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Abstract. The population of the bear cuscus *Ailurops ursinus* (Temminck, 1824), an arboreal marsupial endemic to Sulawesi, Indonesia, and its satellite islands, is declining rapidly due to poaching and habitat loss, even in protected areas. However, despite concerns over its persistence, little is actually known of this secretive species. This research investigated the characteristics of the selected habitats and diet of the bear cuscus in four ecosystem types (lowland non-dipterocarp forest, lowland limestone forest, lowland monsoon deciduous forest, lowland monsoon evergreen forest). Habitat use data were collected through direct encounters and indirect observations (tracks, signs, secondary information), and analyzed using a chi-square goodness-of-fit test. Habitat characteristics and diet availability were determined using vegetation analysis. Diet data were obtained using direct observations, feed remains, and interviews. The lowland non-dipterocarp forest ecosystem was used significantly more by bear cuscus populations. Its habitats across the four ecosystem types had similar environmental conditions. Fifty-five plant species, eaten mostly as young leaves and leaf buds, encompassed the bear cuscus' diet, with the Moraceae family being the most representative. Considering the ubiquity of Moraceae in the bear cuscus' habitat, these results highlight the impact unchecked deforestation will continue to have on lowland Indonesia and its endemic species.
Keywords: Endemic species, habitat characteristics, habitat selection, marsupial, Wallacea

1. Introduction

The bear cuscus *Ailurops ursinus* (Temminck, 1824) is one of the threatened endemic cuscuses of the Phalangeridae family. This tree-dwelling marsupial is listed as vulnerable in the IUCN Red List of Threatened Species, and its population, which is restricted to Sulawesi and its satellite islands [1, 2], is declining due to deforestation and poaching for consumption and illegal trade [3, 4]. These threats to its population are exacerbated by its specific habitat requirements: it relies heavily on the presence of contiguous canopy cover [5, 6], and thus forest degradation and deforestation can ultimately reduce its habitat availability. The bear cuscus has been found inhabiting tropical lowland forest [5, 7], mixed natural forest [8], and lowland limestone forest [9], and has also been encountered in four types of land cover; i.e., primary forest, secondary forest, scrub, and farmland [10].

Together with the talaud bear cuscus, the bear cuscus is one of only two species of folivorous cuscuses, differing from the other, frugivorous cuscuses [1, 11]. To date, studies on the bear cuscus' diet have been conducted in North Sulawesi [1] and Southeast Sulawesi [5], with a total of 31 and 80 plants,

respectively, recorded as its diet. A study on the bear cuscus diet has also been conducted in four provinces of Sulawesi [12], the results of which listed 74 species of plants. Thus far, in South Sulawesi, information on the diet of the bear cuscus has only been obtained from one resort in Bantimurung Bulusaraung National Park (BBNP) [9] and in Hasanuddin University Educational Forest (HUEF) [13], with four plant species identified through direct observations. The information in these aforementioned studies is still too insufficient to develop a comprehensive understanding of this arboreal mammal's diet. In comparison, this study covers six resorts in BBNP and four ecosystem types, with both direct and indirect observations made, for determining the bear cuscus' diet.

Understanding the bear cuscus' feeding requirements and habitat are important factors in the management and conservation of this species. It is also essential that more be known about its habitat use, so that more cogent actions can be taken to ensure its survival. Habitat use is the way a particular species makes use of the biological and physical resources in a habitat [14]. For the bear cuscus, a selected habitat with an optimum condition can maintain a sustainable population, as well as support the management of its habitat. This study therefore aimed to (1) investigate the habitat use of the bear cuscus in various forest ecosystem types; (2) determine the characteristics of the bear cuscus' habitat; and (3) identify the species of plants serving as the bear cuscus' diet.

2. Materials and methods

2.1. Study areas

Research took place in the lowland limestone forest (LLF) and lowland non-dipterocarp forest (LnDF) ecosystems in Bantimurung Bulusaraung National Park (BBNP), along with the lowland monsoon deciduous forest (LMDF) and lowland monsoon evergreen forest (LMEF) ecosystems in Hasanuddin University Educational Forest (HUEF), all of which are located in the southern part of South Sulawesi, Indonesia. BBNP (4º42'49"S–5º06'42"S, 119º34'17"E–119º55'13"E) has a total area of ~43,700 ha, which is composed of three ecosystem types; i.e., LnDF, LLF, and the lower montane forest. BBNP's landscape is dominated by a karst topography, whose surface varies from flat to wavy, hilly, and mountainous. Its highest elevation is 1,565 masl [9]. Meanwhile, HUEF (4º58'07"S–5º00'30"S, 119º44'34"E–119º46'17"E) has a total area of ~1,454 ha, which encompasses four ecosystem types; i.e., LMDF, LMEF, the monsoon lower mountain forest, and lowland herbaceous peat swamp. HUEF is a Forest Area with Special Purpose, whose function is focused on educational activities. The elevation of HUEF ranges from 300 to 800 masl, with a mountainous topography dominated by volcanic tuff and sandstone [15].

The LLF ecosystem is made up of steep karst cliffs with vegetation dominated by Moraceace stands mainly composed of fig trees, with a moderate to high canopy cover and sparse undergrowths. The LnDF ecosystem has a moderate to high canopy cover consisting of non-dipterocarp vegetation, such as Anacardiaceae and Moraceae members, with a thick layer of undergrowth. The LMDF ecosystem has a low to moderate canopy cover, dominated by *Polyscias diversifolia* stands, with a thick layer of undergrowth. The LMEF ecosystem is dominated by a large tract of pine forest with a low to moderate canopy cover and sparse undergrowth.

