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The two faces of Mt Gede, Java –
Species richness, composition and
zonation of epiphytic bryophytes

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The two faces of Mt Gede, Java – Species richness, composition and zonation of epiphytic bryophytes

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ABSTRACT

Bryophytes have been included in rather few studies of elevational gradients and studies on epiphytic bryophytes on different slopes of a single mountain have not been conducted in Indonesia. This research aims to compare species richness pattern, species composition, and zonation of epiphytic bryophytes on tree trunks on two different slopes of Mt Gede, West Java, Indonesia. We established an elevational transect on the North-North-East (Cibodas) and the South-South-West (Selabintana) slopes of the mountain. The transects ranged from 1500 to 2700 m each and sampling was carried out at 200 m intervals. The Cibodas slope is richer than the Selabintana slope, with 160 species (71 mosses and 89 liverworts) compared to 149 species (57 mosses and 92 liverworts), respectively. Species richness pattern on both slopes showed quadratic responses for mosses and cubic responses for liverworts. Pairwise elevation comparison between slopes showed that species composition is significantly different except for the highest plot (2700 m). Pairwise elevation comparison within the two transects revealed significant species composition changes at different elevations, indicating the presence of an elevational zonation of epiphytic bryophytes along the slopes. Based on overall bryophyte species composition, five elevational zones were recognized on each slope.

KEY WORDS

Elevational gradient,
mountain slope,
mosses,
liverworts,
Indonesia.

RÉSUMÉ

Les deux visages du mont Gede, Java – Richesse en espèces, composition et zonation des bryophytes épiphytes. Les bryophytes n'ont été considérés que dans peu d'études de gradients altitudinaux. Les études sur les bryophytes épiphytes le long des pentes d'une même montagne n'ont pas été menées en Indonésie. La recherche, présentée ici, compare le patron de richesse en espèces, la composition spécifique et la zonation des bryophytes épiphytes sur des troncs d'arbres de deux pentes différentes du mont Gede, Java ouest, Indonésie. Un transect altitudinal a été réalisé sur les pentes nord-nord-est (Cibodas) et sud-sud-ouest (Selabintana) du mont Gede. Les transects organisés entre 1500 à 2700 m et l'échantillonnage ont été conduits tous les 200 m. La pente Cibodas avec 160 espèces (71 mousses et 89 hépatiques) est plus riche que la pente Selabintana, avec 149 espèces (57 mousses et 92 hépatiques). Le patron de richesse spécifique sur les deux pentes a montré des réponses quadratiques pour les mousses et cubiques pour les hépatiques. La comparaison par paires entre les pentes a montré que la composition des espèces est significativement différente sauf pour les points les plus hauts (2700 m). La comparaison par paires de l'altitude dans les deux transects a révélé des changements significatifs de la composition spécifique à différentes altitudes, montrant la présence d'une zonation altitudinale des bryophytes épiphytes le long des pentes. Sur la base de la composition spécifique globale des bryophytes, cinq zones altitudinales ont été reconnues sur chaque pente.

MOTS CLÉS

Gradient d'altitude,
aspect de la pente,
mousses,
hépatiques,
Indonésie.

INTRODUCTION

Biodiversity changes along elevational gradients have fascinated scientists around the world, starting in the early 1800s with Humboldt in the Ecuadorian Andes, Darwin in the Chilean Andes in 1839 and 1859, and Wallace in Indonesia in 1876 and 1878 (Lomolino 2001). Various aspects of species response to the environmental differences along these gradients have been addressed since then. For bryophytes, these aspects include: 1) species richness patterns, composition, distribution, biomass, cover, and life form changes; 2) bryozone formation based on those community descriptors and assessment of the significance of certain taxa for each zone; 3) comparison between mountains; and 4) understanding the factors influencing the subjects above.

Few studies specifically dealt with richness and composition of epiphytic bryophytes along elevational gradients (e.g. Van Reenen & Gradstein 1983; Wolf 1993; Mucina *et al.* 2000; Ah-Peng *et al.* 2012; Sanger & Kirkpatrick 2015; Song *et al.* 2015; Tabua *et al.* 2017), and even fewer focused on South-East Asian countries (Thailand, Chantanaorrapint 2010; Indonesia, Gradstein & Culmsee 2010; Permadi 2015; Malaysia, Suleiman & Jotan 2015). As in other groups of organisms (Rahbek 1995; 2004; Nogués-Bravo *et al.* 2008; Fischer *et al.* 2011), the most common pattern observed for epiphytic bryophytes is the hump-shaped (quadratic) pattern. While species richness was shown to follow a common pattern, species composition changes along the elevational gradient were not as clear. Kessler (2000) found distinct elevational boundaries in the floristic composition of epiphytic bryophytes in a Colombian transect analyzed by Wolf (1993), but those boundaries were not distinctly detected along a Peruvian transect studied by Gradstein & Frahm (1987). Variation within one transect was observed by Sanger & Kirkpatrick (2015), where moss species com-

position was similar between the two highest elevations and most significantly different between the lowest ones. Distinct epiphytic bryophyte communities were recorded on eastern Viti Levu, Fiji Islands (Tabua *et al.* 2017). Floristic composition of bryophytes, species numbers, the combination of those two, estimation of cover, the spectra of life form, and phytomass estimation were used to infer forest zonation (Frahm 1990; Frahm & Gradstein 1991; Frahm *et al.* 2003). In South-East Asia, studies of the bryophyte zonation and the species associated with them were conducted on Huon Peninsula of Papua New Guinea (Enroth 1990) and Mt Kinabalu (Frahm 1990; Kürschner 1990; Frey *et al.* 1990).

Very few studies of elevational gradients included different slopes of the same mountain. Van Reenen (1987) summarized a comparison of the three Colombian Cordilleras using total percentage cover of terrestrial and epiphytic bryophytes, showing differences in zone boundaries between east and west slopes. Subsequently, Gradstein *et al.* (1989) compared two slopes of the central of the three Cordilleras, where the wet western slope has more understory bryophyte species than the drier eastern slope. No studies have been conducted in South-East Asia comparing different slopes of a mountain.

