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Habitat Ecology, Structure Influence Diversity, and Host-Species Associations of Wild Orchids in Undisturbed and Disturbed Forests in Peninsular Malaysia

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Abstract: As an attempt to examine the causes of forest disturbance and degradation of the orchid community, a comparative study on diversity and ecology in eight undisturbed and ten disturbed forests in Peninsular Malaysia was conducted that varied in areas, elevations, vegetation types, and disturbance regimes. Density and individual-based rarefaction curves were used to describe the abundance. Univariate and multivariate analyses were also performed to explore the associations of species abundance with biotic and abiotic factors. The study reported 239 orchid species belonging to 65 genera. Species richness, abundance, density, and diversity of orchids varied by locality. Higher density of orchids (2.433 plants/km^2) occurred in the undisturbed forests than in the disturbed forests (0.228 plants/km^2). As with the character of undisturbed forests, the temperature was between 27.8 ± 0.3 °C and 31.2 ± 0.2 °C, humid ($77.1 \pm 1.2\%$–$89.6 \pm 0.9\%$), and with low light intensity (23.8 ± 3.3 µmol m^{-2}s^{-1}–171.7 ± 18.8 µmol m^{-2}s^{-1}), thus supporting the high density of the plants. Disturbed forests had higher diversity (H = 4.934 and 1-D = 0.990) and abundance (183 species of 57 genera) but were determined to be highly influenced by the higher abundance of epiphytic orchids on the fallen trees and ease of accessibility in the logged forests. Terrestrial and mycoheterotroph orchids were much lower in density and abundance in the disturbed habitat indicating a gradual reduction in their niche availability following the disturbance. Additionally, the ecology data show that the microclimate conditions of the canopy-covered forest was influenced by proximity to the logged area which had eventually reduced the orchids' habitat quality. Furthermore, the results show that the abundance of epiphytic orchid communities was associated with the host plant characteristics. Host types and bark texture preference were apparent for the epiphytic orchid species, with certain types and textures hosting more orchid species than others. Overall results show that extreme temperature, humidity, and light intensity caused by the canopy opening inflicted damages to the habitat conditions and bark textures of the host plants and limits recolonisation of the orchids in the disturbed forests. The species diversity and density patterns of orchids in undisturbed and disturbed forests revealed in this study provide a baseline for conservationists, policy makers, and forest authorities in expanding the understanding of the forest ecology and vegetation along the disturbance gradient, forest regeneration, and criteria for plant selection for forest restoration in Peninsular Malaysia.

Keywords: diversity; environmental factor; epiphytic distribution; host plant; logging; orchid

1. Introduction

Orchids are diverse and a very good group for studying diversity, ecology, distribution, and host-species associations in undisturbed and disturbed habitats [1]. The diversity study focused on the orchids occurring in Peninsular Malaysia, where previously a total of 982 orchid species were recorded and most of them were epiphytes (personal observation). Apart from focusing on their diversity, ecology, distribution patterns, and conservation,

this paper explores the associations between diversity and distribution of epiphytic orchids and host characteristics in different vegetation types of Peninsular Malaysia. Although the association between epiphyte diversity and different host characteristics are well studied for plants, very little is known about variation in the abundance of epiphytic orchids and their host associations in tropical rainforests. Host plant characteristics play an important role in colonisation of host-dependent species [2–4]. In studies of relationship between tree size and epiphyte species richness, the host's size matters due to greater bark surface available for colonisation on large trees and the creation of additional microhabitats [5,6]. Host position and type, and growth of epiphytic orchid species are influenced by microclimate conditions, including annual precipitation, light intensity, and humidity [3,7]. Conservation-wise, the degree of orchids' host specificity is important to look at, because being host specialists, wild orchids are threatened by co-extinction with their hosts due to habitat alterations and climate change [8–10].

Lack of monitoring programs assessing the before or aftereffects of disturbances in Malaysian rainforests is one of the major limitations to quantifying the commonalities and differences of disturbance effects on forest ecosystem and its inhabitants. Epiphytes are a diverse group with very interesting niche ecology [11–13]. Unlike terrestrial species, epiphytes are highly reliant on their hosts and are thus likely to be affected by host species and host traits [14–17]. Notwithstanding their economical and conservation importance, the understanding of the wild orchid diversity and ecology under wide range of microclimate conditions in the undisturbed and disturbed forests is still rather poor, especially when the impacts come under different disturbance regimes. A comparative study of different undisturbed and disturbed forest types including scoring for different agents of disturbance will give unbiased and general views on the effect of forest and ecological disturbance on the orchid community. Additionally, if only protected areas are targeted, more wild orchids will be lost, and these species could disappear from large areas of former range. Thus, the present study includes several forest types, vegetation types, and disturbance regimes. This diversity and ecology study determines the suitability of the plants, especially trees as protectors and homes to epiphytic plants along with threats and limiting factors.

Specifically, in this paper, the following questions were addressed: (1) Does the diversity of orchids in undisturbed and disturbed forests of Peninsular Malaysia differ? (2) What are the factors determining diversity and composition of orchids in the undisturbed and disturbed forests? (3) What is the significance of ecological alterations on the orchid community in two adjacent forests that are located next to each other or connected to each other, but with distinct levels of disturbance? (4) How much do the number of host plants and host characteristics influence the number of epiphytic orchid species?

2. Materials and Methods

2.1. Study Area

Samplings were conducted between November 2016 and April 2021 in 18 different localities in Peninsular Malaysia (Figure 1). The systematic sampling involved choosing exploration sites in Peninsular Malaysia. We collected information on each of the site conditions (e.g., area, vegetation type, elevation, disturbance regime, and disturbance origin) (Tables 1 and 2). Major disturbances were classified as either natural or anthropogenic in origin. To disentangle the effects of anthropogenic and natural disturbance regimes, there were two main forest types varying in vegetation: undisturbed (Table 1) and disturbed (Table 2) forests, with several subsidiary study sites, eight undisturbed and ten disturbed forests, were selected. The sub-classified disturbed forest types were defined according to the vegetation, disturbance, and period of disturbance. Classification of the vegetation types was based on [18] (modified from [19], and [20] for Bukit Pedu, Kedah. These sites represent some of the major ecosystem and vegetation types in Peninsular Malaysia. To characterise and compare disturbance regimes amongst disturbed forest types, the Disturbance Index (DI) based on five variables (Severity (D), Extension (E), Frequency (F), Duration (D), and Patch Type (PT)) were evaluated following a scoring method and ordinal

