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研究報告

蕨類多樣性與環境之關係—以臺灣中部蓮華池地區杉木人工林為例

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摘　要

本研究目的在瞭解杉木人工林小尺度空間微環境變化對於蕨類多樣性與分布的影響。研究地點位於臺灣中部蓮華池地區坡度小於30°的杉木人工林，在0.2 ha的樣區劃分成80個5 m × 5 m小區調查蕨類物種與株數。調查結果發現樣區出現19種蕨類(10科，13屬)，並分析其與林分密度、冠層開闊度、及土壤水分的關係。回歸分析的結果顯示蕨類豐富度、密度、物種多樣性指數均與乾季的冠層開闊度、土壤水分有顯著相關。以雙向指標種分析蕨類植群可分成網脈突齒蕨群、扇葉鐵線蕨群及深山雙蓋蕨群等3群。降趨對應分析結果顯示，各樣方蕨類分布排列與分群結果大致相符。典型對應分析顯示冠層開闊度為影響蕨類多樣性之主要因子，而土壤水分亦扮演重要角色。其中，網脈突齒蕨群樣區的土壤水分與冠層開闊度相對最高，扇葉鐵線蕨群最低，深山雙蓋蕨群則居中。研究結果反映不同蕨類社會組成對林下環境適應的差異性。

關鍵詞：典型對應分析、冠層開闊度、降趨對應分析、林分密度、雙向指標種分析

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Research paper

The Correlation between Fern Diversity and Environmental Factors—Case Study in a Chinese Fir Plantation in Lienhuachih, Central Taiwan

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ABSTRACT

The purpose of this study was to understand the impact of micro-environmental changes on fern diversity and distribution in a Chinese fir plantation. We selected a Chinese fir plantation with a slope less than 30° in the Lienhuachih lowland area of central Taiwan as the study area. A 0.2 ha plot was established within the plantation to investigate fern species and individual numbers. We identified a total of 19 fern species (10 families and 13 genera) in the plot and then analyzed them for their relationship to stand density, canopy openness, and soil moisture. Regression analysis revealed that fern richness, density, and diversity significantly correlated with canopy openness and soil moisture during the dry season. Based on the results of two-way indicator species analysis (TWINSPAN), the fern communities were classified into three distinct groups: *Pleocnemia winitii*, *Adiantum flabellulatum*, and *Diplazium mettenianum* groups. The result of detrended correspondence analysis (DCA) confirmed that the distribution of fern groups was consistent with the TWINSPAN classification. Canonical correspondence analysis (CCA) revealed canopy openness as the primary factor affecting fern diversity, followed by soil moisture, which also played a significant role. Among the three plant groups, the *Pleocnemia winitii* group exhibited the highest correlation with soil moisture and canopy openness, followed by the *Diplazium mettenianum* group and the *Adiantum flabellulatum* group. This study highlights the distinct adaptations of different fern communities to the understory environment of a Chinese fir plantation.

Keywords: canonical correspondence analysis (CCA), canopy openness, detrended correspondence analysis (DCA), stand density index, two-way indicator species analysis (TWINSPAN)

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緒言

由於物種在空間分布的尺度不同，大自世界(Antonelli et al. 2018, Weigand et al. 2020, Suissa et al. 2021)、區域(region)尺度(Condit et al. 1996, Tang et al. 2013, Liu et al. 2015)，小至地方(local)、樣區尺度(Chang et al. 2010, 2013, Kluge and Kessler 2011, Condit et al. 2017)，物種多樣性都有不同的研究議題進行探討。以世界尺度而言，一般認為在南、北回歸線之間是生物物種多樣性最高的區域(Wright 1996)。然而就地方尺度而言，環境中的水、光度、及營養素等諸多因子交互作用，塑造地區生態系構成生境分化(Niche partitioning) (Silvertown 2004, Beck and Givinish 2021)，促使不同物種擇其適合生境而存活，遂而產生物種多樣性。

低緯度的熱帶動態樣區研究顯示，每1 ha分布有超過300種樹木(Wright 1996)。雖然溫帶地區樹木種類不如熱帶地區豐富，但是在林下地被層卻也佔有高度植物多樣性，每ha也有50-100種林下植物種類(Gilliam 2007, Barbier et al. 2008)。不論在哪個緯度，森林裡最直接容易觀察到的就是地被植物，透過探討林下地被植物組成與分布，可間接瞭解上層樹木所形成的環境對於林下植物的影響(Barbier et al. 2008, Klynge et al. 2020)。蕨類不僅是維管束植物第二大類群，約有10,500現生物種(PPG 2016)，也是森林地被植物的重要組成，尤其是熱帶及亞熱帶之山麓地帶，被視為蕨類多樣性最高的地區(Smith et al. 2006, Suissa et al. 2021)。至於熱帶及亞熱帶之山麓地帶為何擁有較高的蕨類豐富度，通常解釋為提供較大的環境異質性，比如坡度、母岩、土壤、微棲地及海拔的不同(Moran 1995)。

若就更小的森林地方尺度，土壤水分被視為主要影響蕨類多樣性及分布的因素之一(Richard et al. 2000, Karst et al. 2005)。Richard et al. (2000)研究加拿大魁北克省一處老熟林，設置1 ha樣區，指出蕨類多樣性隨土壤水分增加而增加。同樣地方Karst et al. (2005)將取樣範圍加大到湖的周邊地區，範圍約6 km^2，土壤水分的重要性同樣影響蕨類組成與分布。

森林地被受到上層樹木的競爭，也受到冠層開闊度(森林未受冠層植群遮蔽的比率，Jennings et al. 1999)的影響(Messier et al. 1998, Yamada et al. 2014, Chang et al. 2015)，而冠層開闊度與相對光度(relative light intensity)間有正向關係(Baudry et al. 2014)。Beukema and Van Noordwijk (2004)提到森林種類(耐陰性種類)適應較陰暗的環境，而非森林種類(非耐陰性種類)則較適應冠層較開闊的環境。蕨類植物是許多森林地被層的主要組成，其豐富度與分布也受到生育地之冠層開闊度所影響。例如，印尼Pono地區老熟林的蕨類豐富度與冠層開闊度有顯著正相關(Jones et al. 2014)，顯示該研究地區蕨類種數隨光度增加而增加。