In a study on the elevational distribution of lichens and mosses on Mt Gede, West Java, Indonesia, Seifríz (1924) recognized two moss-rich zones on the Cibodas slope of the mountain, each with a distinct species composition. The first zone was located at *c.* 1700–2100 m a.s.l. and the second at *c.* 2400–2700 m. According to Seifríz (1924), the zones below 1700 m and above 2700 m were moss-poor zones dominated by lichens. Enroth (1990) argued that Seifríz's collecting efforts were insufficient and that some species reported to be exclusive to Seifríz's zones were actually widespread. He then mentioned that there were separate moss



FIG. 1. — Mt Gede, showing the SSW (left side) and the NNE (right side) slopes.

zones, but they were not as clear-cut as Seifríz suggested. The existence of what seemed like two hump-shaped patterns of bryophyte species richness on this mountain, each with a distinct species composition, and the question whether the same zonation occurs on other slopes of the mountain, still needs to be investigated.

Here we deal with the elevational gradients of epiphytic bryophytes of Mt Gede by comparing the North-North-East (NNE) slope with the South-South-West (SSW) one in terms of species richness and composition. We hypothesize that a hump-shaped species richness pattern exists on each slope for epiphytic mosses, liverworts, and total bryophytes. Species composition is hypothesized to indicate the presence of an elevational zonation corresponding to vegetational and topographic differences within slope, and to differ between slopes at the same elevation due to climate. We further discuss the zonation formed by dissimilarities of species composition in the light of climate and vegetation differences.

MATERIAL AND METHODS

STUDY AREA

The study was conducted in Gede-Pangrango National Park, West Java, Indonesia. It is the oldest National Park in Indonesia and encompasses two volcanoes, Mt Gede (2958 m a.s.l.) and Mt Pangrango (3109 m). Both mountains are connected through a saddle at approximately 2400 m. Following Van

Steenis (1972), the vascular plant vegetation consists of three zones, the Submontane (<1500 m), Montane (1500–2400 m), and Subalpine (>2400 m) zone.

SAMPLING

Along an elevational gradient ranging from 1500 to 2700 m, bryophytes were sampled in two transects on Mt Gede: one transect on the NNE slope explored through the Cibodas track and the other transect on the SSW slope along the Selabintana track (Fig. 1). Along each transect, seven sample sites were chosen with 200 m intervals. At each site, ten trees with diameter at breast height (DBH) larger than 20 cm were sampled. Trees selected were separated from each other by at least 15 m, belonged to different species and differed in bark texture as much as possible. Tree species, DBH and elevation above sea level of each tree were recorded. At higher elevations, where tree diameters were smaller, we summed up smaller trunks of the same tree in order to balance sampling effort. Epiphytic bryophytes (mosses and liverworts) were collected from the first zone of tree zonation (Johansson 1974; 0–2 m above ground). All material associated with this study is vouchered and deposited at Cibodas Botanic Garden Herbarium (CHTJ). Voucher specimens were identified by standard practice of using identification keys, mainly Bartram (1939), Eddy (1988, 1990, 1996), and Gradstein (2011), and followed the nomenclature within “Tropicos” (n.d.) and Söderström *et al.* (2010, 2016). Only specimens identified to species level were used in the data analysis. The identification results were recorded as presence and absence

of species per tree per elevation site, representing species richness per elevation.

DATA ANALYSIS

All statistical analyses were performed using R software (R Core Team 2018) packages. Overall species richness similarity between Selabintana and Cibodas slope was tested using permutation test with function 'independence_test' in 'coin' package (Hothorn *et al.* 2008). Multiple pairwise comparisons of species richness among elevations from both slopes were tested using Kruskal-Wallis test. Dunn post hoc test with p-values adjusted with Benjamini-Hochberg method was performed following rejection of null hypothesis of Kruskal-Wallis test. Dunn tests were performed using 'FSA' package (Ogle *et al.* 2018) function 'dunnTest'. Correlations among variables were checked using correlation test with Spearman index. Correlation test function 'rcorr' was used from 'Hmisc' Package (Harrell Jr. *et al.* 2018). These tests were performed to match the data properties following data exploration procedure by Zuur *et al.* (2010).

Generalized Linear Models (GLM) with Poisson distribution and log link were used to relate species richness and elevation, with tree surface area added as covariate. Since overdispersion was detected, the standard errors were corrected using quasipoisson-GLM models. Generalized Linear Models were performed using 'glm' function. Comparison of full model (polynomials of third-degree order) with simpler models was used to choose for best model. Nonsignificant terms were dropped stepwise by eliminating the most complex term and re-running the selection until only the significant term and the lower order term were left. Best models were chosen after running diagnostic tests.

The relation between species composition and elevation was analyzed using Permutational Multivariate Analysis of Variance (PERMANOVA) with Bray-Curtis dissimilarity index. The homogeneity of dispersion on the species composition was checked using Permutational Analysis of Multivariate Dispersions (PERMDISP). Each elevation site was used as grouping. Permutation tests (9999 for PERMANOVA and 999 for PERMDISP, respectively) were applied to test the significance. Package 'vegan' (Oksanen *et al.* 2018) functions 'adonis' and 'betadisper' were used to compute PERMANOVA and PERMDISP, respectively. Species composition of a particular elevation was assigned to a different zone than the adjacent elevation when PERMANOVA results showed significant p-values ($p \leq 0.01$) and PERMDISP showed non-significant p-values.

Indicator Species Analysis was conducted to test whether zones distinguished by their bryophyte species composition were associated with elevation. The Indicator Species Analysis was performed using 'indicspecies' package (De Cáceres & Legendre 2009) functions 'multipatt' with 9999 permutations. Indicator species were selected when the Squared Indicator Value $>30\%$ and Benjamini-Hochberg p-adjusted value = 0.05, the latter correcting for false positives in the original, lower p-values that resulted from the analysis (De Cáceres & Legendre 2009).

RESULTS

SPECIES RICHNESS

The Cibodas slope yielded a higher number of bryophyte species (160, of which 71 mosses and 89 liverworts) than the Selabintana slope (149, of which 57 mosses and 92 liverworts) ($Z = -3.1451$, $p\text{-value} = 0.0017$), as shown in Figure 2. Overall species richness of bryophytes in each elevational belt was higher on Selabintana slope, and species richness of liverworts was generally higher than that of mosses on both slopes, albeit not significantly (data not shown). Exceptions were observed at 1500 and 1900 m on Cibodas slope, where richness of mosses was higher.