variables modified from [21] (Table 3). The DI was calculated by multiplying the assigned scores describing the five disturbance variables: DI = S × E × F × D × P × T. A low DI indicates a low impact of a given disturbance agent for a particular ecosystem, whereas a high DI indicates a large impact.
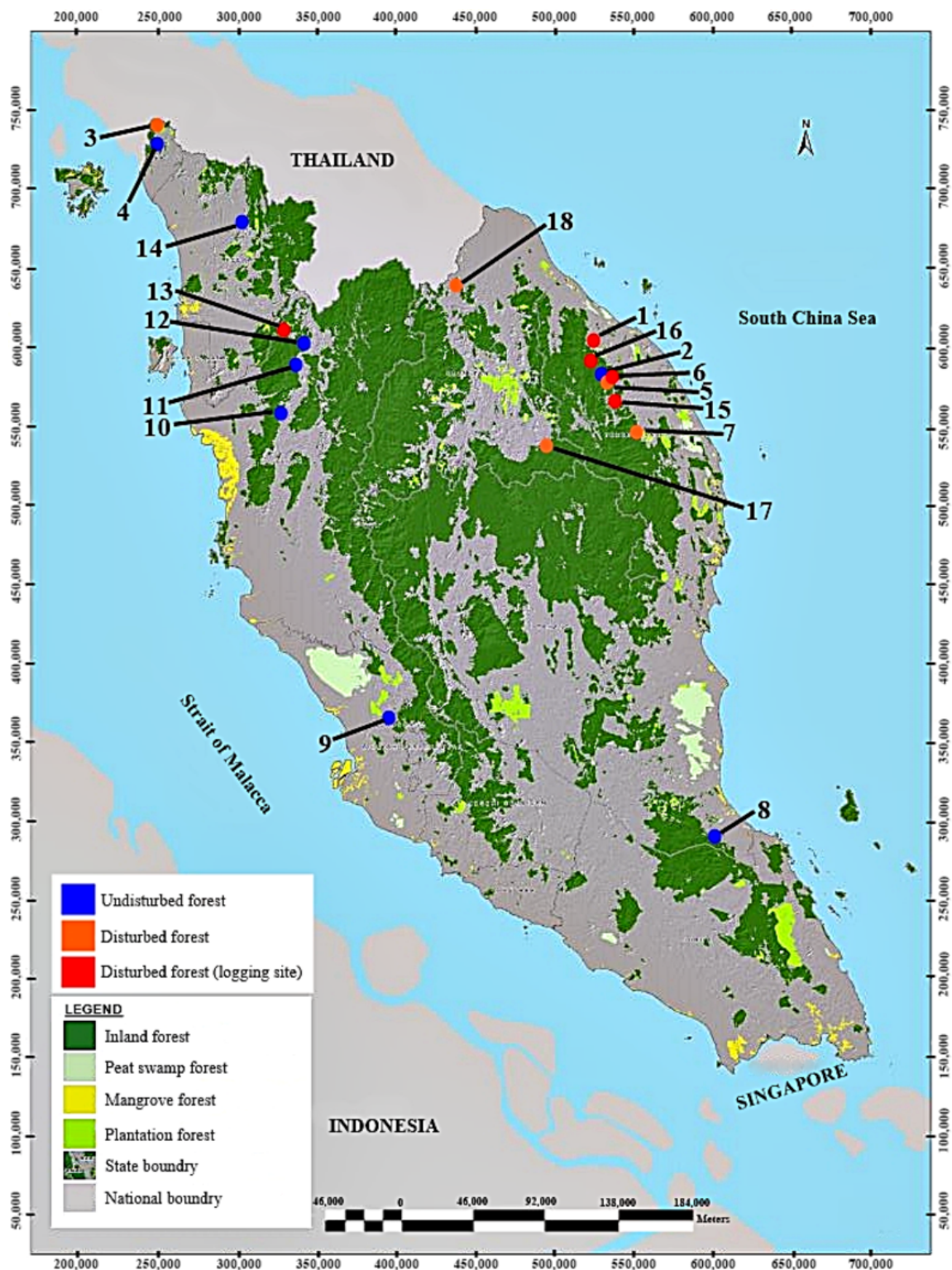

Figure 1. Map showing the study localities (modified and reproduced with permission from JPSM (2019)): 1: Hulu Setiu, logged lowland dipterocarp forest (LHS), 2: Bukit Batu Kapal, lowland riparian

forest (BK), 3: Gunung Perlis, hill dipterocarp forest (GP), 4: Bukit Rongkit, hill limestone forest (BR), 5: Bukit Batu Kapal, forest margin of a mixed dipterocarp forest (BK(M)), 6: Bukit Batu Kapal, logged hill dipterocarp forest (LBK), 7: Bukit Sekayu, lowland riparian forest (BS), 8: Padang 7, hill mixed dipterocarp forest (PG7), 9: Taman Rimba Komanwel, lowland dipterocarp forest (TRK), 10: Lata Kekabu, lowland riparian forest (KB), 11: Lata Lawin, lowland riparian forest (LW), 12: Lata Tanjung Kala, lowland riparian forest (TK), 13: Bintang Hijau, logged lowland dipterocarp forest (LB), 14: Bukit Pedu, conglomerate hill forest (BP), 15: Gawi, logged lowland dipterocarp forest (LG), 16: Petuang, logged lowland dipterocarp forest (LP), 17: Kuala Koh, lowland dipterocarp forest (KH), 18: Tanah Merah, lowland forest (TM). Source: Jabatan Perhutanan Semenanjung Malaysia (JPSM).

Table 1. General characteristics of undisturbed forests in Peninsular Malaysia considered in this study.

Sites	States	Vegetation Types	Elevation (m)	No. of Transect Plots	Totals Transect Size/Area (km^2)
Padang 7 (Rompin) (PG7)	Pahang	Hill mixed dipterocarp forest (with coastal mountain outcrops or *kerangas*)	268–600	4	0.9
Bukit Rongkit (BR)	Perlis	Hill limestone forest	300–400	2	14.4
Taman Rimba Komanwel (TRK)	Selangor	Lowland dipterocarp forest	100–200	6	16.8
Bukit Batu Kapal (BK)	Terengganu	Lowland riparian forest	100–200	5	5.6
Lata Kekabu (KB)	Perak	Lowland riparian forest	100–200	5	5.5
Lata Lawin (LW)	Perak	Lowland riparian forest	100–200	3	3.6
Lata Tanjung Kala (TK)	Perak	Lowland riparian forest	100–200	2	12.0
Bukit Pedu (BP)	Kedah	Conglomerate hill forest	200–400	1	9.0
Total				28	67.8

Table 2. General characteristics of disturbed forests in Peninsular Malaysia considered in this study.

Site	State	Vegetation Types	S	E	F	D	PT	DI	Disturbance Regime	Disturbance Origin	Elevation (m)	No. of Transect Plots	Totals Transect Size/Area (km^2)
Bukit Sekayu (BS)	Terengganu	Lowland riparian forest	1	1	1	3	1	3	Low	Fragmentation caused by palm oil estate	90–100	1	11.8
Gunung Perlis (GP)	Perlis	Hill dipterocarp forest (granite)	1	1	1	3	1	3	Low	Erosion of trail due to heavy ecotourism activities	500–800	4	34.0
Bukit Batu Kapal [BK(M)]	Terengganu	Mixed dipterocarp forest	1	1	1	1	1	1	Low	Timber extraction (a forest margin bordered by logged forests)	100–400–600	1	12.6
Tanah Merah (TM)	Kelantan	Lowland forest	1	1	1	1	1	1	Low	Timber extraction, plantation, mud-flood	40–100	2	0.3
Hulu Setiu (LHS)	Terengganu	Lowland dipterocarp forest	2	2	1	2	1	8	Mild	Timber extraction	40–100	6	13.0
Kuala Koh (KH)	Kelantan	Lowland dipterocarp forest	2	2	1	2	1	8	Mild	Timber extraction (an encroachment), mud-flood	90–130	8	0.8
Bukit Batu Kapal (LBK)	Terengganu	Hill dipterocarp forest	3	2	2	2	1	24	Severe	Timber extraction	300–500	1	33.3
Bintang Hijau (LB)	Perak	Lowland dipterocarp forest	3	2	3	3	2	108	Severe	Timber extraction	100–200	3	1200.0
Gawi (LG)	Terengganu	Lowland dipterocarp forest	3	2	3	3	2	108	Severe	Timber extraction	90–250	1	19.5
Petuang (LP)	Terengganu	Lowland dipterocarp forest	3	2	3	3	2	108	Severe	Timber extraction	200–330	2	53.0
Total												29	1409.7

Notes: Disturbance Index (DI) = Severity (D) × Extension (E) × Frequency (F) × Duration (D) × Patch Type (PT). Interpretation modified from Calderon-Aguilera et al. (2012): Low DI (1–5) = low impact, Intermediate DI (6–20) = mild impact, High DI (>20) = large impact.

Table 3. Ordinal variables assessed to characterise and compare disturbance regimes amongst the disturbed studied sites.

Variables	Definition	Scoring Value
Severity (S)	Loss in ecosystem quality based on the different types of disturbance	(1) small (disturbed ground vegetation due to flood or heavy human trampling) (2) medium (disturbed ground vegetation and forest canopy due to fallen trees and mud flood) (3) large (massive removal of ground vegetation and forest canopy due to clear-felled timber extraction and logs' dragging extraction by tractor
Extension (E)	Area affected by a given disturbance	(1) small (>20% of area) (2) medium (>20% ≤ 50% of area) (3) large (>50% of area)
Frequency (F)	Occurrence of disturbance event in a given time period	(1) low (occurring at intervals longer than 10 years) (2) medium (once every 2–10 years) (3) high (once every year or seasonal)
Duration (D)	Length in time of the disturbance event	(1) <1 year (2) <3 years (3) >3 years
Patch type (PT)	Type of habitat patch created by the disturbance	(1) embedded (disturbed patches within a continuous undisturbed ecosystem) (2) isolated (disturbed patches isolated from an undisturbed ecosystem)

2.2. Sampling Design, Samples, and Data Collection

Samplings were carried along the existing and off-road four-wheel trails using the line-transect method designed at accessible trail(s) in the selected study sites and established randomly by selecting a point along the trail in each locality. To accommodate sampling in the large areas such as logging sites and skid trails, the study areas were calculated based on the distance travelled of each trail multiplied by the width of 5–10 metres on each side of the trail, as shown in Figure 2. Observers walk along lines and count all orchid plants observed within the specified width. The length, width, and number of transect plots were not fixed considering the topography, accessibility, time constraint, movement restrictions due to the pandemic, and budget. Due to the limitations, the comparative study focused on different forest types irrespective of the total size area. Square kilometre (km^2) is used as the unit for total transect plots' area for ease of density calculation, graph scaling, and plotting.