林下光度與上層開闊度相關，同時也可能影響林分密度，例如Comeau (2002) 研究加拿大英屬哥倫比亞東北部12至40年生白楊(*Populus tremuloides*)林，指出當林下光度小於40%時該林分的底面積會超過14 m^2/ha，而當光度小於60%時底面積會超過8 m^2/ha；也就是說林下光度越低時，林分密度就越高。然而，Montgomery and Chazdon (2001)卻指出在哥斯大黎加的森林，林分密度與林下光度並沒有強烈相關，僅在老熟林中的樹木密度與散射光透率有顯著相關。許多研究提到林分密度對於林下地被組成與分布有所影響(Chen and Cao 2014, Ali et al. 2019, Wang et al. 2020)，而蕨類也可能受到林分密度的影響。

蕨類對環境敏感是個良好的生物指標，臺灣蕨類植物多樣性極高(Kuo et al. 2019)，但相關的研究不多(Chang 1998, Lai 2002, Lin 2019, Chen 2020)，對於單一樣區尺度探討蕨類多樣性與分布之研究不足。本研究選擇臺灣中部低海拔山地一處坡度小於30°的杉木(*Cunninghamia lanceolata*)人工林，設立一座 0.2 ha 樣區，探討小尺度蕨類多樣性與環境之關係。

材料與方法

研究區概況

研究樣區位於臺灣中部南投縣魚池鄉境內，為林業試驗所蓮華池研究中心管轄林區(23°54’53”N, 120°53’05”E, Fig. 1a)，屬於楠櫧林帶(*Machilus-Castanopsis* zone)(Su 1984)。樣區為1980年代栽植之杉木人工林，但造林後鮮少撫育，森林逐漸被原生樹種包括頷垂豆(*Archidendron lucidum*)、長尾尖葉櫧(*Castanopsis cuspidata* var. *carlesii*)、火燒柯(*C. fargesii*)、鵝掌柴(*Schefflera octophylla*)等取代。由生態氣候圖可知(Fig. 1b)，本區年均溫約21.2℃，年平均降水量約2,178 mm，降雨集中

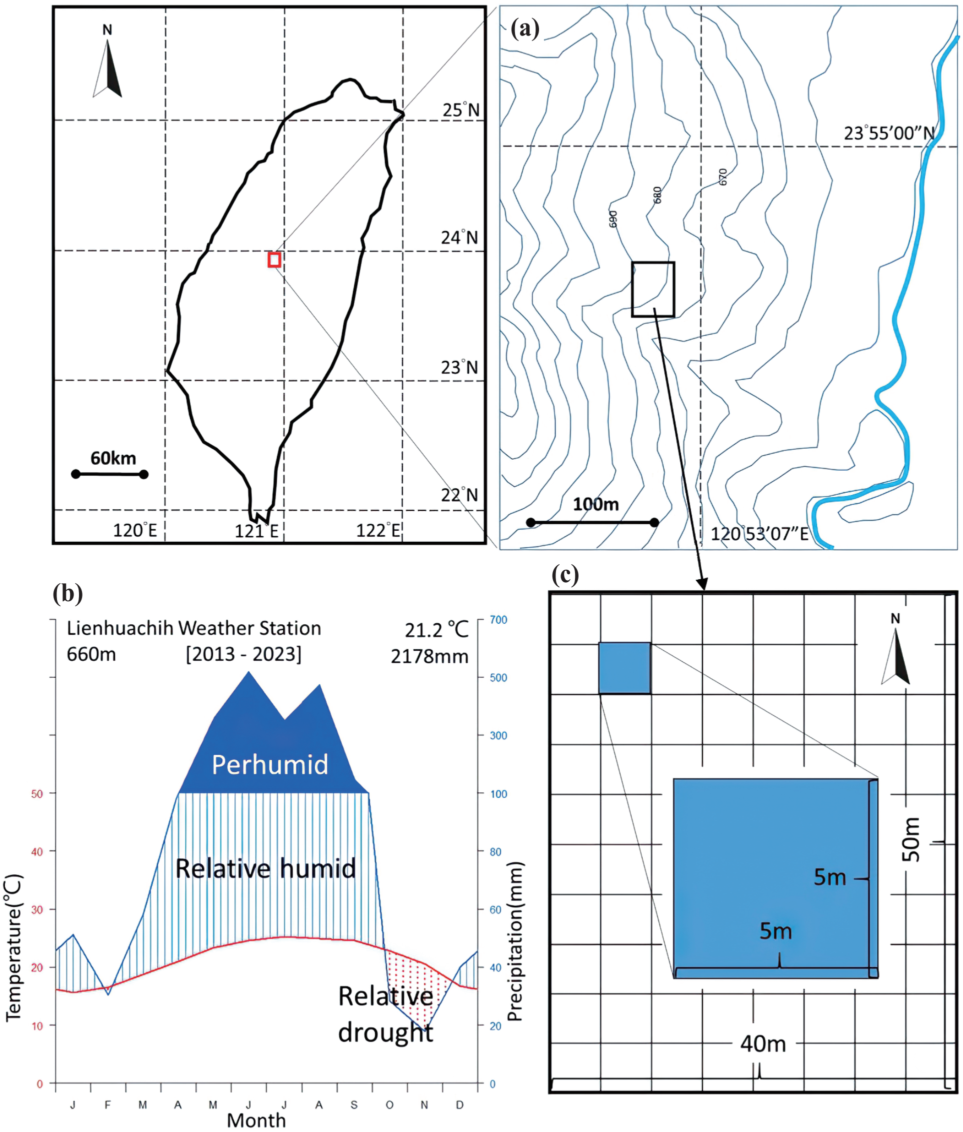

Fig. 1. Study site location and climate characteristics of the Lienhuachih area. (a) Study site location in central lowland Taiwan. (b) Climate diagram of the Lienhuachih area. (c) Schematic diagram of the 0.2 ha sampling plot.