SPECIES RICHNESS PATTERNS

The variable 'tree surface area' was eliminated during the process of selecting the best model, leaving elevation as the only variable in the model. Total bryophyte species richness showed a significant quadratic response pattern, resulting in a hump-shaped curve for Cibodas slope that peaked at 2000 m (Fig. 3A). For Selabintana slope, in contrast, a cubic (hump-shaped, then increasing) response was observed peaking at 1900 m (Fig. 3A). Both Cibodas and Selabintana species richness showed a quadratic response pattern for mosses and a cubic pattern for liverworts (Fig. 3B, C). Moss species richness peaked at 1900 m on the Cibodas slope and at 2100 m on Selabintana, whereas liverwort richness peaked at 1900 m on both slopes and increased again above 2400 m.

SPECIES COMPOSITION

The PERMANOVA analyses for pairwise elevations within each slope (Table 1A) revealed different species compositions of bryophytes on both slopes, indicating the presence of an elevational zonation of epiphytic bryophytes. The PERMDISP analyses revealed that bryophyte compositions were homogeneous ($p\text{-value} < 0.01$) except for Cibodas pairwise elevation at 2500-2700 m. At corresponding sampling elevations on opposite slopes, total bryophyte species composition was generally different (Table 1B).

The zones and respective indicator species are listed in Table 2 and their diagrammatic visualization is shown in Figure 4. Within each slope, five bryophyte zones were distinguished based on the compositional similarity between elevations (Table 2, Fig. 4). Selabintana slope had a wider zone 2, which was comprised of three sampling elevation instead of only two on Cibodas. On the other hand, zone 5 on Cibodas slope was one sampling elevation wider than the corresponding zone on Selabintana. Other than that, the zonation between those two were similar in width. Except for zone 4 on Selabintana, each bryophyte zone had its own indicator species (Table 2, Fig. 4). No indicator species were shared among zones of Cibodas and Selabintana, except for *Syrrhopodon tristichus* Nees ex Schwägr. in zone 2. On Cibodas slope, 10 species were resolved as indicator species with indicator values ranging from 32.7% to 77.1%, while Selabintana slope had 13 indicator species with indicator value ranging from 31.3% to 90.9% (Table 2).

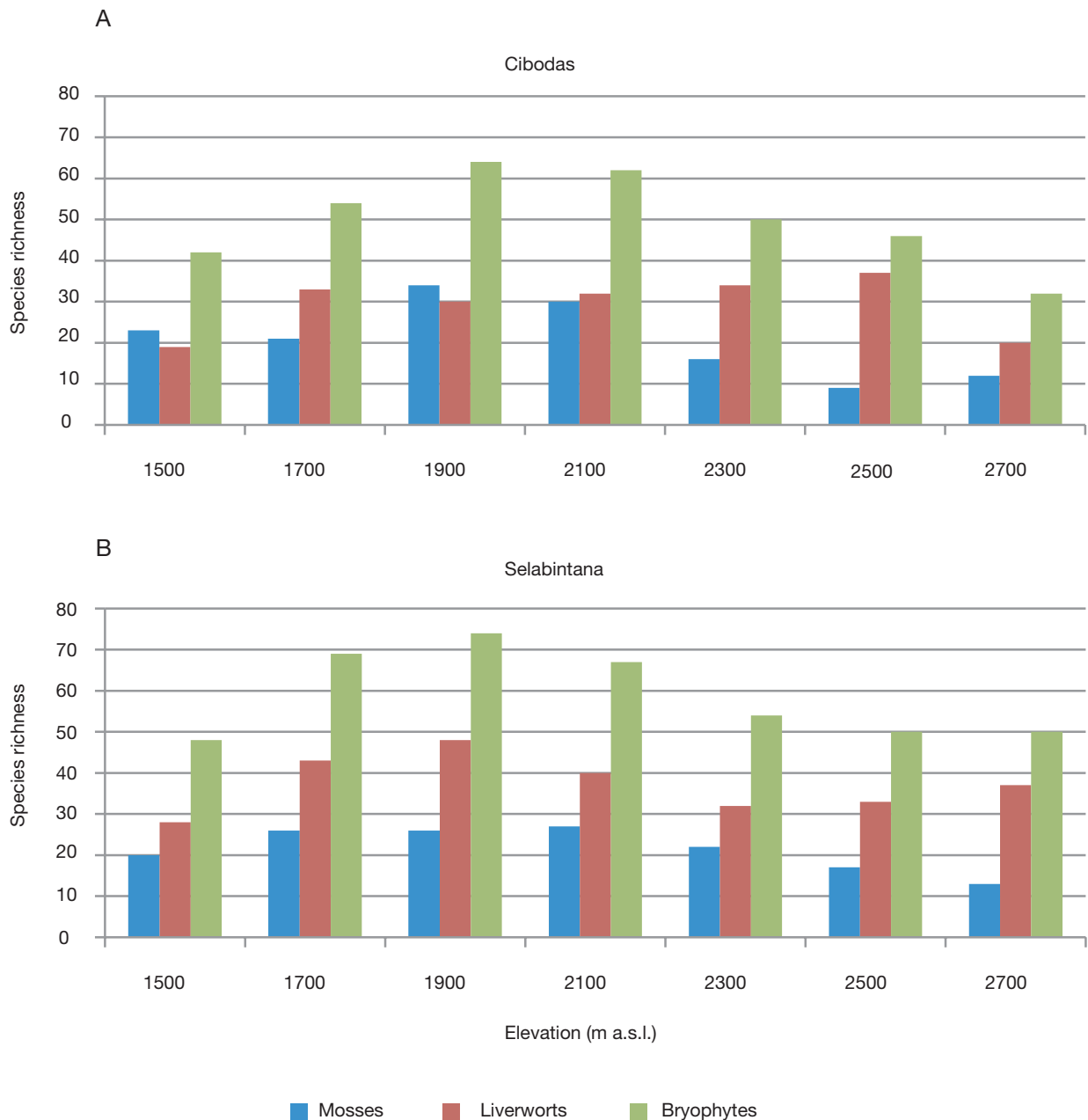


FIG. 2. — Species richness of **A**, Cibodas and **B**, Selabintana slopes along the elevational gradient.

