton RB. 1990. An exploratory use of correspondence analysis to study relationships between avian foraging behavior and habitat. Stud Avian Biol 13:309-17.
Pianka ER. 1973. The structure of lizard communities. Ann Rev Ecol Syst 4:53-74.
Rottenborn SC. 1999. Predicting the impacts of urbanization on riparian bird communities. Biol Conserv 88:289-99.
SAS Institute. 1989. SAS/STAT user's guide. Vers. 6. Cary, NC: SAS Institute. 846 p.
Schoener TW. 1974. Resource partitioning in ecological communities. Science 185:27-39.
Shiu HJ. 2003. Spatial and seasonal variations in avian assemblages in Taiwan [dissertation]. Taipei, Taiwan: National Taiwan Univ. 187 p. [in Chinese with English summary].
Shiu HJ, Ding TS, Sheu JE, Lin RS, Koh CN, Lee PF. 2005. Morphological characters of bird species in Taiwan. Taiwania 50:80-92.
Snow DW. 1971. Evolutionary aspects of fruit-eating by birds. Ibis 113:194-202.
ter Braak CJF. 1985. Correspondence analysis of incidence and abundance data: properties in terms of a unimodal response model. Biometrics 41:859-73.
ter Braak CJF. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-79.
Thompson JN, Willson MF. 1979. Evolution of temperate fruit/bird interactions: phonological strategies. Evolution 33:973-82.
Wallace MP, Temple SA. 1987. Competitive interactions within and between species in a guild of avian scavengers. Auk 104:290-5.

Appendix 1. Fruit type, life-form, and vegetation level of 39 plant species used by 3 frugivores in the Fushan Experimental Forest

Family Species	Type of fruit	Life-form	Vegetation level[1)]	Used by[2)]
Dicotyledon				
Actinidiaceae				
Actinidia callosa var. *formosana*	berry	liana	C	F
Anacardiaceae				
Rhus succedanea	drupe	tree	C	F
Aquifoliaceae				
Ilex ficoidea	drupe	tree	S	F
Ilex formosana	drupe	tree	S	F
Araliaceae				
Aralia bipinnata	drupe	small tree/tree	S	F
Aralia decaisneana	drupe	small tree/tree	S	B, F
Schefflera arboricola	drupe	liana/small tree	S	B, BB, F
Schefflera octophylla	drupe	tree	C	B, BB, F
Caprifoliaceae				
Sambucus formosana	drupe	shrub	U	F
Ebenaceae				
Diospyros morrisiana	berry	tree	S	B
Euphorbiaceae				
Glochidion acuminatum	capsule	small tree/tree	S	F
Mallotus japonicus	capsule	small tree/tree	S	F
Lauraceae				
Litsea acuminata	drupe	tree	C	B, BB
Persea japonica	drupe	tree	C	B, BB
Persea thunbergii	drupe	tree	C	B, BB
Persea zuihoensis	drupe	tree	C	B, BB, F
Phoebe formosana	drupe	tree	C	B, F
Melastomataceae				
Melastoma candidum	capsule	shrub	U	F
Pachycentria formosana	berry	shrub	U	F
Moraceae				
Ficus erecta var. *beecheyana*	achene	shrub/small tree	S	F
Myrsinaceae				
Ardisia sieboldii	drupe	tree	S	F
Maesa tenera	berry	shurb	U	F
Polygonaceae				
Polygonum chinense	achene	herb	U	F
Rosaceae				
Prunus campanulata	drupe	tree	S	B
Rubus taiwanianus	aggregate fruit	herb	U	F
Rubus	aggregate fruit	herb/liana	U	F

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Rubiaceae				
Lasianthus fordii	drupe	shrub	U	F
Mussaenda parviflora	berry	liana	S	F
Tricalysia dubia	berry	small tree	U	F
Symplocaceae				
Symplocos cochinchinensis laurina	drupe	shrub/small tree	U	F
Theaceae				
Adinandra formosana	berry	tree	C	F, B
Eurya acuminata	berry	small tree	U	B, BB, F
Urticaceae				
Villebrunea pedunculata	achene	shrub/small tree	U	B, F
Verbenaceae				
Callicarpa formosana	drupe	shrub/small tree	U	B, F
Callicarpa kochiana	drupe	shrub/small tree	U	F
Vitaceae				
Ampelopsis cantoniensis	berry	liana	C	B, BB, F
Cayratia japonica	berry	liana	U	F
Monocotyledon				
Araceae				
Pothos chinensis	berry	liana	S	BB, F
Gramineae				
Miscanthus floridulus	caryopsis	herb	U	F

1) The vegetation level of fruit is based on availability data of fruit in the Fushan Experimental Forest collected in this study. C, canopy; S, subcanopy; U, understory.

2) B, Taiwan Barbet; BB, Black Bulbul; F, Grey-cheeked Fulvetta.