3-9月，乾季在10-11月 (Fig. 1b)。地質為新生代北部第三紀沈積岩，由暗灰色頁岩和泥質砂岩互層構成，土壤屬典型濕潤極育土(Typic Paleudults) (King 1986, Chiang et al. 1994)；土壤為趨紅化作用之黃壤，屬砏質黏土(Chuang et al. 2008)。

樣區設置與調查方法

本研究於2023年4月1–30日，在一處坡度小於30°的杉木人工林設置40 m × 50 m樣區，樣區方向正南北向，地形坡向由西北朝東南向，以西北點海拔最高(alt. 690 m)，東南點海拔最低(alt. 670 m)。每5 m × 5 m設立樣方(square)，以每一樣方為調查單位，共80個樣方(Fig. 1c)。以樣方為單位，調查樣方內的地生蕨類物種與株數；植株為成熟植株，意即能生產孢子葉的個體。若植株長走莖，則以長出葉子處為一個植株。調查之蕨類植物學名依據Kuo et al. (2019)更新版臺灣植物名錄。本研究每一蕨類物種取1–5個植株量測葉長(包括葉柄及葉身)與葉寬，並取平均值，以了解蕨類大小對環境的適應性。此外，調查每個樣方內 DBH ≥ 1cm 的木本植物種類、株數與胸徑。

土壤水分含量(%)使用RiXEN M-700S測計，探針插入土壤約5 cm 深，測點以5 m × 5 m樣方為單位，每一樣方內在對角線方向平均取3個點。冠層開闊度(canopy openness)測量參考前人使用之方式(Fournier et al. 2017)，以魚眼相機(CASIO EX-FR200)進行拍攝，每一樣方中央高度150 cm處拍攝一張相片，並使用Gap Light Analyzer計算冠層開闊度。土壤水分及冠層開闊度之調查除於同年濕季進行(分別是6月9–19日與8月30日)，以及同年乾季 (12月15–19日)進行調查。

資料處理

以樣方為單位，計算各個樣方內蕨類的物種豐富度(species richness，以物種數表示)、密度(單位面積之株數)、及物種多樣性(以夏農指數Shannon-Wiener index表示，Shannon 1948)。計算各樣方之林分密度指數(stand density index, SDI)。林分密度指數使用Reineke (1933)所用的計算方法，公式：$SDI\% = N(25.4/\sqrt{\sum(DB^2/n)})^{-1.605}$，DB：胸徑，n：物種株數，N：單位公頃內株數。為了解小尺度樣區內蕨類植物之物種多樣性與環境關係，本研究將各樣方之物種豐富度、物種多樣性、密度等變數作為依變數，林分密度指數、冠層開闊度、及土壤水分等作為自變數，進行線性回歸分析。為了解樣區內各樣方蕨類植物社會組成特性，本研究以雙向指標種分析(Two-way Indicator Species Analysis, TWINSPAN) (Hill 1979)進行歸群分析，資料使用各樣方之蕨類種類密度，使用Modified TWINSPAN (Roleček et al. 2009)，並設定布雷–柯蒂斯相異度(Bray-Curtis dissimilarity) (Legendre and Legendre 1998)作為測計植群異質性之方法。植群命名方式以特徵種命名，表示一種植物對於該植群的忠誠度(Su and Liou 2004)，在其他植群不出現或出現較少。此外，本研究針對各植群型間的物種豐富度、密度及物種多樣性進行變異數分析，探討各植群間的差異。

本研究使用排序分析了解樣區內各樣方蕨類植物社會組成特性及其與環境之關係，分析方法包括降趨對應分析(detrended correspondence analysis, DCA) (Hill and Gauch 1980)與典型對應分析(canonical correspondence analysis, CCA) (ter Braak 1986)。DCA以物種與樣方之矩陣資料(當中參數為密度)作多變量統計並加以排序，使用前兩變異軸的資料作排序圖，以觀察物種與所在樣方的排序情況(Shiu and Lee 2003)。若DCA的軸長大於4個標準偏差(standard deviation, SD)，則將植群資料與環境因子矩陣進行CCA，透過繪製雙序圖，直觀了解影響植群與環境因子間的關係(ter Braak and Verdonschot 1995, Shiu and Lee 2003)。環境因子以箭頭表示，箭頭指的方向顯示因子值越高；反之，相反方向表示因子值越低。CCA分析後得出前3個序列軸，與前述3種環境因子使用斯皮爾曼等級相關係數(Spearman's rank correlation coefficient)分析，此為一種無母數相關分析，將資料化為等級，以符合本研究物種–樣方及環境因子資料結構(僅林分密度與土壤水分達常態分布，其餘為非常態分布)。以上分析使用R軟體進行分析，使用「vegan」與「fossil」套件。

結果

物種多樣性與環境

本研究調查DBH ≥ 1cm 的木本植物共有52種(Appendix 1)，冠層優勢喬木(H ≥ 5 m)除了杉木外，主要優勢樹種有頜垂豆、長尾尖葉櫧、火燒柯、鵝掌柴等，灌木層(H < 5 m)常見有柏拉木(*Blastus cochinchinensis*)、桃實百日青(*Podocarpus nakaii*)、九節木(*Psychotria rubra*)、茜草樹(*Randia cochinchinensis*)等。樣區內出現10科，13屬，19種蕨類，共1,582株(Table 1)；其中以金狗毛蕨(*Cibotium barometz*)密度最高(*n* = 389)，而落鱗鱗毛蕨(*Dryopteris sordidipes*)的株數最少(*n* = 1)；蕨葉尺寸以逆羽裏白(*Diplopterygium blotianum*)最長，圓葉陵齒蕨(*Lindsaea orbiculata*)最短(Table 1)。若以超過100株的優勢蕨類而言，金狗毛蕨最長最寬，再者是網脈突齒蕨(*Pleocnemia winitii*)，

Table 1. Compositions, number of individuals, leaf size (length and width, units: cm), quadrat ratio (%) and number of quadrats (within parentheses) of fern groups (analyzed by TWINSPAN) in the 0.2-ha plot at the Chinese fir plantation in the Lienhuachih area, central Taiwan. Groups represented by characteristic species are the *Pleocnemia winitii* group (PLEOWI), *Adiantum flabellulatum* group (ADIAFL), and *Diplazium mettenianum* group (DIPLME).