DISCUSSION

Our study shows that elevational gradients of epiphytic bryophytes on Mt Gede are expressed by changes in species richness as well as species composition, and differ among slopes. The differences between slopes seem to be associated with climatic and vegetational differences.

SPECIES RICHNESS: DIFFERENT PATTERNS FOR MOSSES AND LIVERWORTS

While the drier Cibodas slope is overall significantly richer in epiphytic bryophyte species, the wetter Selabintana slope

has more species than Cibodas at corresponding elevations although the differences were not significant. Dearborn & Danby (2017) observed similar patterns in alpine-subarctic plant communities. In that study, the drier, south-facing slope had a higher β -diversity than the wetter, north-facing slope, while the mean species richness per elevation between aspects was similar, which might have been caused by less pronounced vegetation changes on the wetter, north-facing slope. On Mt Gede a more variable topography and more pronounced forest stand changes are seen on the Cibodas slope. Climbing up this slope from lower elevation, one passes a river, small lake, swamp, hot water river, waterfall, and a steep

TABLE 1. — Non-parametric analysis of variance for pairwise elevation comparison within slope **A** and between slopes **B** for Cibodas and Selabintana bryophytes. Pairwise comparisons of group mean dispersions are shown as F ratio and p value (9999 permutations). Pairwise comparisons of permutational analysis of variance are shown as coefficient of determination R² and p value (999 permutations). ** = p ≤ 0.01; *** = p ≤ 0.001.

A	Permdisp		Permanova	
	F	p	R ²	p
Pairwise elevation				
Cibodas				
1500-1700	0.814	0.370	0.155	0.001 ***
1700-1900	0.096	0.760	0.120	0,027
1900-2100	0.255	0.618	0.139	0.005 **
2100-2300	0.000	0.998	0.202	0.001 ***
2300-2500	1.137	0.299	0.173	0.001 ***
2500-2700	21.700	0.0001 ***	0.298	0.001 ***
Selabintana				
1500-1700	0.162	0.697	0.160	0.004 **
1700-1900	0.570	0.458	0.115	0,018
1900-2100	0.580	0.452	0.078	0,138
2100-2300	4.154	0.055	0.258	0.001 ***
2300-2500	3.762	0.067	0.202	0.001 ***
2500-2700	0.114	0.741	0.281	0.001 ***

B	Permdisp		Permanova	
	F	p	R ²	p
Pairwise elevation				
Cibodas-Selabintana				
1500	0.557	0.465	0.156	0.001 ***
1700	0.281	0.602	0.168	0.003 **
1900	0.331	0.572	0.170	0.003 **
2100	0.241	0.630	0.241	0.001 ***
2300	2.111	0.163	0.326	0.001 ***
2500	0.014	0.906	0.308	0.001 ***
2700	17.781	0.0005 ***	0.336	0.001 ***

trail up to the summit, whereas the trail on the Selabintana slope mainly follows a ridge and then passes a river up to the summit, without much topographic variation. The more variable topography and more pronounced forest stand changes on the Cibodas slope probably caused the higher epiphytic bryophytes species richness seen on this slope.

The generally higher liverwort diversity observed on each elevational gradient in this study is in accordance with Frahm (2002), Gradstein *et al.* (1989), Santos *et al.* (2017), Song *et al.* (2015), Tabua *et al.* (2017) and Wolf (1993). In Neotropical moist forests, liverworts are the dominant component in the epiphytic layer (Cornelissen & Ter Steege 1989; Gradstein *et al.* 2001). This is also the case with Mt Gede, where mosses are outnumbered from the very beginning of the elevational gradients. According to Gradstein *et al.* (1989), the ratio of mosses and liverworts reflects the humidity of a location, where a higher proportion of liverworts signifies higher humidity. The higher liverwort richness in Selabintana should reflect the wetter climate on this slope as compared with Cibodas.

The quadratic response pattern for total bryophytes richness on the Cibodas slope, resulting in a hump-shaped curve, confirms previous observations (Wolf 1993; Ah-Peng *et al.* 2012; Sanger & Kirkpatrick 2015; Song *et al.* 2015). However, different patterns were observed for mosses (quadratic) and liverworts (cubic) on both slopes of Mt Gede. A similar cubic pattern was observed for terrestrial bryophytes along

an altitudinal gradient in China (Sun *et al.* 2013). In contrast, Grau *et al.* (2007), Henriques *et al.* (2016) and Tabua *et al.* (2017) did not find differences between mosses and liverworts, both showing quadratic patterns. Another pattern was found by Bruun *et al.* (2006), who observed increasing species richness with elevation for both mosses and liverworts in an alpine environment, the increase being steeper for liverworts. In the Canary Islands, on the other hand, Hernández-Hernández *et al.* (2017) found a significantly quadratic pattern for liverworts but not for mosses. In Cibodas, moss and total bryophyte richness exhibited a similar pattern, while in Selabintana liverworts matched the total bryophyte richness pattern. In the Colombian Andes, Wolf (1993) also observed that the overall bryophyte pattern was mainly determined by the liverwort component, while the moss pattern was similar to that of lichens.

The quadratic response pattern on Mt Gede for total bryophytes is attributed to the suitability of the microclimate at mid-elevation for bryophyte growth. The peak richness of total bryophytes at mid-elevation coincides with maximum humidity due to cloud belt formation at 2000 m (Van Steenis 1972). The decline towards higher elevation is most likely due to the combination of lesser cloud frequency (pers. obs.) and the decrease in tree size above 2000 m (Van Steenis 1972), providing less substrate for epiphytic bryophytes. Another possible explanation for the quadratic pattern would be the Mid Domain Effect (MDE), where the peak of the species richness at mid elevation is formed by the stochastic overlapping of species ranges along the gradient. In the latter case, the pattern observed should be the same for mosses and liverworts, which was not the case in the present study. Grau *et al.* (2007) found quadratic patterns for mosses and liverworts in the Himalayas that peaked at different elevations and argued that such patterns could be explained by the interaction between climate and species richness. They suggested that MDE may not be important for bryophytes. On Mt Gede, the vegetation zonation of the forest stands might explain the cubic pattern for liverworts. The last increase in liverwort richness with elevation occurs at approximately 2400 m and coincides with the upper limit of the montane vegetation zone. Above that elevation the subalpine zone starts, characterized by lower, denser, thinner-stemmed, more open forest with single canopy layer (Van Steenis 1972). This zone promotes liverworts better than mosses, presumably due to the higher light intensity. Increasing humidity along a transect causes an increase in liverwort richness (Frahm & Ohlemüller 2001). More open forest means higher overall light intensity and light transmission to the forest floor, allowing sun-tolerant species to grow at lower heights on the trunks (Acebey *et al.* 2003) and thus adding to liverwort species richness. Another explanation could be non-proportional sampling, with taxa sampled from the smaller trees at high elevation possibly including those of higher tree zones. Since more liverworts are known to inhabit higher vertical zones within a tree in tropical rainforests (Cornelissen & Ter Steege 1989; Wolf 1993; Holz 2003; Mota de Oliveira & Ter Steege 2013), the species richness of liverworts is thus further increased.