2.2. Bear cuscus presence data collection

Data collection was carried out during a three-month fieldwork period in October 2020–January 2021. Bear cuscus presence data were collected based on direct encounters and indirect observations through signs (claw marks, feed remains, calls), information from indigenous people and local guides, as well as inventory data supplied by BBNP (see supplementary data; https://doi.org/10.5281/zenodo.5516079). Exploration tracks and bear cuscus presence signs were marked and tracked using the Garmin GPSMAP 64s GPS device.

2.3. Vegetation analysis and environmental parameters data collection

Vegetation analysis was conducted to determine the habitat characteristics of the bear cuscus, as well as its diet availability. Fifteen plots of 20 x 20 m were established in each ecosystem type, leading to a total of 60 plots (see supplementary data; https://doi.org/10.5281/zenodo.5515918). The plots were constructed at the locations of bear cuscus sightings, with three plots allocated per location (figure 1). Sightings were based on either direct encounters during the research or indirect encounters noted in the data provided by the local guides.

Vegetation data were collected from various growth forms—namely, seedlings (height <1.5 m), saplings (height ≥1.5 m and dbh <10 cm), poles (dbh 10–19.9 cm), and trees (dbh ≥20 cm)—using the nested plot method (figure 1). Seedling data were sampled from 2 x 2 m subplots, sapling data from 5 x 5 m subplots, pole data from 10 x 10 m subplots, and tree data from 20 x 20 m plots. Seedling and sapling data comprised species' local names and the number of individuals, while the data on poles and trees comprised species' local names, the number of individuals, trunk diameters at breast height, first branch heights, total tree heights, and canopy length in north–east–south–west directions.

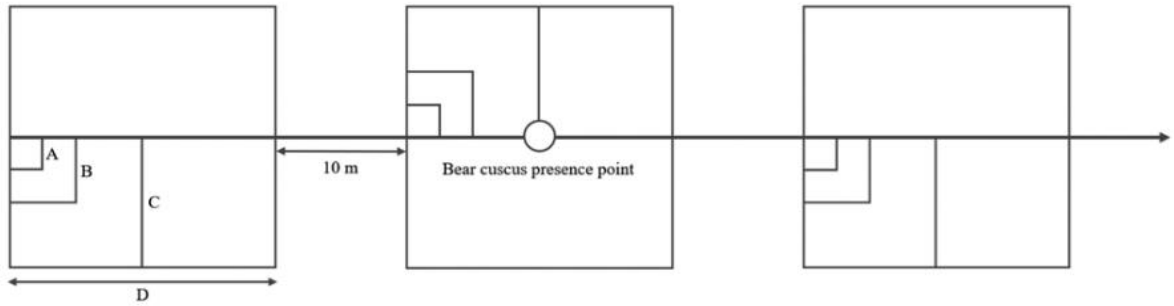

Figure 1. Nested plot design used to collect vegetation data. A: 2 x 2 m subplot for seedling data (height <1.5 m); B: 5 x 5 m subplot for sapling data (height ≥1.5 m, dbh <10 cm); C: 10 x 10 m subplot for pole data (dbh 10–19.9 cm); D: 20 x 20 m plot for tree data (dbh ≥20 cm).

The environmental parameters collected in each plot were air temperature, air humidity, light intensity, elevation, and slope. Canopy cover was also estimated in each plot using the Gap Light Analysis Mobile App (GLAMA) version 3.0. All of the vegetation data were collected using the Plant Inventory (Inventum) mobile application version 2.0.0-twa. Identification of plant species was carried out using the BBNP and HUEF plant list database, and the remaining unidentified species were sampled and thereafter identified at the Herbarium Bogoriense, Research Centre for Biology, Indonesian Institute of Sciences (LIPI).

2.4. Bear cuscus habitat use analysis

To determine the habitat use of the bear cuscus, each ecosystem type was categorized into various types of land cover based on a 2020 land cover map provided by the Ministry of Environment and Forestry of Indonesia; i.e., primary forest, secondary forest, shrubland, farmland, and mixed farmland. Using QGIS version 3.18.1, presence data of the bear cuscus were spatially partitioned into several populations according to the similarities between land cover types. Bear cuscus populations consisted of direct and indirect encounter points; the area available for these populations in each land cover type within each ecosystem type was estimated by constructing a 10 m buffer area from the exploration tracks in QGIS. A chi-square goodness-of-fit (GoF) test with a confidence interval level of 95% was used to analyze the use of different land cover types [16]. The parameters measured and calculated were area (a, in ha), proportion of the area (p, in percent), observed presence signs (O_i), expected presence signs ($E_i = \sum O_i.p_i$), and the chi-square values ($\chi^2=(O_i-E_i)^2/E_i$) (see supplementary data; https://doi.org/10.5281/zenodo.5516206).

2.5. Bear cuscus habitat characteristics analysis

Vegetation data from each ecosystem type were analyzed to obtain the densities, relative densities, frequencies, relative frequencies, and importance value index (IVI) of seedling and sapling species. For poles and trees, the same analysis was performed with the additional parameters of pole and tree dominances, relative dominances, and size of canopy area [17]. Species richness and Shannon's index were estimated using the Abundance-based Coverage Estimator (ACE) and the Chao and Shen estimator, respectively [18, 19], both provided by the SpadeR (Species-Richness Prediction and Diversity Estimation with R) package in R-Studio version 1.4.1717 [20, 21]. Plant community similarities were analyzed using the Morisita-Horn index of multiple-community similarity among all pairs of ecosystem types [22].

Air humidity, light intensity, elevation, and slope data were first transformed using a Tukey's Ladder of Powers transformation, before going through statistical analyses. To determine the variations in environmental parameters between ecosystem types, A one-way analysis of variance (ANOVA) test with a post-hoc Tukey HSD test was conducted for light intensity, slope, and canopy cover, while a Welch's ANOVA test with a post-hoc Games-Howell test was conducted for air temperature and air humidity, the latter due to their unequal variance data. Elevation was tested using a Kruskal-Wallis test with a post-hoc Dunn test, due to its non-normality of data distribution. All statistical analyses were carried out using R-Studio version 1.4.1717.