Species		Individuals	Length	Width	PLEOWI	ADIAFL	DIPLME
Adiantum flabellulatum L.	扇葉鐵線蕨	148	41	19	14(8)	100(16)	83(5)
Alsophila podophylla Hook.	鬼桫欏	19	250	102	26(15)	-	-
Asplenium normale D.Don	生芽鐵角蕨	10	29	3	9(5)	-	-
Cibotium barometz (L.) J. Sm.	金狗毛蕨	389	313	106	88(51)	88(14)	67(4)
Dicranopteris tetraphylla (Rosenst) C. M. Kuo	蔓芒萁	17	239	117	10(6)	6(1)	33(2)
Diplazium dilatatum Blume	廣葉鋸齒雙蓋蕨	3	118	59	5(3)	-	-
Diplazium donianum var. *donianum* (Mett.) Tardieu	細柄雙蓋蕨	256	65	29	69(40)	-	-
Diplazium mettenianum (Miq.) C. Chr.	深山雙蓋蕨	137	50	20	22(13)	-	100(6)
Diplopterygium blotianum (C. Chr.) Nakai	逆羽裏白	2	401	42	2(1)	-	-
Dryopteris integriloba C. Chr.	羽裂鱗毛蕨	38	60	24	21(12)	13(2)	-
Dryopteris sordidipes Tagawa	落鱗鱗毛蕨	1	58	25	2(1)	-	-
Lindsaea bonii Christ	海島陵齒蕨	53	33	7	10(6)	69(11)	33(2)
Lindsaea heterophylla Dryand	異葉陵齒蕨	5	36	15	-	19(3)	-
Lindsaea orbiculata (Lam.) Mett. *ex* Kuhn	圓葉陵齒蕨	23	13	2	3(2)	63(10)	50(3)
Microlepia calvescens (Wall. *ex* Hook.) C. Presl	光葉鱗蓋蕨	7	86	30	2(1)	-	-
Microlepia hookeriana (Wall. *ex* Hook.) C. Presl	虎克氏鱗蓋蕨	14	57	17	16(9)	-	-
Pleocnemia winitii Holttum	網脈突齒蕨	289	142	70	88(51)	-	-
Pteris semipinnata L.	半邊羽裂鳳尾蕨	36	85	27	28(16)	19(3)	17(1)
Tectaria harlandii (Hook.) C. M. Kuo	沙皮蕨	135	64	34	69(40)	13(2)	33(2)

-: does not exist.

這兩種屬於大型蕨類(平均葉長142-313 cm，葉寬70-106 cm)；扇葉鐵線蕨(*Adiantum flabellulatum*)屬於小型蕨類(平均葉長41 cm，葉寬19 cm)；中型優勢蕨類有細柄雙蓋蕨(*Diplazium donianum* var. *donianum*)、深山雙蓋蕨(*Di. mettenianum*)、及沙皮蕨(*Tectaria harlandii*)(平均葉長50-65 cm，葉寬20-34 cm) (Table 1)。全區的夏農指數為2.16，每樣方之夏農指數介於0.00-1.88間 (mean = 1.2, SD = 0.37)。

樣區內各樣方的林分密度介於1-22% (mean = 11.2, SD = 4.9)，冠層開闊度介於7.4-16.4% (mean = 10.1, SD = 2.1)，以及土壤水分介於33.8-38% (mean = 35.7, SD = 0.8)；各樣方環境因子數值如Appendix 2。由於蕨類豐富度、密度、物種多樣性指數均與乾季的冠層開闊度、土壤水分相關顯著性較高(Table S)，加上乾、濕季的冠層開闊度與土壤水分具顯著相關性(土壤水分：r_s = 0.34, p = 0.002；冠層開闊度：r_s = 0.25, p = 0.03；r_s: Spearman's rank correlation coefficient)，因此後續報告討論以乾季為主。蕨類各項變數與3項環境因子的回歸分析顯示(Table 2)，蕨類的物種豐富度與夏農指數對3項環境因子均呈現顯著正向關係($p < 0.05$)，而蕨類密度與冠層開闊度、土壤水分呈顯著正向關係($p < 0.05$)。

蕨類植群組成特性分析

杉木人工林蕨類組成分析結果可切分成3個植群(Appendix 3)，以特徵種命名，分別為網脈突齒蕨群(*Pleocnemia winitii* group；簡稱網脈群，PLEOWI；n = 58)、扇葉鐵線蕨群(*Adiantum flabellulatum* group；簡稱扇葉群，ADIAFL；n = 16)、以及深山雙蓋蕨群(*Diplazium mettenianum* group；簡稱深山群，DIPLME；n = 6)。由Table 1及Fig. 2a可知，網脈群為樣區內的優勢蕨類植群，扇葉群分布在樣區東南方，深山群則分布於網脈群樣方邊緣；並且，網脈群的平均蕨葉尺寸最大(mean length = 151.9 ± 45.8 cm, mean width = 59.8 ± 15.9 cm)，與其他2群達顯著差異(p <

Table 2. Linear regression relating richness, density, and Shannon-Wiener index of ferns to three environmental factors: stand density index (SDI), canopy openness, and soil water in the 0.2 ha plot at the Chinese fir plantation in the Lienhuachih area, central Taiwan. Three fern groups were classified using TWINSPAN.

Response \ Factors	Coefficient (ß)			R^2
	SDI	Canopy openness	Soil water	
Richness	0.08*	0.22**	0.52**	0.23
Density	0.003	1.93***	2.47*	0.26
Shannon-Wiener index	0.02*	0.05**	0.16**	0.25
PLEOWI group				
Richness	0.06	0.21*	0.46	0.16
Density	-0.04	1.77**	1.91	0.20
Shannon-Wiener index	0.01	0.05*	0.13*	0.17
ADIAFL group				
Richness	0.13	0.43	0.62	0.25
Density	0.70	-0.47	1.17	0.14
Shannon-Wiener index	0.03	0.26	0.09	0.31
DIPLME group				
Richness	0.29	0.04	-0.28	0.73
Density	0.37	2.22	-6.23	0.21
Shannon-Wiener index	0.06*	-0.03	0.29	0.95

*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

0.05)，而2群間平均蕨葉尺寸無顯著差異(扇葉群：112.6 ± 65.4 cm, 40.2 ± 21.6 cm；深山群：67.1 ± 25.5 cm, 26.5 ± 11.1 cm)。

從植群間的變異數分析可知，各植群的種數與夏農指數沒有顯著差異；蕨類密度則有顯著差異，以扇葉群的蕨類密度最少，而網脈群的密度最高。以各植群環境因子而言，植群間林分密度沒有顯著差異，冠層開闊度與土壤水分有顯著差異，這兩者均以扇葉群的值最小(Table 3)。此外，我們還分析樹木密度(單位面積之樹木株數)