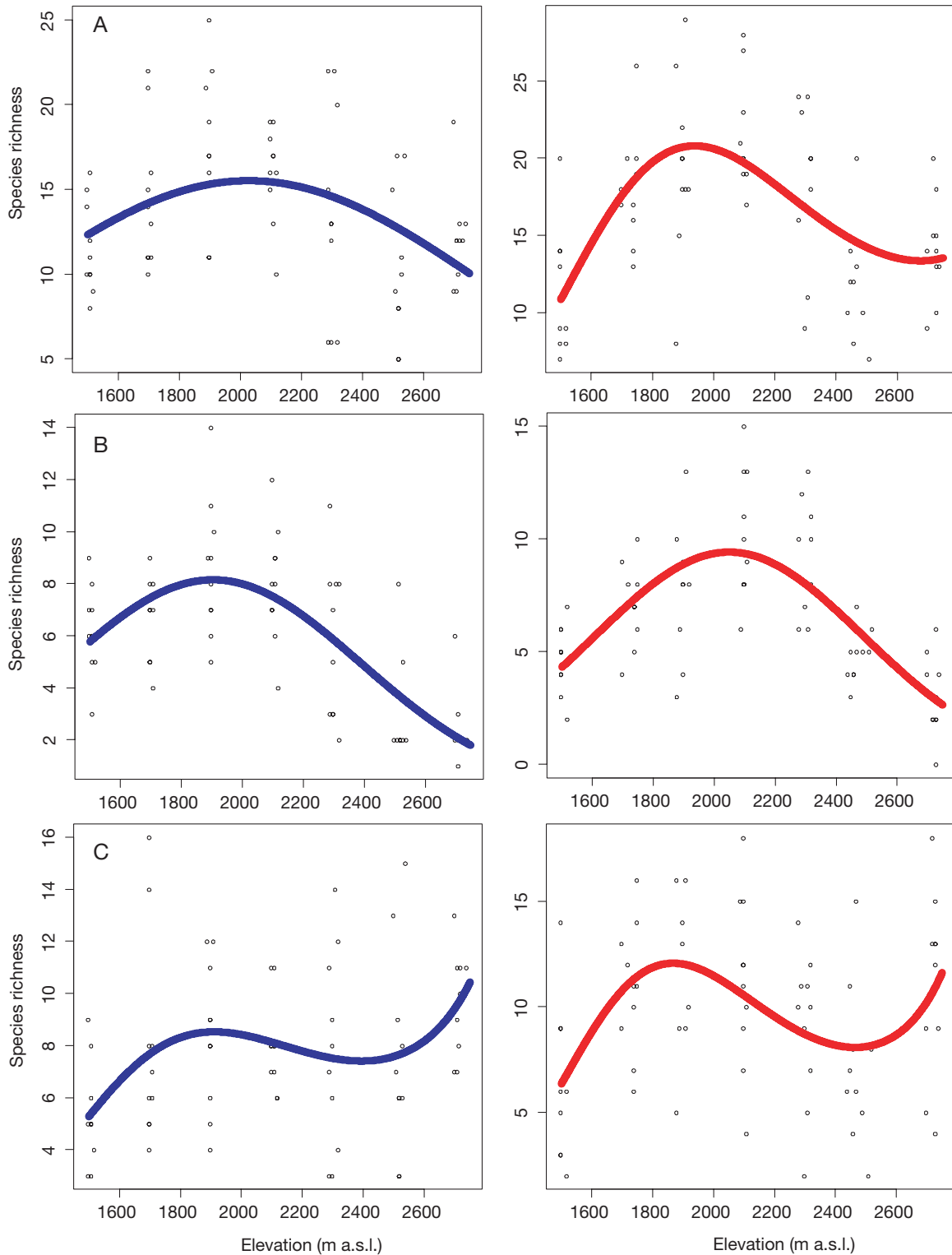


FIG. 3. — The relationship between species richness of **A**, bryophytes; **B**, mosses; and **C**, liverworts and elevation with GLM functions superimposed for the Cibodas (left) and Selabintana (right) slopes.

SPECIES COMPOSITION: SLIGHT DIFFERENCES IN ZONATION ACCORDING TO SLOPE

Comparing pairwise elevations across the Cibodas and Selabintana slopes, in general, species richness did not significantly differ, but species composition did. This might be due

to the different climate on each slope, with Cibodas (NNE) being drier than Selabintana (SSW). The moisture brought by western monsoon winds from the Pacific and Indian Ocean is released as rain on the windward Selabintana slope, leaving the leeward Cibodas slope relatively less wet. The difference

TABLE 2. — Indicator species of elevational zones on the Cibodas and Selabintana slopes. **A** and **B** represent the ‘specificity’ and the ‘fidelity’ components of indicator value. Only $(\text{IndVal})^2 > 30\%$ and $p\text{-adj.} \leq 0.05$ are shown.