One individual of the flowering specimens was collected and all occurrence pertaining to the same species were successively pooled for each transect and trail. Samples with floral structures were preserved using a standard herbarium technique [22] and voucher specimens were deposited in the Herbarium of Universiti Putra Malaysia (UPM) at the Department of Biology, Faculty of Science. The robust non-flowering individuals were brought back to UPM and transplanted into the ex situ conservatory as living collections. However, some of the non-flowering individuals that are also fragile, minute size, and found growing in few populations were not collected during the first visit until flowering. The flowering individuals were then collected during the revisits. Additionally, some sterile individuals were simply determined at generic level or to the closest affinity on the basis of their vegetative morphological characters. The exact locality is withheld to protect the population from illegal collections.
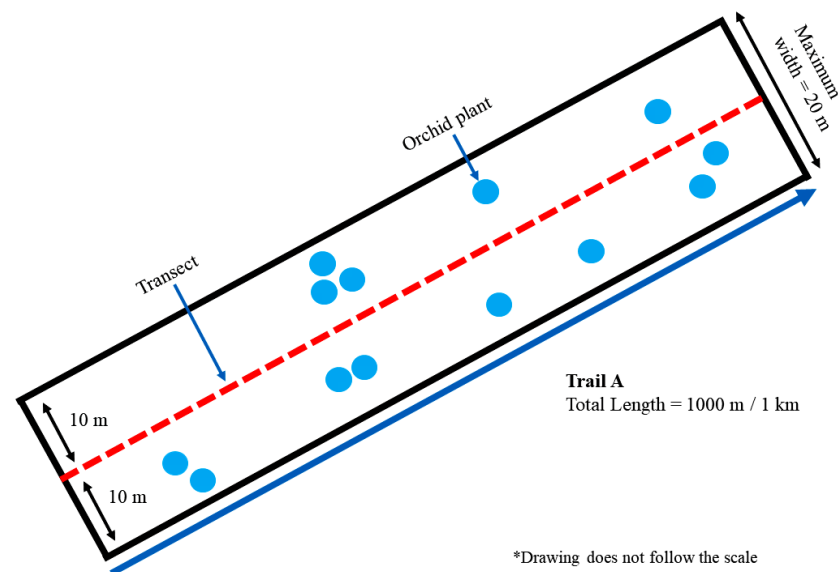
Figure 2. An example of a line-transect (1000 m × 20 m transect plot). The total transect plots' area was converted to the unit of square kilometre (km^2).

For species identification and evaluation of each species' distribution status, reliable taxonomic and floristic literatures were referred and studied, e.g., [23–26]. Digitalised images of herbarium collections, botanical drawings, and records deposited in the National Herbarium of the Netherlands (NHN) accessed through Browse Dutch Natural History Collections: BioPortal (Naturalis) (http://bioportal.naturalis.nl/ (accessed on 27 October 2022)), Herbarium of Singapore Botanic Gardens (SING) accessed through BRAHMS Online managed by the University of Oxford (http://herbaria.plants.ox.ac.uk/bol/sing (accessed on 27 October 2022)), Swiss Orchid Foundation [https://orchid.unibas.ch/index.php/en/ (accessed on 27 October 2022)), Kew Herbarium Catalogue (http://apps.kew.org/herbcat/gotoSearchPage.do (accessed on 27 October 2022)), Natural History Museum Specimen Collection (https://data.nhm.ac.uk/ (accessed on 27 October 2022)), Herbarium of Aarhus University (AAU)(https://www.aubot.dk/search_form.php (accessed on 27 October 2022)), Museum National D'Histoire Naturelle (MNHN) (https://science.mnhn.fr/all/search (accessed on 27 October 2022)), and Plants of the World Online (POWO) (http://www.plantsoftheworldonline.org/ (accessed on 27 October 2022)) were examined prior to the taxonomic treatment and assessment on the range of distribution for each species. The accepted names were validated via KEW World Checklist of Selected Plant Families (WCSP) [27] and POWO.

Occurrence of the host plants containing epiphytic orchids was recorded within the studied transect plots. For each sampled host plant, parameters, and characteristics: height, bark's texture, canopy's structure, crown's forms and classes, and substrate cover were recorded in a spreadsheet. Height was measured either using clinometer and visual interpretation or measuring tape for fallen trees. Each character was described and photographed on the field. The presence of epiphytic orchids was recorded for the entire host plants. The host species and associated epiphytic orchids were mostly identified in the field and verified using different local floras, e.g., [28–38]. The unidentified species of host plants were photographed in detail along with their flowers, leaves, and fruits (if present) and later identified with expert consultation. Studying epiphyte diversity is challenging because it is difficult to observe and identify the plants in the tree canopy from the ground [39]. Each host plant was examined from the ground at different points, thereby assuring a clear view of all the orchids and host's parts [4,40]. Hence, for large and tall host plants, the inaccessible epiphyte growing up on it were only photographed and captured using a Nikon D5100 and a macro lens AF-S DX NIKKOR 55–300 mm f/4.5–5.6 G ED VR

(very high-powered telephoto zoom) as evidence, and on-field visual identification were employed.

2.3. Ecological Study Design and In Situ Measurement of Microclimate Data

In this study, intact undisturbed area and adjacent disturbed area were compared to understand the significant impacts of ecological dynamics towards orchid diversity. Four ecological parameters were logged from morning (9 am) to afternoon time (4 pm) under the influence of varying spatial-temporal conditions; temperature (°C), relative air humidity (10%–100%), and light intensity (μmol m^{-2}s^{-1}) (number of photons received per unit time (s) on a unit area (m)) of the study areas, and bark moisture (0%–100%) of the host plants. The temperature and humidity were measured with Extech Hygro-Thermometer (Extech Instruments, Inc., Nashua, NH, USA) at 2 m above the ground during the study period [41]. The light intensity was first measured in Lux unit with Milwaukee MW700 Standard Portable Lux Meter (Milwaukee Instruments, Inc., Rocky Mount, NC, USA) and then value was converted to the Photosynthetic Photon Flux Density (PPFD) unit. Given an illuminance value (Lux), similarly, we calculated the PPFD in micromoles per second per square metre (μmol m^{-2}s^{-1}) for the given light source [42,43]. Unit Lux is simply based on visual sensitivity and does not provide information on the energy or photon content of light, which truly influence the photosynthesis or sugar production in the leaf. Hence, in order to understand better the light intensity for a study relating to plant responses, the suitable unit is the μmol m^{-2}s^{-1}. The bark moisture was measured with HoldPeak HP-2GD Wood Moisture Meter (Zhuhai Jida Huapu Instrument Co., Ltd., Zhuhai, Guangdong Province, China) at 2 m above the basal area.

2.4. Diversity Analyses

Recorded information about the total individual species were analysed statistically and mathematically for clearer identification of diversity in the area. Diversity analyses were estimated using PAleontological STatistics Version 4.04 (PAST4) [44,45]. To determine the species richness and species evenness, Shannon–Wiener Diversity Index (H) and Simpson's Diversity Index (1-D) were used in this study. Inclusion of both diversity indices improves the output information of the dataset, which is unique for each community or sample analysed. The H and 1-D indices allow data on species richness and relative abundance to be combined [46]. The Simpson Index was explained by presence of the predominant species, and the Shannon Index assumed that individuals were randomly selected, and that all species were represented in the sample [47]. The effect of the sample size is generally insignificant for both indices. However, these methods could not tell which factors contributed more to the value. Hence, Evenness (E) was used to determine how close in numbers each species in each studied area were [48]. Higher values indicate greater community diversity and more even distribution of different individuals within a species. Dominance (D) gives the abundance of the most abundant species and ranges from 0 (all taxa are equally present) to 1 (one taxon dominates the community completely) [44].