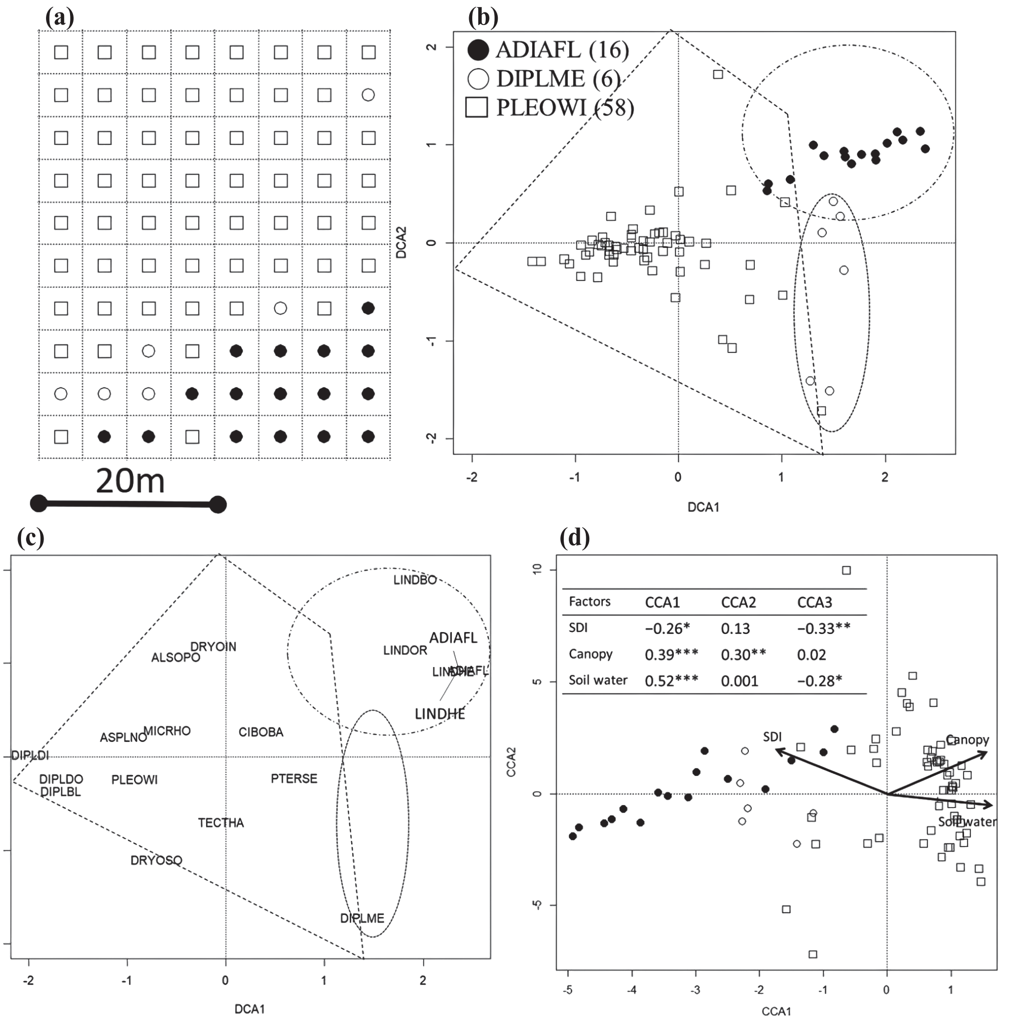

Fig. 2. Distribution of fern groups and ordination analysis of the 0.2 ha plot of the Chinese fir plantation in the Lienhuachih area, central Taiwan. (a) Fern groups analyzed by TWINSPAN and distribution within the plot. (b) Ordination plot of detrended correspondence analysis (DCA) for fern groups. (c) Ordination plot of DCA for fern species. (d) Bi-ordination plot of canonical correspondence analysis (CCA) for fern groups. □: PLEOWI group, ●: ADIAFL group, ○: DIPLME group. Arrows indicate environmental factors including: stand density index (SDI), canopy openness (Canopy), and soil water. Spearman's rank order correlation coefficients appear inside the table between the first three axes of CCA and the environment factors.

Table 3. ANOVA among the groups analyzed by TWINSPAN in the 0.2 ha plot of the Chinese fir plantation in the Lienhuachih area, central Taiwan. Variables include fern richness, density, and Shannon-Wiener index. Environmental factors include stand density index (SDI), canopy openness (%), and soil water (%). Different letters on the same line indicate significant differences between the groups (*p* < 0.05).

Groups / Variables	PLEOWI		ADIAFL		DIPLME	
	Mean	Interval	Mean	Interval	Mean	Interval
Fern						
Richness	4.8^{a}	1–9	3.8^{a}	2–6	4.2^{a}	2–6
Density	21.9^{a}	2–44	13.5^{b}	2–35	15.8^{ab}	2–35
Shannon-Wiener index	1.27^{a}	0–1.88	1.03^{a}	0.3–1.5	1.03^{a}	0.3–1.61
Factors						
SDI	10.94^{a}	0.96–22.02	11.39^{a}	5.87–17.50	13.91^{a}	7.67–19.85
Canopy openness	10.5^{a}	7.8–16.4	8.6^{b}	7.4–9.2	9.7^{ab}	7.9–13.1
Soil water	36^{a}	33.8–38	35^{b}	33.9–35.5	35.6^{ab}	34.8–36.3

在3個蕨類植群的平均值，分別為12.1 (網脈群)、18.9 (扇葉群)、及25 (深山群)，變異數分析結果以網脈群的樹木密度顯著小於其他2個植群；若杉木不列入估算，其餘樹木的更新密度依序為11.4、18.9、23.5，變異數分析結果與前述相同。若單獨將網脈群的58個樣方進行線性回歸發現冠層開闊度對蕨類豐富度及多樣性均有正向顯著關係，其餘兩個植群僅有深山群對林分密度有顯著關係外，其餘因子均無顯著關係(Table 2)。

植群排序與環境分析

降趨對應分析(DCA)結果顯示(axis rescaling = 4, segments = 26)，前3軸特徵值分別為0.6006、0.4713、及0.2355，軸長分別為3.8068、3.4369、及2.2277。DCA前兩軸的排序圖顯示扇葉群與深山群分佈於第1軸 的右側，而網脈群在第1軸的最左側；第2軸則將扇葉群與深山群區分開(Fig. 2b)。Fig. 2c顯示蕨類物種在DCA排序圖的主要分布位置，在扇葉群樣方的主要物種包括：扇葉鐵線蕨及圓葉陵齒蕨複合群(*Lindsaea orbiculata* complex, 包含圓葉陵齒蕨*L. orbiculata*、海島陵齒蕨*L. bonii* 及異葉陵齒蕨*L. heterophylla*)；在深山群樣方主要為深山雙蓋蕨；而在網脈群樣方除網脈突齒蕨尚包括前述以外的多種物種(Table 1)。