Slope	Elevation (m a.s.l.)	zone	Indicator species	A	B	IndVal	(IndVal) ² (%)	p-adj.	
Cibodas	1500	1	<i>Leucophanes angustifolium</i> Renaud & Cardot	1.000	0.400	0.632	40.0	0.007	
		2	<i>Plagiochila spathulifolia</i> Mitt. <i>Syrrophodon tristichus</i> Nees ex Schwägr. <i>Lejeunea micholitzii</i> Mizut.	0.929	0.650	0.777	60.4	0.001	
	2100	3	<i>Hypnodendron dendroides</i> (Brid.) A. Touw <i>Trachyloma indicum</i> Mitt.	1.000	0.400	0.632	40.0	0.005	
		4	<i>Pogonatum cirratum</i> (Sw.) Brid. <i>Distichophyllum brevicuspis</i> M. Fleisch	0.714	0.500	0.598	35.7	0.012	
	2300	4	<i>Trachyloma indicum</i> Mitt. <i>Pogonatum cirratum</i> (Sw.) Brid.	0.546	0.600	0.572	32.7	0.023	
		5	<i>Distichophyllum brevicuspis</i> M. Fleisch <i>Bazzania japonica</i> (Sande Lac.) Lindb.	0.875	0.700	0.783	61.3	0.001	
	2500-2700	5	<i>Bazzania japonica</i> (Sande Lac.) Lindb. <i>Herbertus dicranus</i> (Gottsche, Lindenb. et Nees) Trevis.	0.750	0.600	0.671	45.0	0.002	
		5	<i>Herbertus dicranus</i> (Gottsche, Lindenb. et Nees) Trevis.	0.857	0.900	0.878	77.1	0.001	
	Selabintana	1500	1	<i>Heteroscyphus argutus</i> (Reinw., Blume et Nees) Schiffn.	1.000	0.650	0.806	65.0	0.001
		1700-2100	2	<i>Heteroscyphus argutus</i> (Reinw., Blume et Nees) Schiffn. <i>Syrrophodon tristichus</i> Nees ex Schwägr. <i>Bazzania javanica</i> (Sande Lac.) Schiffn.	0.600	0.600	0.600	36.0	0.013
3			<i>Syrrophodon tristichus</i> Nees ex Schwägr. <i>Bazzania javanica</i> (Sande Lac.) Schiffn.	0.944	0.567	0.732	53.5	0.002	
2300		3	<i>Symphysodontella attenuatula</i> M. Fleisch. <i>Fissidens wichurae</i> Broth. & M. Fleisch	0.842	0.533	0.670	44.9	0.006	
		4	<i>Symphysodontella attenuatula</i> M. Fleisch. <i>Fissidens wichurae</i> Broth. & M. Fleisch	0.909	1.000	0.953	90.9	0.001	
2500		4	—	1.000	0.400	0.632	40.0	0.009	
		5	<i>Plagiochila arbuscula</i> (Brid. ex Lehm. et Lindenb.) Lindenb. <i>Lepidozia stahlilii</i> Steph.	—	—	—	—	—	
2700		5	<i>Plagiochila arbuscula</i> (Brid. ex Lehm. et Lindenb.) Lindenb. <i>Lepidozia stahlilii</i> Steph.	0.900	0.900	0.900	81.0	0.001	
		5	<i>Lepidozia stahlilii</i> Steph. <i>Cylindrocolea kiaeri</i> (Austin) Vána <i>Cryptolophocolea ciliolata</i> (Nees) L.Söderstr.	1.000	0.500	0.707	50.0	0.001	
5		<i>Cylindrocolea kiaeri</i> (Austin) Vána <i>Cryptolophocolea ciliolata</i> (Nees) L.Söderstr.	0.636	0.700	0.667	44.5	0.002		
5		<i>Cryptolophocolea ciliolata</i> (Nees) L.Söderstr. <i>Heteroscyphus aselliformis</i> (Reinw., Blume et Nees) Schiffn.	0.833	0.500	0.645	41.7	0.005		
5		<i>Heteroscyphus aselliformis</i> (Reinw., Blume et Nees) Schiffn. <i>Drepanolejeunea ternatensis</i> (Gottsche) Schiffn.	0.833	0.500	0.645	41.7	0.005		
5		<i>Drepanolejeunea ternatensis</i> (Gottsche) Schiffn. <i>Frullania junghuhniana</i> Gottsche	0.500	0.800	0.632	40.0	0.011		
5	<i>Frullania junghuhniana</i> Gottsche <i>Bazzania praerupta</i> (Reinw., Blume et Nees) Trevis.	0.800	0.400	0.566	32.0	0.024			
5	<i>Bazzania praerupta</i> (Reinw., Blume et Nees) Trevis.	0.625	0.500	0.559	31.3	0.023			

between wet and dry season in the West Javan mountains is not as pronounced as in East Java. Rainfall recordings on Mt Gede’s twin peak Mt Pangrango show that even during the driest months, rain still falls every other day (Docters van Leeuwen 1933; Van Steenis 1972). And since Java is positioned south of the equator, the NE side of Mt Gede receives more sunshine than its SW side (Van Steenis 1972). Similar climatic conditions are observed on Mt Kilimanjaro (Pepin *et al.* 2017) – also located in the southern hemisphere – where the SW slope is generally cooler and moister, and receives sunshine later during the day than the NE slope.

The climatic settings of different slopes influence the vegetation, as observed on Mt Kilimanjaro (Hemp 2006) and on Baima Snow Mountain (Yang *et al.* 2016) where changes in forest species composition along the elevational gradient differ between slopes. This, in turn, together with microclimatic differences, affects the species composition of the epiphytic vegetation component, including the bryophytes. In the case of Mt Gede, there are more bryophyte species in Selabintana at single sampling elevations than in Cibodas, but the differences were not significant.

The forest stand components create a microclimate suitable for particular bryophytes assemblages. The degree of vegetation density around the phorophyte might influence the effect of sunlight and wind at the lower trunk. Király & Ódor (2010) found that sapling density increased the epiphytic bryophyte species richness significantly and had a considerable effect on species composition. In addition, tree species contribute to epiphytic bryophyte composition (Barkman 1958, Sim-Sim

et al. 2011, Mežaka *et al.* 2012) through variation in bark texture (Szövényi *et al.* 2004), bark chemical properties (Mežaka *et al.* 2012, Batista & Santos 2016, Dislich *et al.* 2018), and shaded cover (Ariyanti *et al.* 2008). The more heterogeneous the phorophyte composition, the more variable the bryophyte species composition.

Another factor possibly causing differences in bryophyte composition between the two slopes is human disturbance. Visitors of Gede-Pangrango National Park usually climb up to the peak via the Cibodas track as it is more easily accessible, the main office of the National Park is located at the entrance, more water resources are available on the way up, and the visitor quota allowed to enter daily through this track is three times that of Selabintana (Ketentuan Umum Penda- kian Gunung Gede Pangrango (n.d.); 300 persons per day). Although this study was conducted in sites with minimal human disturbance, it is possible that human activities along the track had influenced the studied bryophyte communities.