2.6. Identification of plant species in the bear cuscus diet

Data of the plant species identified as constituting the bear cuscus diet were obtained from direct observations, feed remains, and information from the local guides (BBNP and HUEF officers). These data consisted of plant species names and the parts eaten by the bear cuscus.

3. Results

3.1. Bear cuscus habitat use

In our research area, the local bear cuscus population was split into smaller populations, each of which was confined to a relatively small home range separated by different types of barriers. The presence data of the bear cuscus revealed six spatial populations in both LLF and LnDF (BBNP), while two bear cuscus spatial populations were revealed in both LMDF and LMEF (HUEF). In LLF, based on the chi-square GoF test results, all populations showed a similar pattern, wherein secondary forest was used less in comparison with shrubland and mixed farmland, although the observed presence signs in secondary forest for population (4-6) was high. None of the land cover types in LLF showed a significant use by their respective bear cuscus populations (table 1).

In LnDF, although there was no significance in the land cover types used by populations 1, 2, and 3, secondary forest was nevertheless used more than shrubland and mixed farmland. Primary forest was significantly overused by population 4, whereas secondary forest was underused, albeit non-significantly. Populations 5 and 6 conversely significantly overused secondary forest, and underused farmland and shrubland, with only farmland being significant. In LMDF, secondary forest was significantly overused by populations 1 and 2, while shrubland was significantly underused. There was no significance in the use of both land cover types used by populations 1 and 2 in LMEF, although secondary forest was used more compared with shrubland.

Table 1. Bear cuscus habitat use in various land cover types based on the chi-square goodness-of-fit test results in each ecosystem type. Farmland in population 4 in the lowland non-dipterocarp forest is excluded from the analysis, as its chi-square value was less than 1. *Significant at $\alpha = 0.05$; **Significant at $\alpha = 0.01$.

Ecosystem type	Population	Land cover	$\chi 2$	Remarks
Lowland limestone forest (LLF)	1, 2, 3	Secondary forest	1.16	Underused
		Shrubland	1.16	Overused
	4, 5, 6	Secondary forest	1.32	Underused
		Mixed farmland	1.32	Overused
Lowland non-dipterocarp forest (LnDF)	1, 2, 3	Secondary forest	2.94	Overused
		Shrubland	1.76	Underused
		Mixed farmland	1.09	Underused
	4	Primary forest	7.08*	Overused
		Secondary forest	3.48	Underused
	5, 6	Secondary forest	31.64**	Overused
		Shrubland	3.84	Underused
		Farmland	14.88**	Underused
Lowland monsoon deciduous forest (LMDF)	1, 2	Secondary forest	13.66**	Overused
		Shrubland	13.66**	Underused
Lowland monsoon evergreen forest (LMEF)	1, 2	Secondary forest	1.06	Overused
		Shrubland	1.06	Underused

3.2. Habitat characteristics of the bear cuscus

In general, the four ecosystem types had different species compositions (see supplementary data; https://doi.org/10.5281/zenodo.5516053). In LLF and LnDF, the specific dominance of tree and sapling species was not prominent, with an IVI of less than 30% each and the dominance spread out among the high number of species recorded. The dominance of tree species in LMDF and LMEF was more notable, as their highest IVI exceeded 40%, with fewer total tree species recorded. The species dominance in the pole category in LMDF and LMEF was more conspicuous, as their species' highest IVI exceeded 80%. In all ecosystem types, the seedling category showed a somewhat similar distribution of IVI among the most dominant species.

In LLF, trees were dominated by *Myristica impressa*, which also co-dominated poles alongside *Syzygium aqueum*. *Myristica impressa* also had the largest canopy area, in both tree and pole categories. The sapling species with the highest density and IVI was *S. aqueum*. This species also had the second highest density and IVI among seedlings, after *Euphorianthus sp*. In LnDF, *Alstonia scholaris* and *Litsea mappacea* were the dominating species in the tree and pole categories, respectively (table 3). The largest canopy cover in the tree category was found in *Melicope latifolia*, while in the pole category it was found in *Heritiera sylvatica*. The dominant species among saplings and seedlings were *Aphanamixis sp.* and *Leea indica*, respectively. In LMDF, *Polyscias diversifolia* dominated both trees and poles, as well as being the species with the largest canopy area in the pole category. Meanwhile, the tree species that had the largest canopy cover was *Aleurites moluccanus*. *Cinnamomum iners* and *Flacourtia jangomas* were the dominating species in sapling and seedling categories, respectively. In LMEF, both tree and pole growth form categories were dominated by *Polyscias nodosa*, which also had the largest canopy area in the pole category, whereas among trees it belonged to *Pinus merkusii*. The dominant species in the sapling and seedling categories were *Garcinia celebica* and *Diospyros celebica*, respectively.

A total of 117 plant species belonging to 46 families were recorded during the research. The contribution of the number of species to the plant diversity of the ecosystem was more prominent than that of the abundance distribution among the species, which is indicated by the near-similar pattern of

the species richness estimates and Shannon's diversity values (figure 2). The highest species richness among seedlings was found in the LMDF ecosystem, whereas LnDF had the highest species richness in saplings and poles. The LLF ecosystem had the highest tree species richness. In terms of species diversity, the highest diversity of seedlings, saplings, and trees was found in LLF, while pole diversity was found to be highest in LnDF. Notably, both ecosystems are located in BBNP.