由於DCA軸長接近4個標準偏差，因此進行典型對應分析(CCA)以了解環境因子與植群的關係。結果顯示前3軸特徵值分別為0.2400、0.0474、及0.0295，累積變異量分別為7.23、8.66、及9.55%：第1軸與林分密度、土壤水分、冠層開闊度呈顯著正向關係($p < 0.05$)；第2軸與冠層開闊度達顯著關係($p < 0.05$)；第3軸與林分密度($p < 0.01$)、土壤水分($p < 0.05$)呈現顯著負向關係。CCA雙序圖顯示土壤水分與冠層開闊度箭頭指向網脈群，而林分密度箭頭指向扇葉群與深山群；表示網脈群的土壤水分與冠層開闊度的值較高，而扇葉群與深山群的林分密度值較高(Fig. 2d)。

討論

光線與水分是影響植物生長與分布的主要因子(Lambers et al. 2006)。許多研究均說明植群的區分與環境分化有密切相關(Chang et al. 2010, 2012, Chao et al. 2010, Mehmood et al. 2021, Thakur et al. 2022)。本研究樣區係1980年造林但未持續強度管理的杉木人工林，調查其林下之蕨類植群後，先利用TWINSPAN進行分群，再與DCA結果進行比較，結果均明顯將樣區群落區分為網脈群、扇葉群及深山群等3個植群，顯示兩個分析結果具一致性。因冠層開闊度與CCA前兩軸均有顯著相關，

故為主要影響因子；而土壤水分與第一軸有顯著相關，也扮演重要角色。

扇葉群在3個蕨類植群中的林下透光較低，有較多的小型蕨類在這裡分布，如：扇葉鐵線蕨、海島陵齒蕨、圓葉陵齒蕨等。網脈群的樣方樹木以大徑木(DBH > 10 cm)的杉木為主，這裡杉木樹幹通直，樹冠幅較其他闊葉樹小，林下透光充足，有比較多的中、大型蕨種，如：金狗毛蕨、網脈突齒蕨、細柄雙蓋蕨等。Hill and Silander (2001)指出乾草蕨(*Dennstaedtia punctilobula*)與紐約蕨(*Thelypteris noveboracensis*)的蕨葉高(代表蕨葉大小)、植株密度與光度呈顯著正相關。杉木人工林網脈群的蕨葉大小與密度最大，推測其生育地之透光較充足有關。深山群的樣方不論DCA、CCA及與環境因子的關係上(林分密度除外)均在扇葉群與網脈群之間，推測其主要特徵種深山雙蓋蕨在本樣區對於光度的適應性介於其他兩個蕨類植群物種之間。各植群間蕨類之豐富度及多樣性指數沒有顯著差異，但從環境因子對於這兩變數的線性回歸卻顯示出顯著影響，且單獨將網脈群的樣方進行線性回歸發現冠層開闊度對於蕨類豐富度與夏農指數均有正向顯著關係，顯示網脈群蕨類的物種組成、多樣性隨著杉木人工林冠層開闊度的增加而增加。

冠層開闊度對蕨類組成可能會造成影響(Jones et al. 2014, Chang et al. 2015)，或不影響(Karst et al. 2005)。本研究調查發現，杉木人工林的冠層開闊度(7.4–16.4%)與地被蕨類豐富度、密度及多樣性指數均達顯著正相關，且對CCA前兩變異軸均具顯著相關，顯示冠層遮蔽的變化是主要影響本區蕨類組成與分布的環境因子之一。

有研究顯示林下光度與林分密度有顯著相關(Comeau 2002, Angelini et al. 2015)，但Montgomery and Chazdon (2001) 對哥斯大黎加森林的研究與本研究之結果並非如此；本研究發現杉木人工林的冠層開闊度與林分密度相關性低(r = –0.11, p > 0.05)。林分密度影響林下植被的多樣性，許多研究指出適中的林分密度會有高度的物種多樣性(Ahmad et al. 2018, Ali et al. 2019, Wang et al. 2020)，如：Ahmad et al. (2018)在中國西北地區落葉松(*Larix principis-rupprechetii*)人工林調查指出，每公頃樹木密度在1,032–1,476株時有最多的林下地被物種。本研究CCA分析與回歸分析結果顯示，林分密度對杉木人工林的蕨類豐富度與多樣性有所影響，但並不是影響蕨類分布的主要因子。雖然林分密度在各植群間沒有顯著差異，但在每一樣方中樹木株數來說，深山群的樣方內樹木株數最多，這也反應在冠層開闊度的差異上面，深山群與扇葉群的冠層開闊度較網脈群低。

水分的多寡也影響蕨類多樣性、組成與分布(Lwanga et al. 1998, Richard et al. 2000, Karst et al. 2005, Weigand et al. 2020, Suissa et al. 2021)。例如，在加拿大魁北克省Gault自然保留區，不論1 ha樣區或較大範圍的分散樣區都指出土壤水分為影響蕨類分布的主要因子之一(Karst et al. 2005)。本研究回歸分析結果顯示土壤水分對於蕨類種數、多樣性與密度呈現顯著正相關，也就是說土壤水分較低的樣方蕨類分布較少。本調查區域之土壤水分介於33.8與38.0%之間，水分之多寡影響下層蕨類多樣性及密度之分布；例如，扇葉群樣方偏向在土壤水分較低的環境，而網脈群則偏向土壤水分較高之處。

森林有大小不同的孔隙(gap)，形成不同程度的冠層開闊度，進而影響土壤中的水分 (van Dam 2001, Gálhidy et al. 2006, Kollár 2017)。小孔隙中土壤在乾季時會比無孔隙的完整森林內或大孔隙的土壤溼潤(van Dam 2001, Kollár 2017)，有助於喜濕植物生長(Gálhidy et al. 2006)。當林木過於密集生長(冠層開闊度趨近於零)導致林下孔隙幾近消失，此時將因林木之大量蒸發(transportation)而導致表層土壤水分迅速流失，反不利土壤溼度之保持(van Dam 2001)。小孔隙表示森林冠層開闊度比大孔隙小，本研究結果顯示本樣區之冠層開闊度(相當於孔隙)如同土壤水分，對於當地林下蕨類之豐富度、密度及多樣性有顯著正向影響。綜合前述各項多樣性數據及環境因子分析，表示本樣區多數蕨類偏好較高之光度與水分，而其中之網脈群主要分布的環境孔隙，較扇葉群及深山群大，也顯示其生育地之低林分密度、高冠層開闊度及土壤水分較適宜當地多數蕨類生長的條件。