BRYOPHYTE ZONATION ON MT GEDE IN A BROADER PERSPECTIVE

Applying the tropical rainforest zonation terminology using bryophytes proposed by Frahm (1990) and Frahm & Gradstein (1991), bryophyte composition changes on Mt Gede correspond with the vegetation zonation in other studies on the Mt Gede-Mt Pangrango twin mountain, as shown in Figure 5.

The numbers and width of zones varied between those studies. A minimum of three zones, Tropical Lower Mon-

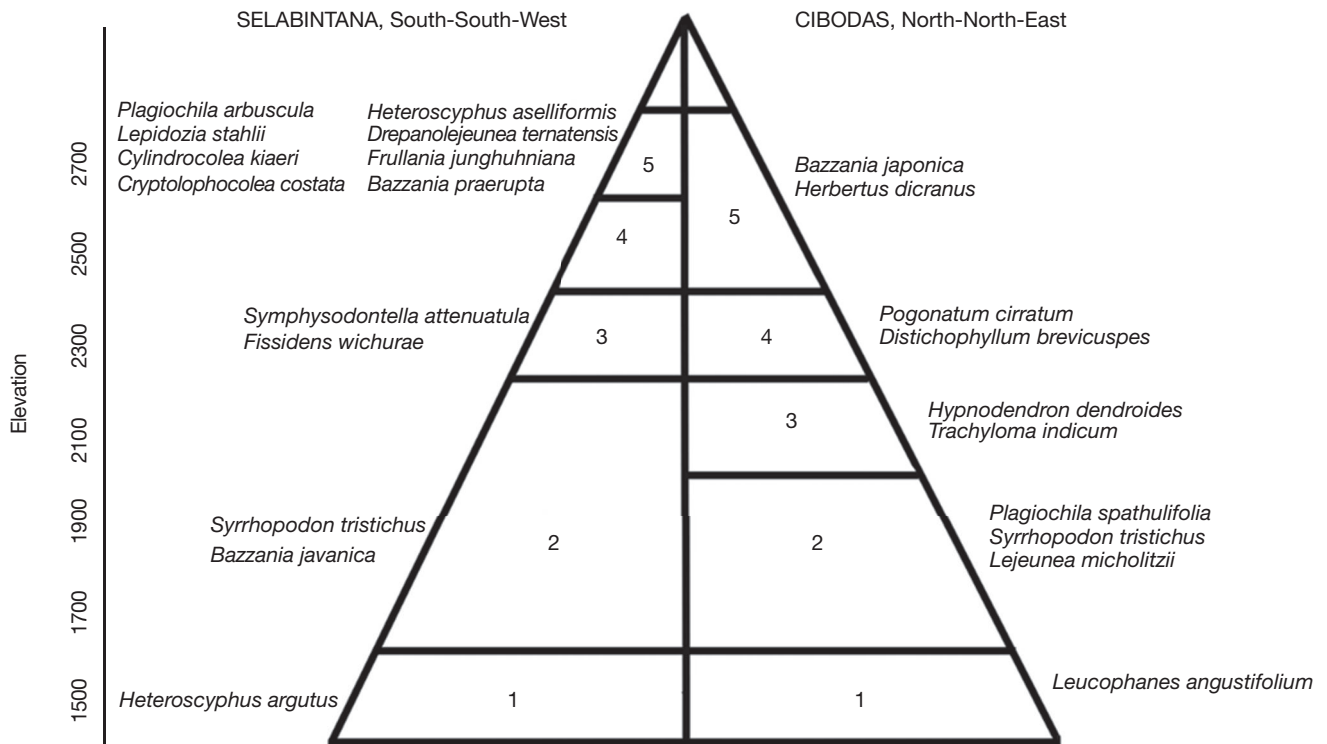


FIG. 4. — Diagrammatic visualization of zonation along the elevational gradient of the Selabintana and Cibodas slopes with their indicator species. For taxa authors see Table 2.

tane, Tropical Upper Montane, and Tropical Subalpine, were recognized in all of them. On Mt Gede, the lowest elevation zone corresponds to the Tropical Submontane zone and the highest to the Subalpine forest of Van Steenis (1972). The Tropical Submontane zone was not part of the transect on Mt Pangrango (Ohsawa 1991) and thus unrecognized. The zones on Mt Gede (zone 2, 4, 5; this study) are mostly narrower than on neighbouring Mt Pangrango (except for zone 2, see below), which may be due to the ‘Massenerhebung’ effect where the width of a forest zone was narrower on the smaller mountain than on the bigger one (Grubb 1971). The wider zone 2 (Tropical Lower Montane zone) on Mt Gede should be due to the wetter climate on the Selabintana slope, as mentioned before. This finding is in accordance with Van Reenen (1987), Gradstein *et al.* (1989), and Frahm & Gradstein (1991) who found that the width of the Tropical Montane zone is narrower on drier slopes, and its boundaries different accordingly. The wider zone 5 (Tropical Subalpine) on the Cibodas slope as shown from the species composition dispersion (PERMDISP) analyses, was due to the nestedness of the species composition, with the species at higher elevation being a subset of the lower one. Phorophyte richness on the Cibodas slope was highly reduced in the summit site and dominated here by *Vaccinium varingiaefolium* Miq., which was also part of the phorophyte composition at lower elevations. The reduced phorophyte richness at the summit might be due to the harsh environmental conditions here, including the effect of toxic substances emitted from the crater of Mt Gede.

Zone 1 (Tropical Submontane) corresponds to Seifriz’s moss-poor *Altingia* zone. The next three zones comprised Van Steenis’ Montane zone. In his elevational zonation scheme of the mountains of Java, Van Steenis (1972) did not divide the Montane zone into subzones. Ohsawa (1991) proposed to divide Van Steenis’ Subalpine zone into an Upper Montane and Subalpine zone, as supported by his recognition of Lower and Upper Montane zones on Mt Pangrango, the twin mountain of Gede. Our study using bryophytes reflects the detailed forest stand zonation of Mt Gede and shows that the Montane zone has three divisions – Tropical Lower Montane, transition, Tropical Upper Montane –, which was also recorded by Arrijani (2008) based on an analysis of tree diversity on the Cibodas slope. These three zones correspond to Seifriz’s *Podocarpus*, herbs, and *Vaccinium* zones, respectively. His observation of the moss-rich zone was also confirmed by the present study in which epiphytic bryophytes peaked in the Tropical Lower Montane zone and then declined in the transition zone. On the opposite slope (Selabintana), Permadi (2015) found a similar bryophyte zonation although he did not further subdivide the Montane zone.