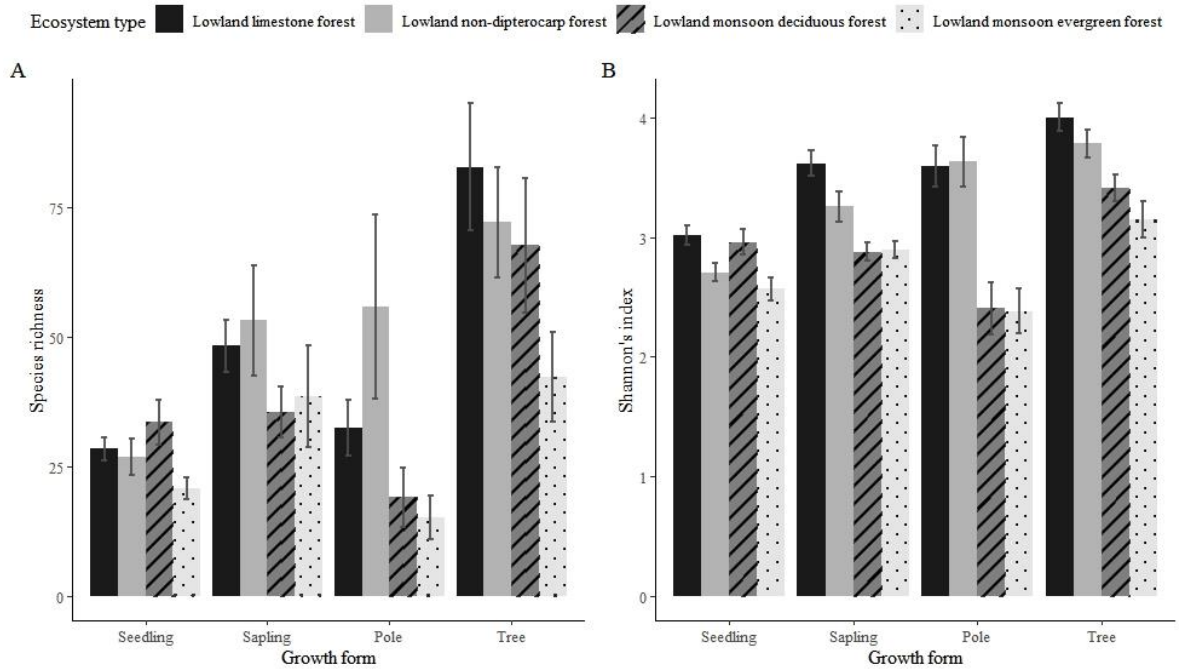

Figure 2. Vegetation diversity estimates of various growth forms in different ecosystem types. A: species richness; B: Shannon's index values. Error bars represent the estimates' standard errors.

The Morisita-Horn similarity index showed that the vegetation composition similarities among the four ecosystem types were relatively low, with the highest similarity found between LMDF and LMEF (0.54), and the rest showing a similarity value ranging from 0.2 to 0.38 (figure 3).

Figure 3. Vegetation compositional similarities between ecosystem types, estimated using the pairwise Morisita-Horn index. LnDF: lowland non-dipterocarp forest; LLF: lowland limestone forest; LMEF: lowland monsoon evergreen forest; LMDF: lowland monsoon deciduous forest.

The measured environmental factors differed significantly among ecosystems, with the exception of air humidity (figure 4). Mean air temperature ranged from 24.43±3.03 to 27.19±2.29ºC, with LnDF's temperature being significantly different from those of LLF (p = 0.043) and LMEF (p = 0.024). Air

humidity did not differ significantly amongst all ecosystems, with the means ranging from 84.77±9.90 to 89.41±5.26%. The highest mean of light intensity was found in LMDF (1308.20±775.29 lux), differing significantly from LLF (p = 0.036) and LnDF (p = 0.025). The ecosystems' elevations were significantly different, with the highest mean found in LnDF (860.53±71.26 masl) and lowest in LLF (268.00±128.90 masl). The highest mean of slope was found in LMDF (26.13±7.25º), which was significantly different from LMEF (p = 0.011), while the rest of the ecosystems differed non-significantly. The mean canopy cover ranged from 70.25±5.98 to 76.14±4.66%, with LMEF's canopy cover being significantly different from those of LLF (p = 0.014) and LnDF (p = 0.013).