蓮華池試驗林本樣區所在之杉木人工林超過30年未進行人工撫育，依據Chou et al. (2021)對於本試驗林演替林型的研究，推測本樣區涵蓋水金京–鵝掌柴林型(*Wendlandia formosana-Schefflera octophylla* forest type)及長尾尖葉櫧–茜草樹林型(*Castanopsis cuspidata-Randia cochinchinensis* forest type)，屬於演替中期階段；以林分發育的演替階段而言，本樣區屬於林下再現期(understory reinitiation) (Oliver and Larson 1996)，而此期間林下的蕨類植群可區分為網脈群與扇葉-深山群等兩種途徑。扇葉-深山群的更新樹木平均株數多於網脈群，推測這兩群的環境較適宜林木更新，並造成土壤水分的減少，因而抑制蕨類生長；而另一種途徑是網脈群，環境適宜蕨類生長，組成多為大型葉且密集生長的蕨類，因而抑制樹苗生長與更新(Liang et al. 2022)。非生物因子(如：光度)的限制或生物資源競爭(如：與樹木幼苗的競爭)，何者為主要影響杉木人工林的蕨類物種組成？則有待後續更進一步分析探討。

結論

本研究於臺灣中部杉木人工林0.2 ha樣區調查蕨類物種有 19種，雙向指標種分析顯示網脈突齒蕨群、扇葉鐵線蕨群與深山雙蓋蕨群 3個群，與DCA比較結果大致相符。CCA結果顯示，影響蕨類分布的主要因子為冠層開闊度與土壤水分。多數蕨類還是需要充足的光線與土壤水分促進生長，尤其葉子尺寸大的蕨類。三種蕨類植群於杉木人工林樣區分布呈現區隔，反映不同蕨類組成對林下環境適應的差異性。本研究結果提供小尺度杉木人工林下地被研究，探討小範圍(< 1 ha)與環境差異小(坡度 < 30°)的影響下，蕨類植物多樣性及分布如何產生變化。

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Appendix 1. Checklist of 52 tree species belonging to 26 families (DBH ≥ 1 cm) recorded within the 40 m × 50 m plot at Lienhuachi in central lowland in Taiwan. The numbers of species recorded are in the parentheses after each family name. "#" indicates endemism; "*" indicates naturalized species; and "†" indicates cultivated species.

裸子植物 Gymnosperms
1. Cupressaceae 柏科 (1)
1. *Cunninghamia lanceolata* (Lamb.) Hook. 杉木 †
2. Podocarpaceae 羅漢松科 (1)
2. *Podocarpus nakaii* Hayata 桃實百日青 #
被子植物 Angiosperms
3. Aquifoliaceae 冬青科 (3)
3. *Ilex ficoidea* Hemsl. 臺灣糊樗
4. *Ilex formosana* Maxim. 糊樗
5. *Ilex goshiensis* Hayata 圓葉冬青
4. Araliaceae 五加科 (1)
6. *Schefflera octophylla* (Lour.) Harms 鵝掌柴
5. Celastraceae 衛矛科 (2)
7. *Euonymus laxiflorus* Champ. ex Benth. 大丁黃
8. *Euonymus tashiroi* Maxim. 菱葉衛矛
6. Daphniphyllaceae 虎皮楠科 (1)
9. *Daphniphyllum glaucescens* Bl. subsp. *oldhamii* T.C. Huang 奧氏虎皮楠
7. Ebenaceae 柿樹科 (1)
10. *Diospyros morrisiana* Hance 山紅柿
8. Elaeocarpaceae 杜英科 (1)
11. *Elaeocarpus sylvestris* (Lour.) Poir. 杜英
9. Euphorbiaceae 大戟科 (1)
12. *Mallotus paniculatus* (Lam.) Müll. Arg. 白匏子
10. Fabaceae 豆科 (2)
13. *Archidendron lucidum* (Benth.) I.C. Nielsen 頷垂豆
14. *Ormosia formosana* Kaneh. 臺灣紅豆樹 #
11. Fagaceae 殼斗科 (5)
15. *Castanopsis cuspidata* (Thunb. ex Murray) Schottky var. *carlesii* (Hemsl.) T. Yamaz. 長尾尖葉櫧
16. *Castanopsis fargesii* Franch. 火燒柯
17. *Lithocarpus konishii* (Hayata) Hayata 油葉石櫟 #
18. *Lithocarpus synbalanos* (Hance) Chun 菱果石櫟
19. *Quercus pachyloma* Seemen 捲斗櫟

Appendix 1. Continued

12. Juglandaceae 胡桃科 (1)
    20. *Engelhardia roxburghiana* Wall. 黃杞
13. Lauraceae 樟科 (6)
    21. *Cinnamomum subavenium* Miq. 香桂
    22. *Cryptocarya chinensis* (Hance) Hemsl. 厚殼桂
    23. *Litsea acuminata* (Blume) Kurata 長葉木薑子
    24. *Machilus thunbergii* Siebold & Zucc. 紅楠
    25. *Machilus zuihoensis* Hayata 香楠 #
    26. *Neolitsea aciculata* (Bl.) Koidz. var. *variabillima* J.C. Liao 變葉新木薑子 #
14. Melastomataceae 野牡丹科 (1)
    27. *Blastus cochinchinensis* Lour. 柏拉木
15. Myrtaceae 桃金孃科 (1)
    28. *Syzygium buxifolium* Hook. & Arn. 小葉赤楠
16. Oleaceae 木犀科 (1)
    29. *Osmanthus matsumuranus* Hayata 大葉木犀
17. Pentaphylacaceae 五列木科 (2)
    30. *Eurya loquaiana* Dunn 細枝柃木
    31. *Ternstroemia gymnanthera* (Wight & Arn.) Sprague 厚皮香
18. Phyllanthaceae 葉下珠科 (1)
    32. *Glochidion acuminatum* Müll. Arg. 裏白饅頭果
19. Primulaceae 櫻草科 (2)
    33. *Ardisia quinquegona* Blume 小葉樹杞
    34. *Ardisia sieboldii* Miq. 樹杞
20. Proteaceae 山龍眼科 (2)
    35. *Helicia cochinchinensis* Lour. 紅葉樹
    36. *Helicia formosana* Hemsl. 山龍眼
21. Rosaceae 薔薇科 (2)
    37. *Prunus phaeosticta* (Hance) Maxim. 墨點櫻桃
    38. *Rhaphiolepis indica* (L.) Lindl. ex Ker var. *tashiroi* Hayata *ex* Matsum. & Hayata 石斑木
22. Rubiaceae 茜草科 (7)
    39. *Gardenia jasminoides* J. Ellis 山黃梔
    40. *Lasianthus bunzanensis* Simizu 文山雞屎樹
    41. *Lasianthus curtisii* King & Gamble 柯氏雞屎樹
    42. *Lasianthus wallichii* (Wight & Arn.) Wight 圓葉雞屎樹
    43. *Psychotria rubra* (Lour.) Poir. 九節木
    44. *Randia cochinchinensis* (Lour.) Merr. 茜草樹
    45. *Tricalysia dubia* (Lindl.) Ohwi 狗骨仔
23. Salicaceae 楊柳科 (1)
    46. *Casearia membranacea* Hance 薄葉嘉賜木
24. Styracaceae 安息香科 (1)
    47. *Styrax suberifolius* Hook. & Arn. 紅皮
25. Symplocaceae 灰木科 (2)
    48. *Symplocos setchuensis* Brand 四川灰木
    49. *Symplocos theophrastifolia* Siebold & Zucc. 山豬肝
26. Theaceae 茶科 (3)
    50. *Camellia sinensis* (L.) Kuntze var. *assamica* Pierre 阿薩母茶
    51. *Pyrenaria shinkoensis* (Hayata) H. Keng 烏皮茶 #
    52. *Schima superba* Gardner & Champ. 木荷