2.5. Data Analyses

Abundance was calculated as Relative abundance of orchid (%Ao): [Number of clump or population of a particular orchid species within the transect plots ÷ Total number of all orchid clumps or populations of the transect plots] × 100. When sampling design is transect-based, orchid and host plants are sampled in unequal numbers due to the variation in size of the studied areas or trails. Hence, the following parameters were computed; Density of the orchid plants within a transect plot (plants/km^2): Number of orchids plants within the transect plot (plants) ÷ Total area of the transect plots (km^2). An ordination method, clustering with UPGMA (Unweighted Pair Group Method with Arithmetic Mean) and Q-mode clustering (grouping variables or associations) by transposing the data matrix [45], was used to look at similarity of host plants (bark textures) amongst the studied vegetation alliances. The similarity was tested using Bray–Curtis Similarity Coefficient [49].

Bray–Curtis is a popular similarity index for abundance data (Hammer et al., 2001). The ordination method was carried out using PAleontological STatistics Version 4.04 (PAST4) [45].

2.6. Statistical Analyses

Ecological data obtained were analysed using software package IBM SPSS version 24 (IBM Corp., Chicago, IL, USA). The measured microclimate parameters were subjected to Shapiro–Wilk for a normality distribution test. As the parametric assumptions could not be obtained for all dependant variables even through transformation (Supplementary Table S1a,c,e,g), non-parametric tests were used for all analyses. The Mann–Whitney test was used to determine the significant relationship of the parameters between the undisturbed and disturbed forests. Statistical significance was determined at $p < 0.05$ (Supplementary Table S1b,d,f). Following the study [50], the significant difference of mean between groups were determined by comparing directly between the minimum values recorded for undisturbed forests with minimum values recorded for disturbed forests and evaluated accordingly for the maximum values. Kruskal–Wallis one-way analysis of variance (ANOVA) was used to determine the significant difference in daily hours' ecological parameters between undisturbed, disturbed, and disturbed 'non-logging sites' forests with distinctively different disturbance types (Supplementary Tables S1h,j,k). The post hoc for Kruskal–Wallis was conducted using the Mann–Whitney test with multiple pairwise comparisons (Supplementary Table S1i,l). To ensure that Type I error does not t exceed 0.05, Bonferroni correction was used by dividing α of 0.05 by the number of tests conducted. Therefore, the statistical significance was determined at $p < 0.017$. Comparing species richness among sites or samples is a statistical challenge because the observed number of species is sensitive to the number of individuals counted or the area sampled [51]. Hence, to describe the orchid species richness in the different localities, we used a rarefaction function for each region. Rarefaction is a method for comparing the species richness of samples of different sizes by calculating species richness for a given number of individuals based on rarefaction curves, which are plots of the number of species as a function of the number of samples [52], in our case number of clumps (one clump = one individual = one occurrence). We conducted individual-based rarefaction as implemented in EstimateS 9.1.0 [53].

2.7. Terminology

Following the study [54], the terms 'host' and 'host species' imply that the focal epiphyte taxon has been observed on the plant individual or species. Since hosts are of several growth forms (trees, shrubs, lianas), the term 'host plants' is used rather than 'host tree'. Note that, in unambiguous contexts, 'host' is often used as a short form of 'host species' or 'host plant'. Therefore, the unoccupied (by epiphytic orchids) plant species were excluded from the analysis. In the current study, 'undisturbed forest' and 'disturbed forest' are the general classification used for the forest types. The terms 'undisturbed forest' and 'disturbed forest' were adopted from [55]. The synonymous terms such as undisturbed and disturbed areas, or undisturbed and disturbed vegetation have been used in other works of literature on biodiversity in the tropics or Malaysia, such as [18,56–61]. 'Undisturbed forest' are primary or protected forests that have experienced little to no recent human disturbance, whereas 'disturbed forest' are forest that have experienced disastrous and large disturbance such as deforestation, extreme floods, tree falls, and human trampling.

3. Results

3.1. Species Richness and Abundance

In total, 389 orchid specimens confined to 239 species and 65 genera were collected (Supplementary Table S2). A plot of species accumulation curve allows comparison of a number of species at different levels of collecting effort. Using the number of individuals, the disturbed forest was the most species-rich for equal sampling effort if compared to the undisturbed forest (Figure 3). Additionally, the curve for the undisturbed forest stopped

at 250 individuals and appeared to approach an asymptote, whereas the curve for the disturbed forest is longer but steeper, indicating that there may be more species found in the disturbed forest if the sampling continues. This may indicate a higher abundance of species which can be found in heterogeneous and larger area sites [62], but nothing of the sort for logging areas as the orchid abundance is influenced by the number of fallen trees and ease of collections for epiphytic orchids on the fallen trees along the skid trails [50].
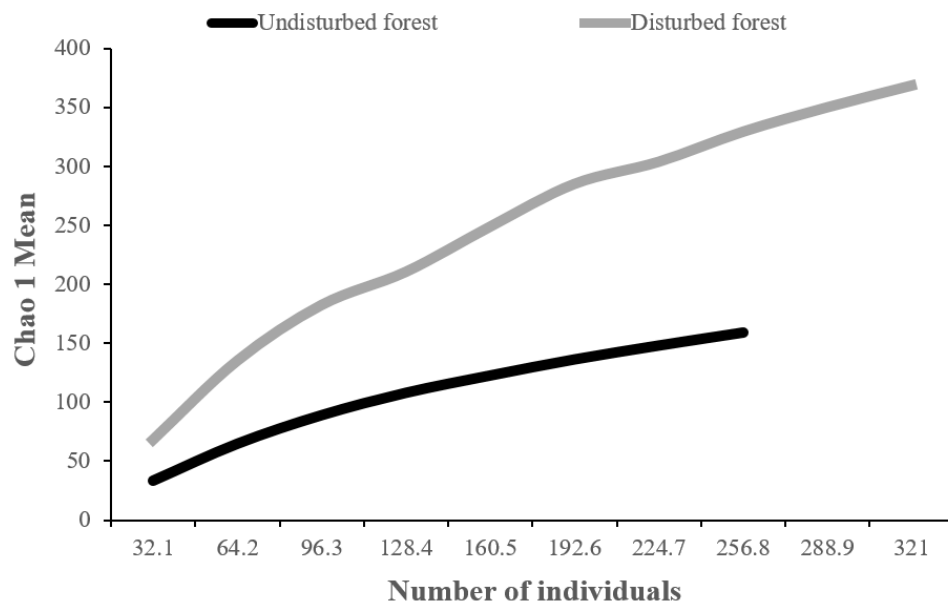
Figure 3. Orchid species accumulation curves (individual-based rarefaction) within grid points of different land-use intensities.