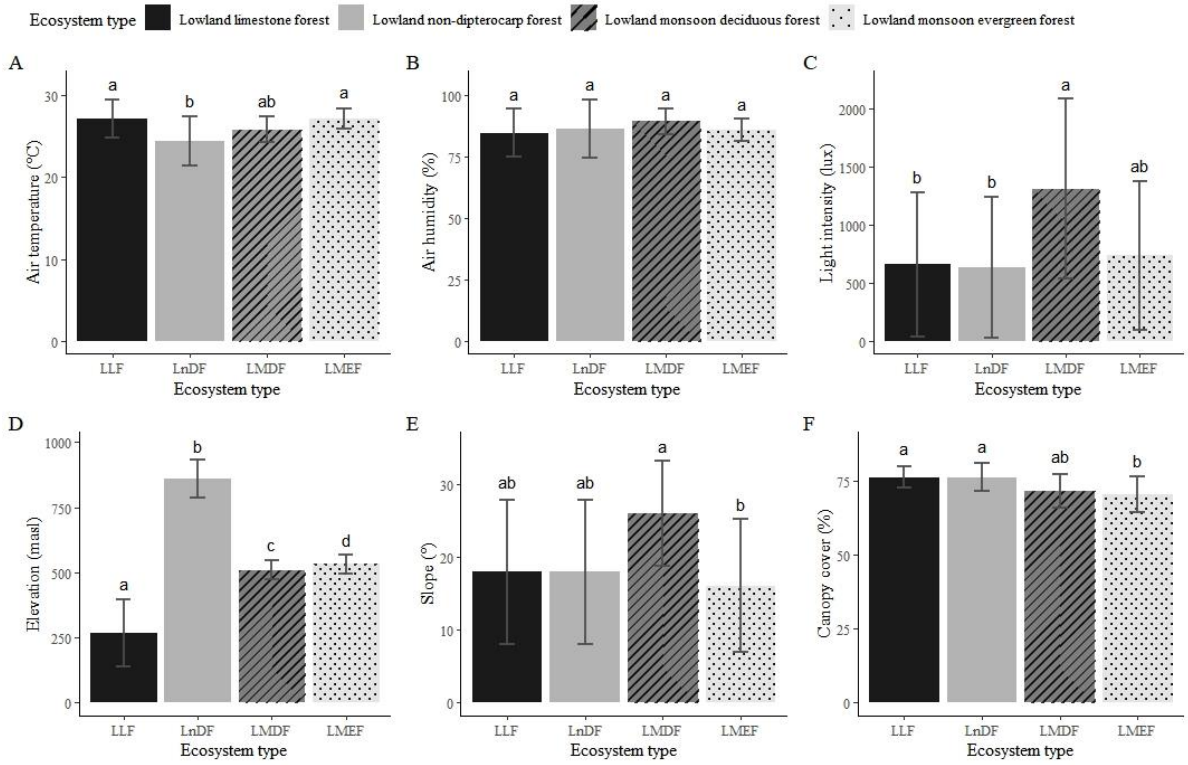

Figure 4. Variations in environmental variables' means in various ecosystem types. A: Air temperature; B: air humidity; C: light intensity; D: elevation; E: slope; F: canopy cover. Error bars represent the standard deviation of the estimates. Different letters above error bars indicate the difference of significance at p = 0.05 between ecosystem types.

3.3. Diet of the bear cuscus

Based on direct observations, feed remains, and information from the local guide, twenty-two plant families consisting of 55 species were recorded as the bear cuscus' diet (see supplementary data; https://doi.org/10.5281/zenodo.5516118), Moraceae among them being the most-consumed family, with 16 species (figure 5). Eight species were observed being consumed by an individual, while ten species were identified from feed remains (table 2). Of the plants eaten by the bear cuscus, the most common parts were young leaves and leaf buds.

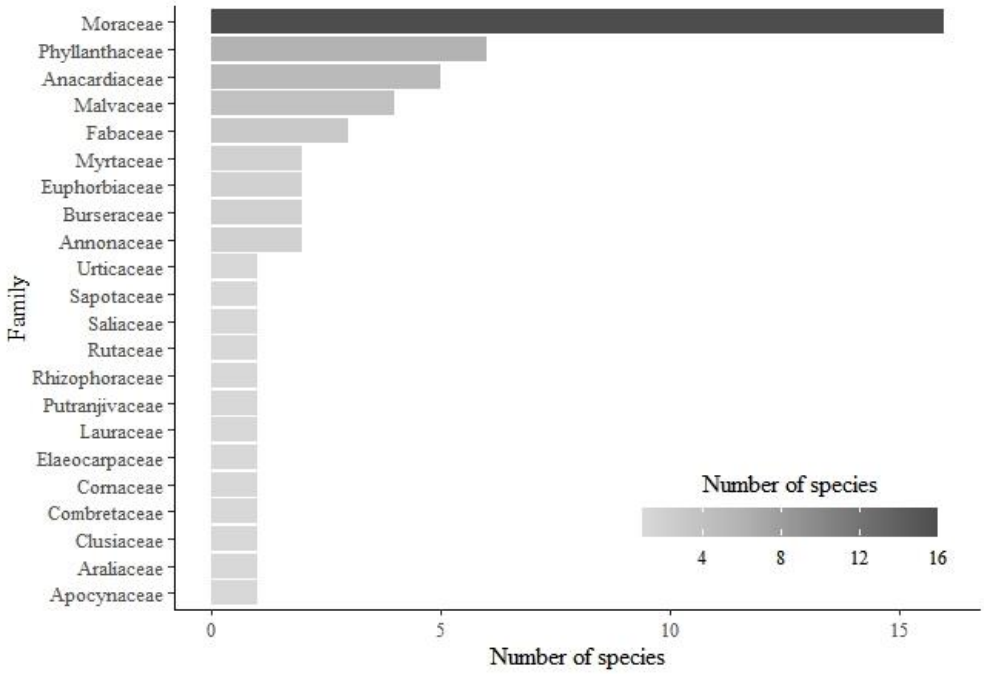

Figure 5. Plant families and number of their member species in the bear cuscus' diet.

Table 2. Plant species recorded as constituting the bear cuscus' diet, based on direct observations and feed remains.

No	Family	Species	Common name	Local name	Part(s) eaten
			Direct observations		
1	Apocynaceae	*Alstonia scholaris*	Blackboard tree	Rita/Pulai	Young leaves, leaf buds
2	Combretaceae	*Terminalia supitiana*	-	Katabo	Young leaves, leaf buds
3	Fabaceae	*Albizia procera*	Silver bark rain tree	Bilalang	Young leaves, leaf buds
4	Fabaceae	*Pterocarpus indicus*	Amboyna-wood	Angsana	Young leaves, leaf buds
5	Malvaceae	*Sterculia foetida*	Java olive	Kalumpang	Young leaves, leaf buds
6	Moraceae	*Ficus ampelas*	-	Kajuara langa langa	Young leaves, leaf buds
7	Moraceae	*Ficus sumatrana*	-	Kajuara karisabatang	Young leaves, leaf buds, mature leaves
8	Phyllanthaceae	*Baccaurea nanihua*	-	Tera-terasa	Young leaves, leaf buds
			Feed remains		
1	Anacardiaceae	*Dracontomelon dao*	Argus pheasant tree	Rao/Dao	Young leaves
2	Anacardiaceae	*Mangifera indica*	Mango	Mangga	Young leaves
3	Anacardiaceae	*Spondias pinnata*	Common hog-plum	Karunrung	Young leaves
4	Araliaceae	*Polyscias diversifolia*	-	Lento-lento cakdi	Young leaves
5	Burseraceae	*Garuga floribunda*	-	Mapala	Young leaves
6	Combretaceae	*Terminalia supitiana*	-	Katabo	Young leaves
7	Ebenaceae	*Diospyros ferrea*	-	Mawai	Young leaves
8	Fabaceae	*Erythrina variegata*	Easter flower	Kane romang	Young leaves
9	Malvaceae	*Sterculia foetida*	Java olive	Kalumpang	Young leaves
10	Moraceae	*Ficus racemosa*	Cluster fig	Biraeng	Young leaves