Appendix 2. Tree density (a, unit = number per 25 m^2), stand density (b, unit = %), canopy openness in the wet season (c, unit = %), and soil water in the wet season (d, unit = %), canopy openness in the dry season (e), and soil water in the dry season (f) in the 0.2 ha plot in the Chinese fir plantation of central lowland in Taiwan. Values are rounded to whole numbers. TWINSPAN results were divided across the 3 groups, including PLEOWI, DIPLME, and ADIAFL (see Results).

4	14	17	18	19	9	7	14
6	4	7	13	6	13	18	12
14	4	10	15	4	13	8	12
9	7	5	5	8	11	8	18
16	16	8	11	8	6	6	5
20	13	13	18	14	9	14	14
20	15	15	15	19	17	19	14
4	23	37	15	20	22	13	13
26	22	36	15	22	25	18	23
32	31	10	16	16	21	24	15

11	18	13	16	7	1	9	22
12	5	8	8	5	5	16	8
14	9	13	15	7	10	8	14
14	6	10	4	15	11	12	7
21	16	8	18	3	6	3	2
10	13	16	22	13	8	5	17
15	8	19	8	10	9	15	10
1	14	17	13	13	7	6	9
19	11	20	9	13	14	13	16
17	17	9	7	13	12	14	8

PLEOWI
DIPLME
ADIAFL

25	21	26	27	25	27	17	11
28	18	17	22	28	24	19	17
20	18	20	23	23	17	24	21
23	16	15	25	38	28	24	17
23	23	24	23	24	28	20	14
14	25	25	14	22	24	21	20
25	26	16	25	24	23	20	11
26	23	14	13	26	21	19	10
27	25	15	13	26	14	27	12
24	13	26	14	23	32	23	26

41	42	42	43	44	42	42	43
43	41	43	42	44	43	43	43
42	42	43	42	42	42	43	43
42	43	44	43	43	42	44	42
44	43	42	45	43	42	43	42
43	42	42	44	42	44	42	41
37	43	41	43	43	43	42	42
40	42	41	41	42	41	42	43
42	44	41	42	41	42	42	42
42	40	43	42	42	43	42	42

a	b
c	d
e	f

20m

14	12	13	13	11	11	10	8
15	16	16	13	10	9	9	8
10	16	12	12	9	13	11	8
12	14	11	9	9	9	9	8
11	12	8	10	13	12	9	8
10	10	8	11	8	8	12	9
9	8	9	11	8	9	11	7
10	8	8	8	9	9	9	9
13	11	8	8	9	9	9	9
9	8	9	9	8	9	8	9

35	36	36	36	36	36	36	36
36	35	37	36	37	36	36	36
36	35	37	36	36	36	35	36
36	36	38	37	37	37	36	35
35	36	36	37	36	36	36	36
36	36	35	38	37	37	35	34
35	37	36	37	37	35	35	34
36	36	36	36	35	34	35	36
36	35	35	35	35	35	35	35
34	35	35	36	35	35	35	34

Table S. Spearman's rank correlation coefficients between fern variables and environmental variables.

Fern variables	Wet season		Dry season	
	Canopy openness	Soil water	Canopy openness	Soil water
Richness	0.19	0.03	0.32**	0.26*
Density	0.17	0.15	0.46***	0.23*
Shannon index	0.19	0.04	0.32**	0.34**

*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

Appendix 3. Species-quadrat table for TWINSPAN at the 0.2 ha plot in a Chinese fir plantation in central lowland Taiwan. Abbreviations of the 19 species (see Table 1) are along the left. The 80 quadrats are in the second row along the top. Vegetation groups (see Results) are across the top row. Numbers in the table represent the conversion value of density (individuals per area) (-: does not exit, 1: 1, 2: 2-4, 3: 5-9, 4: 10-19, 5: >19)

```
                                      PLEOWI                                    ADIAFL      DIPLME
       15756630133334556667000012233444700111122222334445670015672367456744751567015722
       24463425357899895687023499304348979467845678365677966855750110200101310222113812
DIPLDI ---------------------------------1----1------1----------------------------------
DRYOSO --------------------1-----------------------------------------------------------
MICRHO ---1-------11----------2----2--2--11--2-----------------------------------------
DIPLBL ----------------------------------------------1---------------------------------
ASPLNO ---1------212-2-----------------------------------------------------------------
DIPLDO ---4-2-2-444-2335443----------11-4332232325414222133442434----------------------
MICRCA ------3-------------------------------------------------------------------------
PLEOWI -3-3222333442242334---22222-32222342322443433322233232233-----------------------
ALSOPO -1----1--1-----------1-2----111---1------------1----2-1221----------------------
DRYOIN ------1--22233231-------11-------1----------------------------1-1---------------
TECTHA -------4222-2412--1-32333311111122322-1-2222--21112-1322------1--1--------22----
CIBOBA ---22122222-111--22223343423323324433442344432223333443-2324232-1221-3213121--11
PTERSE --2111-11---122--212-----------21--------------------2---21-1-----2-----------1-
DIPLME 53-334-----2---------3--12----------1----------------112------------------254123
DICRTE ------1----21------1------1-2-----------------------------2-------------------22
ADIAFL --------1--2-2------------121---1------1------------------2123344443322112211-21
LINDBO ----2-1-1-2-----------1---1-------------------------------1222223322-1--------13
LINDHE -----------------------------------------------------------1---1-1--------------
LINDOR -------1---1------------------------------------------------1-1-211-1-222121-1--
```