Species richness in the disturbed forests was 183 species with the logging sites harbouring the most abundant orchids species if compared to the undisturbed forests with 100 species (Figure 4A). Despite that, undisturbed forests had a higher orchid density (2.4 orchids) when compared with the disturbed forests (0.2 orchids). However, disturbed habitats, especially the logging sites, showed greater impoverishment than the undisturbed habitats as very few surviving plants were found or collected. Similarly, *Agrostophyllum stipulatum* was recorded with highest relative abundance in both undisturbed (3.6%) and disturbed forests (4.6%). The species composition of the orchids differed significantly in between undisturbed and disturbed forests. Disturbed forests comprised mostly epiphytic orchids (Figure 4B), of which the highest collection was from logging sites. Terrestrial species occurred the most in the undisturbed habitats. Only few to none were marginally more frequent in a more open and disturbed habitat. Additionally, species density of orchids based on growth habits was lower in disturbed habitats than in the undisturbed or pristine ones (Figure 4C). The two forest types were *Dendrobium* and *Bulbophyllum* as of the most abundant genera which were also mostly epiphytic (Figure 5).
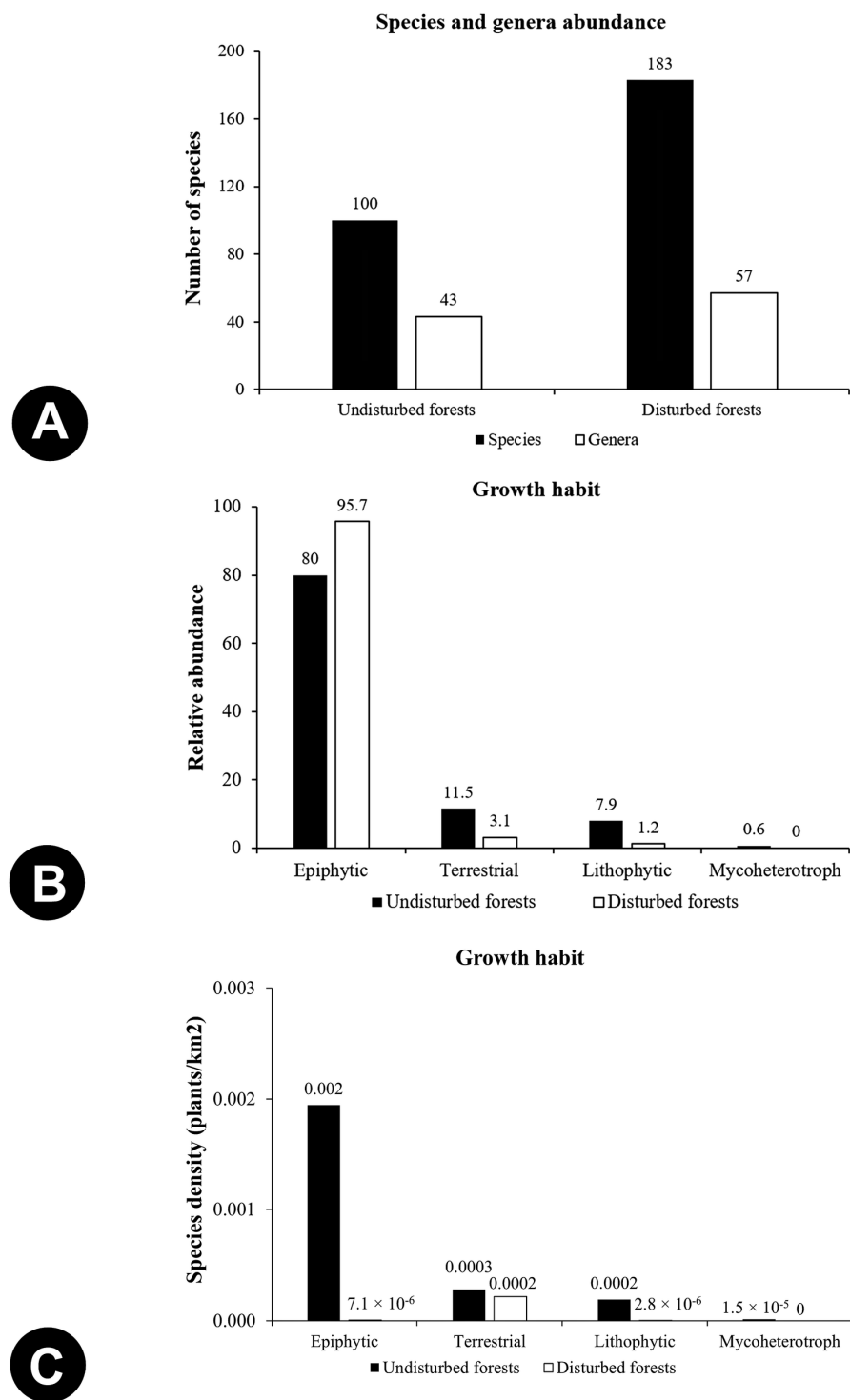
Species and genera abundance

Growth habit

Growth habit

Figure 4. Comparison of species abundance and density between undisturbed and disturbed forests: (**A**) Species and genera abundance, (**B**) Relative abundance based on growth habit, (**C**) Species density based on growth habit.
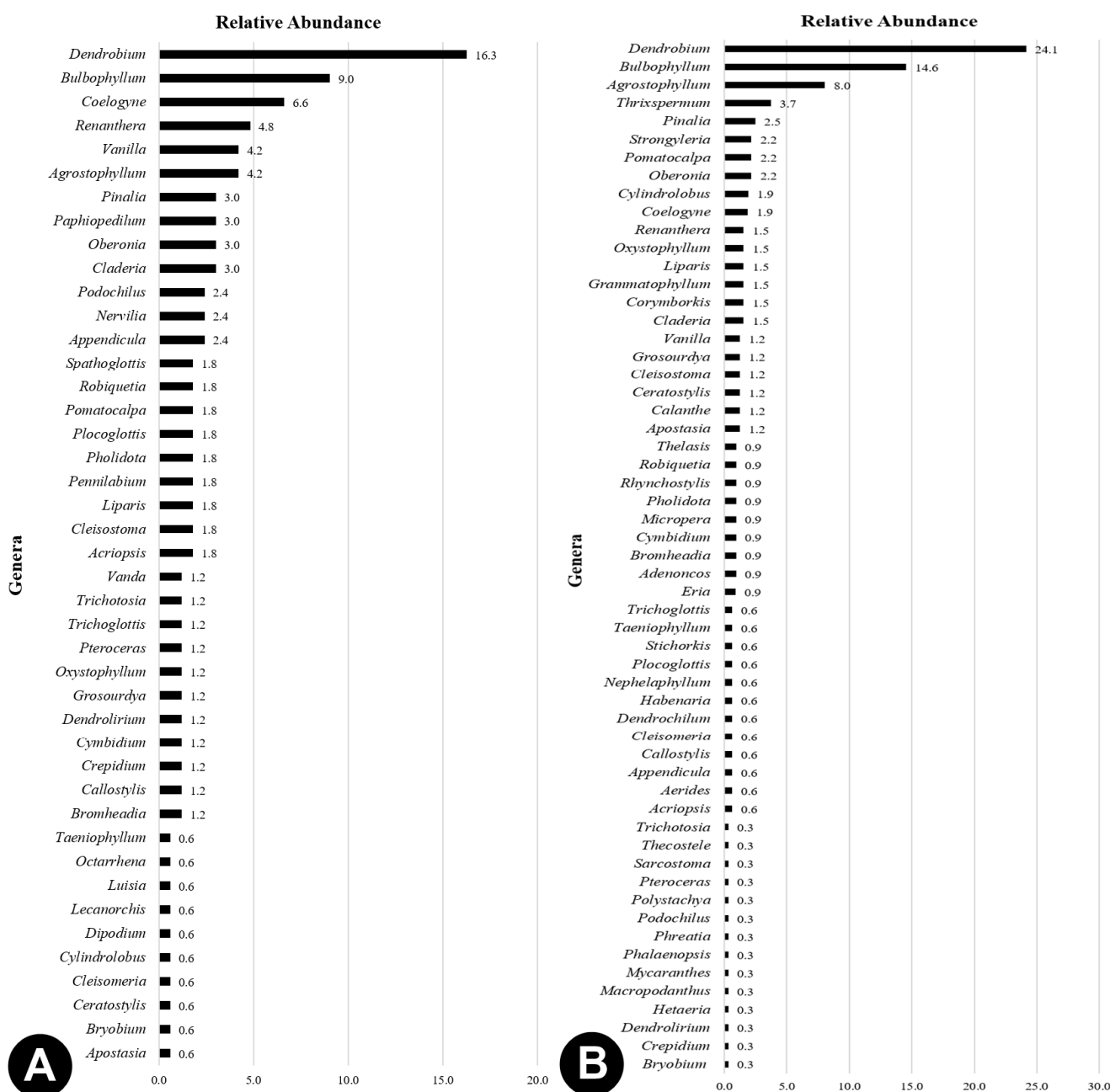
Figure 5. Comparison of species abundance based on genera for (**A**) undisturbed and (**B**) disturbed forests in Peninsular Malaysia.

3.2. Species Diversity

Shannon–Wiener Diversity Index (H) (Figure 6A) and Simpson's Diversity Index (1-D) (Figure 6B) were showing similar patterns of diversity for the undisturbed and disturbed forests. Both indices showed that disturbed forests harboured higher species diversity than the undisturbed forests. Theoretically, H is strongly influenced by species richness, evenness, and presence of rare species. Meanwhile, 1-D gives more weight to evenness and presence of common species. In this sense, H has an advantage over 1-D because it depends more on species richness and less on abundance, so it is very sensitive to even small diversity changes, and thus is widely used to assess the actual state of environment. Although the finding suggests that disturbed forests could retain a high richness of orchid taxa, there are several detrimental aspects that need consideration—the high abundance of orchids in the disturbed forests might overstate the species richness.