4. Discussion

4.1. Habitat use of the bear cuscus

In LLF, shrubland was used more than secondary forest by populations 1, 2, and 3, albeit not significantly. Here, shrubland was located adjacent to secondary forest, thus providing the species with the ability to move between land cover through the interlocked canopies. A study in Southeast Sulawesi reported that bear cuscuses were frequently encountered in the forest-edge ecosystems, as well as found occupying the shrubland [10]; it is thus possible that, while foraging, bear cuscuses spread out to shrubland, where a contiguous canopy cover connected it with secondary forest. During data collection in LLF, populations 1, 2, and 3 were found in shrubland occupying *Sterculia foetida*, using this species, which is also part of their diet, as a resting tree. Although not significant, the use of mixed farmland by populations 4, 5, and 6 in LLF was more pronounced than that of secondary forest, having four times as many observed presence signs compared with mixed farmland. The mixed farmland, which consisted of *Tectona grandis* and corn, may be used more by bear cuscuses because the *T. grandis* tree could serve as a shelter for bear cuscuses. Furthermore, the local guide also reported that bear cuscuses frequently use *T. grandis* branches to help them cross to the other side of the mixed farmland where there are plenty of *Terminalia catappa* trees as its diet source. A study in North Sulawesi reported that the talaud bear cuscus, a relative of the bear cuscus, could be seen in man-made habitats adjacent to primary forest [23].

Populations 1, 2, and 3 in LnDF made use of secondary forest more than shrubland and mixed farmland, although to a non-significant degree. Secondary forest is known to have an intermediate species richness [24], with numerous native forest plant species [25], which is preferred by the bear cuscus. During the research, populations 1, 2, and 3 in LnDF were encountered occupying *Baccaurea nanihua, Sterculia foetida,* and *Pterocarpus indicus* trees in the secondary forest, the leaves and buds of which also form part of the bear cuscus' diet. The mixed farmland in LnDF were composed of *Syzygium aromaticum* and *Coffea* sp., or a combination of *Aleurites moluccanus*, *Syzygium aromaticum*, *Coffea* sp., and *Arachis hypogaea*. *Syzygium aromaticum,* which dominated in mixed farmland, is a small tree with a small crown, arranged at a distance between individuals, making it less preferable for the bear cuscus or any of its activities. Population 4 in LnDF significantly overused primary forest compared with secondary forest. Primary forests in Central Sulawesi hold a higher species richness in comparison with forest gardens, secondary forests, and cacao plantations in the same area [24]. Accordingly, these forests could be more preferred as a bear cuscus habitat, owing to the potential presence of plant species that serve important functions for this animal. In North Sulawesi, the talaud bear cuscus was observed to be highly dependent on the primary forest [6], and thus it served as the key habitat for this bear cuscus species [24]. It is consequently likely that the primary forest in LnDF is similarly important to the sustainability of the bear cuscus population (namely 4) inhabiting it. Meanwhile, populations 5 and 6 in LnDF used secondary forest significantly more than they did shrubland and farmland. The farmland in LnDF consisted of *Coffea* sp., which is unused by the bear cuscus due to its small tree characteristics, as well as the absence of large trunks and branches.

In both LMDF and LMEF, secondary forest was used more than shrubland by each population, with the most signficant usage occurring in LMDF. Research in Southeast Sulawesi recorded the bear cuscus in the secondary forest of Buton and Kabaena islands [10]. This was also the case with populations 1 and 2 in LMDF, which were found in the secondary forest occupying *Albizia procera*, *Alstonia scholaris*, and *Pinus merkusii*. These species were used as both a shelter and diet source by the bear cuscus.

4.2. Bear cuscus habitat vegetation composition

Of the studied growth form categories, trees and poles were the most essential to bear cuscus daily activities. As a dominant tree species in LLF, *Alstonia scholaris* was considerably important to the bear cuscus, because of its contribution to the animal's diet. A pair of bear cuscuses were encountered at this tree species during data collection, while a report from local guides also confirmed that bear cuscuses were seen occupying *A. scholaris*. A previous study in four provinces of Sulawesi also mentioned that

the bear cuscus occupied *A. scholaris* as its sleeping tree [12]. However, the regeneration of this species seemed low since none of the sapling and seedling categories of *A. scholaris* were sampled in LLF during the research. *Melicope latifolia* had the largest canopy coverage of the tree species in LLF. This species is also a part of the bear cuscus diet, and with its large canopy area, *M. latifolia* serves a double function for the species, as both food and a resting place. As a dominant species in the pole category in LLF, *Litsea mappacea* might also continue to be dominant when it reaches the tree category. This is advantageous since *L. mappacea* were used by the bear cuscus as its diet and a bridge tree, indicated by the claw marks found on this plant species.

In LnDF, many individuals of *Myristica impressa*, the tree species with the highest density and IVI, were found to contain claw marks, highlighting that they had been frequented as a bridge tree to help bear cuscuses traverse across the landscape. Many of the species identified as part of the bear cuscus' diet were also found in the vicinity of *M. impressa.* The fact that *M. impressa* also had the highest canopy cover in LnDF might have contributed to the proclivity of the species to use it as a resting tree, due to the dense canopy, which helps to conceal them. *M. impressa* also co-dominated with *Syzygium aqueum* in the pole category. Both *M. impressa* and *S. aqueum* appeared to have good regeneration, as indicated by their saplings' and seedlings' high density and IVI values. The bear cuscus also presumably used *S. aqueum* as a bridge tree, based on the claw marks discovered on different individuals of this species.