Zone 3 can be regarded as a transition zone between the Tropical Lower Montane and Upper Montane zone, due to its significantly different species composition that consists of a mix of species from adjacent zones. Yamada (1976) mentioned the presence of a forest transition zone on Mt (Gede-) Pangrango, situated on the saddle shared by the two mountains with a maximum width at 2300 m.

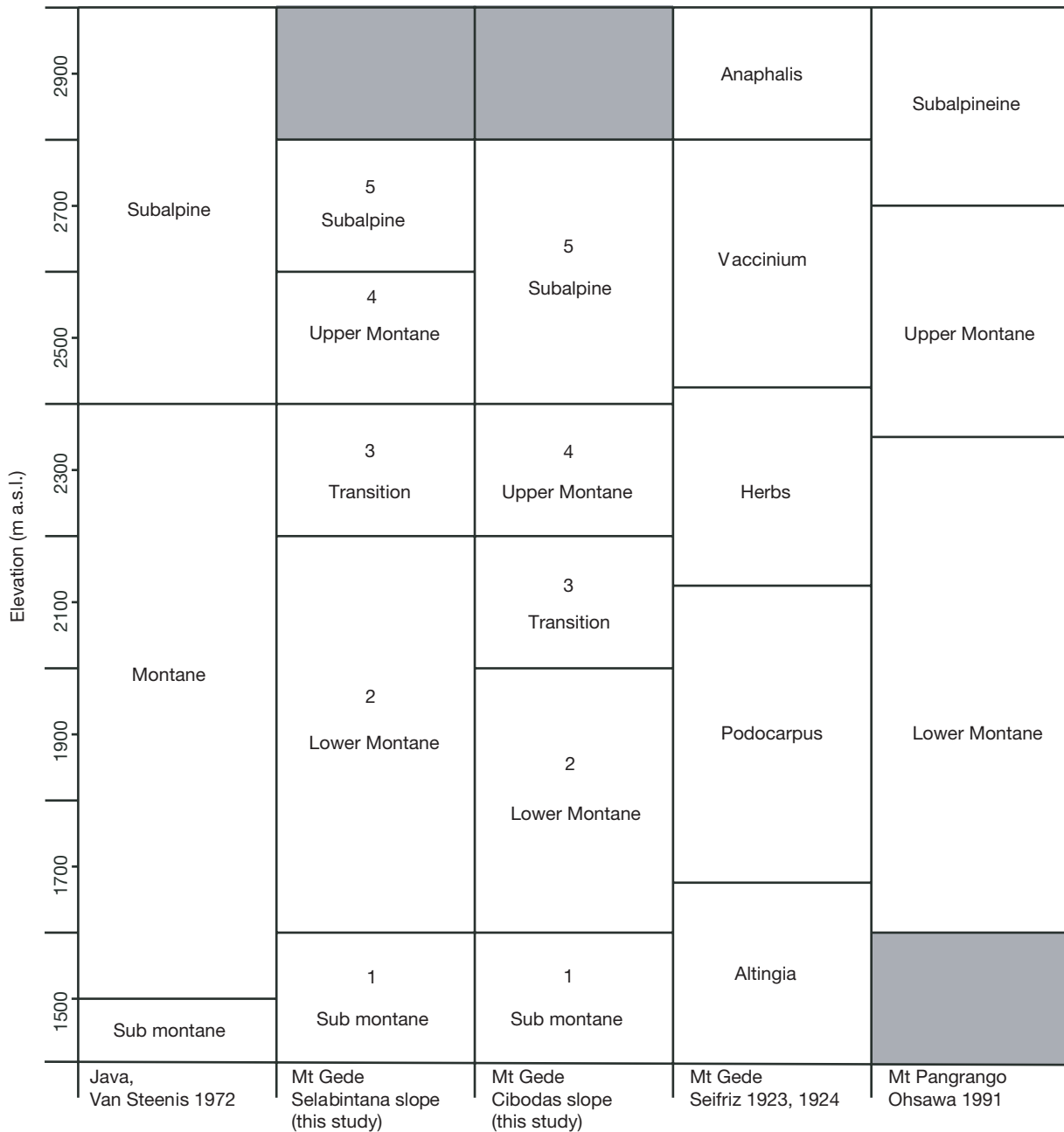


FIG. 5. — Elevational zonation comparison on mountains of Java, especially Mt Gede-Pangrango. Zonations were based on bryophytes coverage (Seifriz 1924), species composition dissimilarity (this study) and higher plants composition (Ohsawa 1991, Seifriz 1923, Van Steenis 1972).

Since bryophyte species composition is influenced by forest stand, the presence of a transitional forest stand along the elevational gradient explains the existence of a bryophyte transition zone. Despite using Yamada’s data, Ohsawa (1991) did not recognize the transition zone and included it in a wider Lower Montane Zone. The methodologies applied by Ohsawa (1991) to determine the zonation of Mt (Gede-) Pangrango probably did not allow for a transition zone to be detected, since such inference would require species turnover analysis (cf. Bach & Gradstein 2011). The Subalpine zone in the latter study coincided within Seifriz’s *Vaccinium* zone (approximately 2400-2700 m). Although described by Seifriz

as the second ‘moss-rich’ zone, the present study found that it is actually a liverwort-rich zone.

The characterization of the zones on the Selabintana and Cibodas slope of Mt Gede by species indicators reinforces the differences in species composition. Different plant communities inhabiting the same zone on opposite slopes were also observed by Kappelle *et al.* (1995) in Costa Rica. Since epiphytic bryophytes are influenced by phorophyte communities, the occurrence of different bryophyte communities in the same zone on opposite slopes is to be expected. Selabintana has more liverworts as indicator species, reflecting the wetter condition and higher liverwort richness on this slope. The

results indicate that altitudinal zonation is more strongly driven by slope conditions than by elevation.

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