The low orchid diversity in the undisturbed forest is supported by the high dominance of the most dominant species (D = 0.015) (Figure 6C), and the slightly higher evenness in the undisturbed forest (E = 0.844) does not seem to affect the H and 1-D values much (Figure 6D). Additionally, the higher diversity of orchids in the disturbed forests might be influenced by the higher number of rare species found on the fallen trees in the logged areas (Figure S1). Moreover, forest margin had lower species diversity (Figure 7A) and density (Figure 7C) than the adjacent undisturbed forest with no terrestrial orchid recorded in the area. It suggests the altered environment caused by the adjacent logging activity reduced the orchid species richness. In logging sites, orchid species were greatest in diversity if compared to the undisturbed forests (Figure 7E), but lower in species density (Figure 7G). It only comprised of epiphytic orchids (Figure 7H). Further details on the occurrence, diversity, and density of orchids in each study site are presented in Table 4.
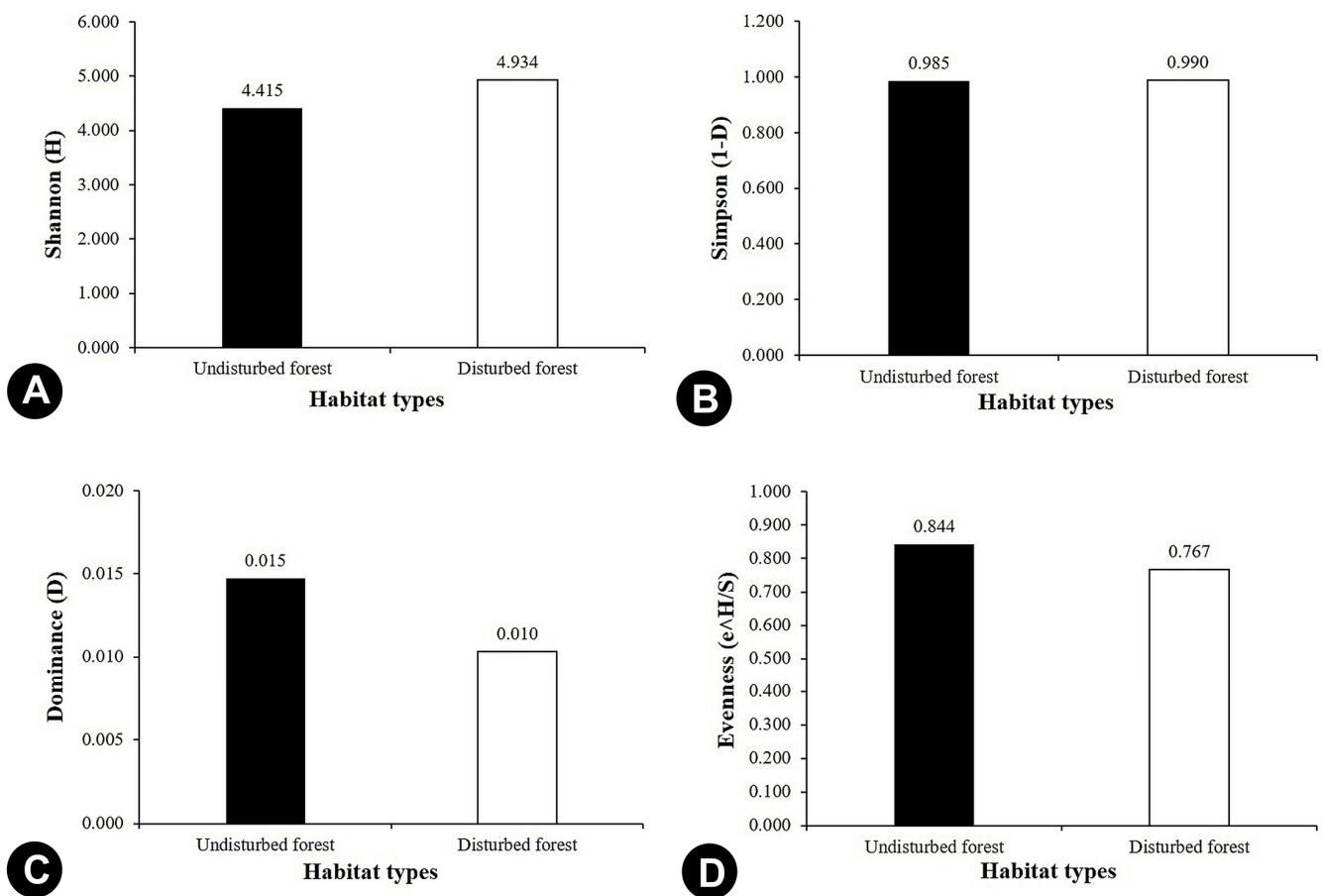

Figure 6. Overall comparison of species diversity between the undisturbed and disturbed forests: (**A**) Shannon (H), (**B**) Simpson (1-D), (**C**) Dominance, (**D**) Evenness (eˆH/S).
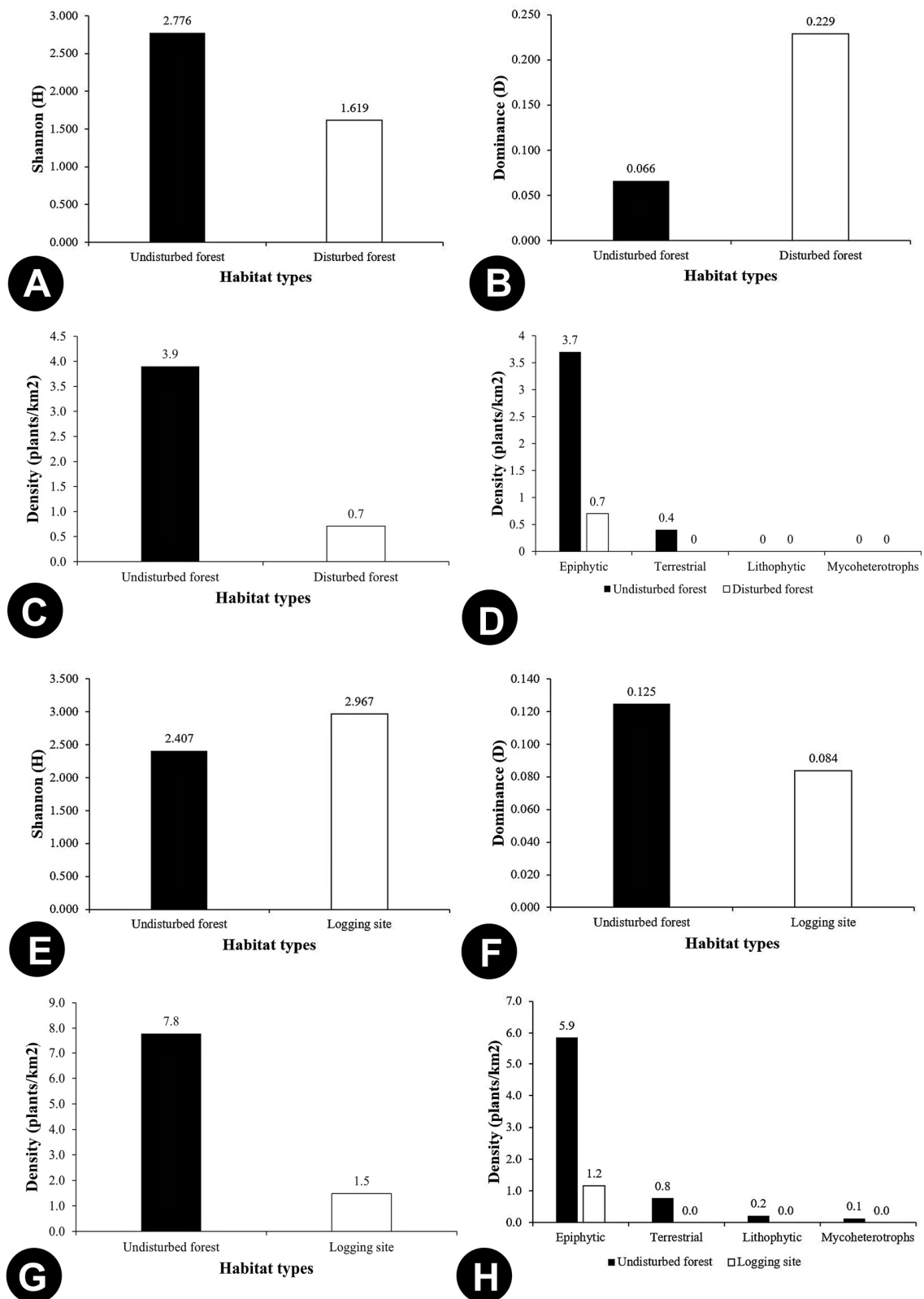
Figure 7. Comparison of species diversity and density for Adjacent Undisturbed vs. Disturbed Forests and Undisturbed Forests vs. Logging Sites: (**A**,**E**) Shannon (H), (**B**,**E**) Dominance (D), (**C**,**G**) Density (plants/km^2) based on forest types, (**D**,**H**) Density (plants/km^2) based on growth habit.