In LMDF, *Polyscias diversifolia*, the dominating species in the tree and pole categories, is also known to be an important component of the bear cuscus' diet. Nevertheless, its regeneration seemed to be low, based on *P. diversifolia* saplings' low IVI value and the lack of seedlings sampled in this ecosystem. Another important tree species (according to its vegetation parameters) in LMDF was *Pinus merkusii*. In spite of its needle-leaved characteristics, which should ostensibly make it less preferable, direct observations showed a bear cuscus sleeping on a *P. merkusii* tree. The bear cuscus used the dense part of the tip of the tree's branch for concealment and sleeping. A previous study in HUEF similarly reported that bear cuscus feces signs were found in the pine forest [8]. In addition, the tree species *Aleurites moluccanus* was found to have a notably large canopy coverage, and thus was often used by the bear cuscus for concealment and as a shelter for resting. That said, both *P. merkusii* and *A. moluccanus* indicated low regenerations in LMDF, since none of these species were sampled in the pole, sapling, and seedling categories.

In contrast to the pattern found in the other ecosystems, the most dominant species in the tree and pole categories in LMEF, *Polyscias nodosa*, was not found in the bear cuscus diet, and a claw mark was found only on one occasion, consequently showing no indications that *P. nodosa* was important to the bear cuscus, either as a source of food or for locomotion. Meanwhile, as previously noted, the co-dominating tree species, *P. merkusii* and *A. moluccanus*, are known to serve important functions in providing shelter and concealment, but are not factors with respect to the diet of the bear cuscus. As in the case of LMDF, the regeneration of these co-dominating tree species appeared to be low in LMEF. Overall, none of the most dominant tree and pole species in LMEF were part of the bear cuscus' diet. This likely explains the low number of presence signs in LMEF (the fewest among all ecosystems), as the bear cuscus tends to prefer habitats that contain a high level of diet availability.

4.3. Bear cuscus habitat vegetation diversity

Both ecosystem types found in BBNP bore higher diversity compared with those in HUEF. The LLF ecosystem reportedly has an extremely diverse flora [26], rich in species, and differing significantly in floristic structure and composition [27]. The high diversity in LLF might be due to its varied microhabitats and the topographic heterogeneity of its karst hills [26], factors which may be beneficial to the bear cuscus in supplying it with a wide diversity of plants to be used as food and shelter.

Despite their adjacency to one another, the structural and compositional similarities between ecosystem types were relatively low. This was probably caused by each ecosystem's differing environmental parameters—i.e., soil conditions, microclimates, elevation, and light intensity—which impact the types of plant species able to grow in each ecosystem, as well as their densities, frequencies,

and dominancies. For bear cuscuses, this ecosystem variability could similarly be beneficial to their persistence, owing to their adaptability within this range of conditions.

4.4. Bear cuscus habitat environmental conditions

Environmental conditions had slight to substantial differences across ecosystem types, with each ecosystem's respective bear cuscus population adapting to its home range's specific conditions. Between the four ecosystem types, the mean air temperature did not range widely, suggesting that the bear cuscus occupied habitats with similar mean temperature conditions. LnDF had the lowest mean air temperature, due to its high altitudinal location compared with the other ecosystems. The elevations where encounters with the bear cuscus took place differed significantly between ecosystems, indicating that bear cuscuses are able to occupy a wide range of elevations, from lowland to midland (ranging 268–860 masl). Even so, bear cuscuses are commonly found in the lowland forest from sea level to over 600 masl [7]. The ability to adapt to the differences in conditions is possibly due to the availability of plant resources, of which there were plenty at the relevant elevation of each ecosystem. The effect of this is that it makes it unnecessary for bear cuscuses to venture far to fulfil their needs, thus resulting in them having a small home range. Meanwhile, the mean air humidity range did not differ significantly, with a difference of 5% between all four ecosystem types. This indicates that the bear cuscus habitats were consistent with each other in terms of air humidity.

The talaud bear cuscus reportedly occupies a slope of approximately 0–14º in Salibabu Island, North Sulawesi [28], concurring with our results, where the mean slope in LLF, LnDF, and LMEF was similar (approximately 17º), while LMDF had the highest mean slope (26º). The difference in the case of this research is likely related to the bear cuscus occupying a higher elevation in BBNP and HUEF, in contrast to Salibabu Island, where the talaud bear cuscus was recorded only at <200 masl [28]. Habitat conditions with steep slopes tend to be less accessible by predators and humans, thus presumably serving as a safe place for the bear cuscus. Meanwhile, because the bear cuscus relies heavily on contiguous canopy cover [5, 6], light penetration through the canopy layer of bear cuscus habitats is consequently expected to be decreased [29], as was found in the relatively low mean light intensity in LLF, LnDF, and LMEF. The results also showed that the mean canopy cover among all ecosystems was >70%, further suggesting that the bear cuscus occupied habitats with high canopy cover regardless of the ecosystem type. A high canopy cover may consequently be an indicator of the bear cuscus' presence [11].

4.5. Diet of the bear cuscus

As the only folivore arboreal mammal in Sulawesi, the bear cuscus occupies its own niche in Sulawesi forest canopies. The results showed that this diurnal marsupial mainly consumed young leaves and leaf buds, probably because their nutrition tends to be higher in protein and lower in condensed tannin and lignin [1, 30]. Young leaves are more easily digestible compared with mature leaves due to their lower crude fiber [1, 31]. The bear cuscus rarely fed on mature leaves [1], as our observations revealed, with an individual found consuming the mature leaves of *Ficus sumatrana* only on one occasion. However, a previous study in HUEF stated that the bear cuscus consumed mature leaves of *Ficus* sp., on more than one occasion [13]. Fruits and flowers also constituted a minor part of the bear cuscus diet [1, 12], especially in the dry season, when young leaves and leaf buds availability was lower.

The bear cuscus fed on 55 species of plants, which is 47% of the total 117 plant species recorded in the field. It showed a preference for young leaves regardless of the plant species [1]. Being the most-consumed plant family by the bear cuscus, Moraceae's leaves are suitable as a protein source [32], and could play a role in supplementing energy intake [33]. Of the 16 plant species in the Moraceae family eaten by the bear cuscus, 14 of them constituted *Ficus* genera. Although Moraceae's members might not be the most nutritive species [33], their availability in terms of abundance—particularly among *Ficus* species—nevertheless provides an ultimately positive trade-off in the fulfillment of the bear cuscus' basic nutritional requirements. A previous study in BBNP reported that the bear cuscus fed on *Ficus ampelas* and *Ficus racemosa* [9], which was confirmed in this study, specifically in terms of their consumption of the young leaves. Based on the information provided by the local guides, another

member of Moraceae, *Artocarpus heterophyllus*, was also eaten by the bear cuscus. A previous study accordingly found that *Artocarpus dadah* and *Artocarpus elasticus*, respectively, were part of the bear cuscus' diet in North Sulawesi [1], and Southeast Sulawesi [5].

Garuga floribunda and *Dracontomelon dao*, which were identified from feed remains, are the two most preferred species of the bear cuscus diet in North Sulawesi [1]. *Koordersiodendron pinnatum, Cananga odorata, Ficus variegata*, and *Syzygium* sp., which were known to be consumed by the bear cuscus based on information obtained from the local guides, were also being consumed by the bear cuscus in North Sulawesi, Gorontalo, Central Sulawesi, and South Sulawesi [1, 11]. Plant species in the bear cuscus diet that was previously recorded in BBNP and HUEF by direct observations were *Dracontomelon dao, Ficus* sp., *Homalanthus populneus, Diospyros celebica,* and *Palaquium obovatum* [9, 13]. The plant species fed by the bear cuscus based on direct observation were consumed by the following age structure of bear cuscus: *Sterculia foetida* by an adult male and adult female; *Alstonia scholaris* by an adult female; *Ficus ampelas* and *Albizia procera* by both adult female and young bear cuscus; *Baccaurea nanihua* and *Terminalia supitiana* by a juvenile male; *Pterocarpus indicus* by a juvenile female; and *Ficus sumatrana* by a young bear cuscus..This research yields additional information of 15 species of plants in the bear cuscus diet in those aforementioned protected areas based on direct observations and feed remains.

4.6. Implication for bear cuscus conservation

In order to maintain the quality of the bear cuscus' habitat, a factor of which is its diet availability, a conservation strategy should focus on protecting the intactness of canopy cover in primary and secondary forest, especially in LnDF, where the habitat proportion used by the bear cuscuses was significantly high. The LnDF ecosystem in BBNP, unlike the lowland dipterocarp forest [34], did not consist of many commercial timber species. However, this ecosystem is under the constant threat of forest conversion—being located adjacent to human settlements—something to which forest areas situated at the forest–human interface are especially prone [35, 36], and leads to a decrease in habitat quality. Declining habitat quality is indicated by the reduction in canopy cover [36], a habitat property on which bear cuscuses rely heavily.

Members of the Moraceae family have been widely known to be the source of food of many frugivore vertebrates [37]. The fact that their leaves are also essential for the folivorous bear cuscus showed that Moraceae is truly an important plant family in the forest ecosystem. *Ficus* species, which are members of Moraceae, encompassed the major proportion of the bear cuscus diet. These trees are known to be adaptable to various environments [38], and thus are a ubiquitous, and consequently reliable, food source for the bear cuscus. However, the rapid destruction of Indonesia's lowland area, mainly by way of land clearing for timber extraction, agricultural land, plantations, and mining [38], is of concern for this species, as the Indonesian lowland is known to be rich in *Ficus* species. Although most of *Ficus*' mature individuals are of practically no or little commercial value [38, 39], another subset of the Moraceae family from *Artocarpus* is known to be a minor commercial timber [40]. As a consequence, curtailing deforestation is critical to maintaining the existence of Moraceae' members, especially *Ficus* species, which are commonly found in primary and secondary lowland forest [38], and form part of the bear cuscus' vital habitat.

5. Conclusion

Our results suggest that the bear cuscus used secondary forest more than other land cover types in the ecosystems of LnDF, LMDF, and LMEF, while underusing the secondary forest in LLF. Bear cuscuses were not highly dependent on primary forest, due to the species' adaptability to using other types of land cover, which paradoxically can expose it to potential harm from humans, including capture. Nevertheless, primary forest is still an essential part of the bear cuscus' habitat. Most of the dominating tree species in LLF, LnDF, LMDF, and LMEF, which were *Alstonia scholaris, Myristica impressa,* and *Polyscias diversifolia,* were used by the bear cuscus either as a resting place or source of food. Overall, the ecosystem types where the bear cuscus populations occurred were dissimilar in their vegetation

structure and composition, suggesting that the bear cuscus could occupy various ecosystems as long as the plant resources necessary for its diet and usage as shelter are readily available. In general, bear cuscuses occupied habitats that were similar in their environmental parameters, except for elevation, which varied across ecosystems. Vegetation with high canopy cover was the main requirement for the bear cuscus' habitat. Meanwhile, its diet consisted of 55 plant species belonging to 22 families, with the members of the Moraceae family being the most-consumed, and the most commonly eaten parts being young leaves and leaf buds. Protection of the Moraceae family, as well as the intactness of canopy cover in secondary and primary forest is needed, to ensure the survival of this threatened endemic marsupial.

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