Table 4. Comparison based on diversity, density, and distribution of life forms of orchid species in undisturbed and disturbed forests in Peninsular Malaysia.

Parameters	Undisturbed Forests								Disturbed Forests									
	PG7	BR	TRK	BK	KB	LW	TK	BP	BS	GP	BK(M)	TM	LHS	KH	LBK	LB	LG	LP
Taxa_S	27	26	5	17	16	4	9	14	25	19	7	4	12	6	5	11	83	61
Occurrence (ni)	34	39	8	22	17	5	17	21	58	21	16	7	12	19	5	15	98	70
Occurrence (ni) (Epiphytic orchids)	31	28	7	21	17	4	17	6	49	19	17	10	13	11	5	16	70	57
Occurrence (ni) (Terrestrial orchids)	4	8	1	2	2	1	0	1	6	2	0	0	0	8	0	0	0	0
Occurrence (ni) (Lithophytic orchids)	0	1	0	0	0	0	0	15	4	0	0	0	0	0	0	0	0	0
Occurrence (ni) (Mycoheterotroph orchids)	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dominance_D	0.047	0.049	0.250	0.066	0.066	0.280	0.142	0.098	0.092	0.057	0.258	0.306	0.083	0.191	0.200	0.102	0.015	0.018
Simpson_1-D	0.953	0.951	0.750	0.934	0.934	0.720	0.858	0.903	0.908	0.943	0.742	0.694	0.917	0.809	0.800	0.898	0.985	0.982
Shannon_H	3.200	3.139	1.494	2.776	2.752	1.332	2.069	2.491	2.801	2.912	1.629	1.277	2.485	1.709	1.609	2.338	4.342	4.063
Evenness_eˆH/S	0.909	0.888	0.891	0.944	0.979	0.947	0.879	0.863	0.658	0.969	0.728	0.897	1.000	0.920	1.000	0.942	0.926	0.953
Area (km^2)	0.900	14.400	16.800	5.618	5.500	3.600	12	9	11.760	34	12.600	0.250	13	0.800	33.300	1200	19.500	53
Density (plants/km^2)	37.800	2.700	0.500	3.900	3.100	1.400	1.400	2.300	4.900	0.600	1.300	28	0.900	23.800	0.200	0	5	1.300
Density of epiphytic orchids (plants/km^2)	34.400	1.900	0.400	3.700	3.100	1.100	1.400	0.700	4.200	0.600	1.300	40	1	13.800	0.200	0	3.6	1.1
Density of terrestrial orchids (plants/km^2)	4.400	0.600	0.100	0.400	0.400	0.300	0	0.100	0.500	0.100	0	0	0	10	0	0	0	0
Density of lithophytic orchids (plants/km^2)	0	0.100	0	0	0	0	0	1.700	0.300	0	0	0	0	0	0	0	0	0
Density of mycoheterotroph orchids (plants/km^2)	1.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

3.3. Microclimate Conditions

Overall data of the microclimate conditions (Supplementary Table S3) show that maximum temperature for the disturbed forests were significantly higher ($p < 0.001$, $df = 58$) than the undisturbed ones. Simultaneously, for the relative air humidity, the disturbed forests had significantly lower values ($p < 0.001$, $df = 58$) if compared to the undisturbed forests (Table 5, Figure S2). Additionally, a comparison on microclimate conditions in between two adjacent forests, an undisturbed forest (BK) and a forest margin (BK(M)) located next to a logging site (LBK), was conducted to see whether there were any significant differences in microclimate between the two forests contrasting in level of disturbance. The result shows there were significant differences in maximum temperature ($p < 0.001$, $df = 38$), minimum and maximum relative air humidity ($p < 0.001$, $df = 38$), and minimum ($p = 0.010$, $df = 38$) and maximum ($p < 0.001$, $df = 38$) light intensity in between the two adjacent forests (Table 5, Figure S3). It indicates that the disturbance caused by adjacent logging projected extreme microclimate conditions on the environment. Also, the result shows significant differences in temperature ($p < 0.001$, $df = 38$), relative air humidity ($p < 0.001$, $df = 38$), and light intensity ($p < 0.001$, $df = 38$) in between the undisturbed forests and extremely disturbed forests (logging areas) (Table 5, Figure S4). The canopy disruptions caused by the selective-cut and clear-cut logging produced openings in the canopy, which had significantly affected the temperature and the light intensity. The temperature could reach up to 40 °C in the afternoon and consequently reduced the humidity to 51%. It indicates extreme dryness in the logging areas, limiting growth and distribution of orchids.

Table 5. Summary of topographic and ecological predictors (mean ± SE) of undisturbed and disturbed forests in Peninsular Malaysia.

Site	Temperature (°C)	Relative Air Humidity (1%–100%)	Light Intensity, PPFD (μmol m^{-2} s^{-1})	Elevation (m)
Undisturbed vs. disturbed forests ($p < 0.005$, $n = 30$, $df = 58$)				
Undisturbed forests	Min: 27.8 ± 0.3 [a] Max: 31.2 ± 0.2 [a]	Min: 77.1 ± 1.2 [a] Max: 89.6 ± 0.9 [a]	Min: 23.8 ± 3.3 [a] Max: 171.7 ± 18.8 [a]	100–600
Disturbed forests	Min: 27.2 ± 0.3 [a] Max: 35.7 ± 0.8 [b]	Min: 64.5 ± 2.3 [b] Max: 88.7 ± 1 [a]	Min: 107.1 ± 16 [b] Max: 456.5 ± 29.6 [b]	40–800
Adjacent undisturbed vs. disturbed forests ($p < 0.005$, n = 20, $df = 38$)				
Undisturbed forests	Min: 30.6 ± 0.1 [a] Max: 30.7 ± 0.1 [a]	Min: 86.5 ± 0.6 [a] Max: 88.2 ± 0.6 [a]	Min: 21.5 ± 2.2 [a] Max: 125.8 ± 17 [a]	100–200
Disturbed forests	Min: 32.2 ± 0.6 [a] Max: 40.6 ± 0.3 [b]	Min: 44.8 ± 1.2 [b] Max: 75.8 ± 1.5 [b]	Min: 51.9 ± 7.7 [b] Max: 406.8 ± 44.3 [b]	200–500
Undisturbed and extremely disturbed (logging sites) forests ($p < 0.005$, n = 20, $df = 38$)				
Undisturbed forests	Min: 28.1 ± 0.3 [a] Max: 31.3 ± 0.3 [a]	Min: 80.7 ± 1 [a] Max: 89 ± 0.5 [a]	Min: 33.4 ± 5 [a] Max: 190.9 ± 24.7 [a]	100–600
Logging sites	Min: 32.9 ± 0.7 [b] Max: 40.2 ± 0.4 [b]	Min: 51.8 ± 2.4 [b] Max: 79.5 ± 1.7 [b]	Min: 132.1 ± 16.6 [b] Max: 410.5 ± 34.5 [b]	200–500

Notes: Different superscripts indicate significant differences ($p < 0.05$) in Mann–Whitney test.

Figure 8 shows the hourly means for temperature and relative air humidity differed between habitats of different disturbance regimes. Hourly means differed between disturbance regimes during daytime from 10 am to 4 pm. The corresponding hourly temperature for the logging sites were significantly higher at the consecutive period of day (morning, H(1) = 26.38, $p = 0.002$, $df = 2$; afternoon, H(1) = 26.75, $p < 0.001$, $df = 2$; late afternoon, H(1) = 20.33, $p < 0.001$, $df = 2$) if compared to the undisturbed forests (morning, H(1) = 14.00, $p = 0.002$, $df = 2$; afternoon, H(1) = 13.10, $p < 0.001$, $df = 2$; late afternoon, H(1) = 5.85, $p < 0.001$, $df = 2$). Similarly, the result shows significantly higher temperature for the logging site (morning, H(1) = 12.63, $p = 0.005$, $df = 2$; afternoon, H(1) = 22.72, $p < 0.001$, $df = 2$; late afternoon, H(1) = 19.35, $p < 0.001$, $df = 2$) than the non-logging site disturbed forests (morning, H(1) = 5.78, $p = 0.005$, $df = 2$; afternoon, H(1) = 11.62, $p < 0.001$, $df = 2$; late afternoon, H(1) = 5.33, $p < 0.001$, $df = 2$). The result also showed significant difference for relative air humidity in between the logging sites (morning, H(1) = 6.56, $p = 0.011$, $df = 2$; afternoon, H(1) = 5.00, $p < 0.001$, $df = 2$; late afternoon, H(1) = 5.44, $p < 0.001$, $df = 2$) and undisturbed forests (morning, H(1) = 13.10, $p = 0.011$, $df = 2$; afternoon, H(1) = 14.50, $p < 0.001$, $df = 2$; late afternoon, H(1) = 14.10, $p < 0.001$, $df = 2$). The result was also with significant difference for relative air humidity in between the logging sites (morning, H(1) = 7.06, $p = 0.050$, $df = 2$; afternoon, H(1) = 5.44, $p < 0.001$, $df = 2$; late afternoon, H(1) = 5.33, $p < 0.001$, $df = 2$) and non-logging disturbed forests (morning, H(1) = 11.94, $p = 0.050$, $df = 2$; afternoon, H(1) = 13.56, $p < 0.001$, $df = 2$; late afternoon, H(1) = 13.67, $p < 0.001$, $df = 2$), except for morning time.
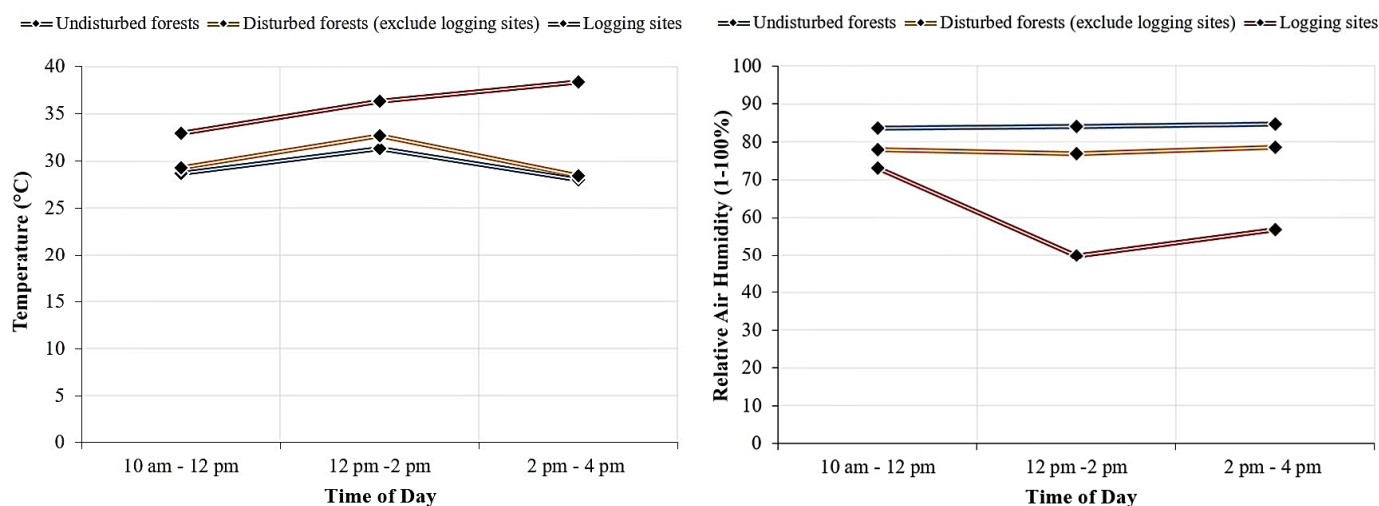
Figure 8. Daily course of temperature and relative air humidity in undisturbed and disturbed forests for different disturbance regimes in Peninsular Malaysia (2016–2020). Note: Each point represents means of period of day, morning (10 am–12 pm), afternoon (12 pm–2 pm), and late afternoon (2 pm–4 pm).

3.4. Factors Influencing Abundance of Epiphytic Orchids: Host Plants and Bark Moisture

Effects of microclimate change due to the anthropogenic and naturogenic activities are now often examined based on the forest canopy species, especially epiphytic orchid species that rely on the host plants. In this paper, the general host characteristics and bark moisture that may influence the distribution and abundance of epiphytic orchids are mainly explored. In total, 102 host individuals harbouring wild orchids were inspected in all the studied line-transect plots. There are five most significant types that accumulate abundant epiphytic orchids, Type 4, 6, 13, 18, and 19 (Table 6), with wide and interlocking crown roofing the understorey part from sun exposure and dryness. Additionally, the study highlights the importance of the host plants that possess bark texture Type 9 and 12 (Table 6), smooth to fissured textures. The result demonstrated that epiphytic orchid diversity and abundance is favoured by rough-barked host. Only 15 families of host species were present in the study localities. Total host species was undetermined because a number of host individual or the fallen trees recorded in the logging sites were only identified to family level due to the missing of important morphological characters, such as leaves and flowers. In the undisturbed and non-logging disturbed forests, epiphytic orchids were prominently abundant growing on *Saraca*, *Sygyzium*, and *Neonauclea* tree species that were growing along the riparian areas. Many clumps of epiphytic orchids were also recorded growing on large snags (dead standing trees) that were covered by moist substrate (mosses and lichens) in riparian forests. On average, an individual host tree could have harboured more than ten epiphytic orchid species. Species abundance of epiphytic orchids correlated with the bark moisture and texture. A box plot analysis shows that host plants having bark moisture 60%–80% generally harboured more epiphytic orchids than hosts with 0%–20%, 20%–40%, 40%–60%, and 80%–100% bark moisture (Figure 9). Fifteen distinct bark textures were recorded and described based on the surface morphology (Table 7 and Figure 10). Using cluster analysis (Figure 11), the difference of bark textures of host plants, those of undisturbed forest or non-logging disturbed forest or logging site were distinguished. Bark textures are generally grouped well based on the vegetation type and disturbance level. This suggests bark textures could be associated with the microclimate conditions of the forest. Furthermore, this explains that the textures that potentially influenced the abundance of epiphytic orchids were likely to be modulated by climate.

Table 6. Types of host plants harbouring orchids in the undisturbed and disturbed forests in Peninsular Malaysia.

| Type	Habit	Crown Form	Crown Class	Substrate Cover	Height (m)	Species
1	Tree	Round	Overtopped	Basal	ca. 3–6	*Greenea corymbosa* (Jack) Voigt (Rubiaceae), *Streblus ilicifolius* (S.Vidal) Corner (Moraceae)
2	Tree	Broad	Codominant	Trunk	ca. 20–30	*Castanopsis* sp. (Fagaceae), *Artocarpus elasticus* Reinw. ex Blume (Moraceae)
3	Tree	Spreading	Dominant	Trunk	ca. 40	*Campnosperma auriculatum* (Blume) Hook.f. (Anacardiaceae), *Castanopsis* sp. (Fagaceae)
4	Tree	Spreading	Intermediate	Basal, trunk, branches	ca. 5	*Ficus fistulosa* Reinw. ex Blume (Moraceae), *Polyalthia cauliflora* Hook.f. & Thomson (Annonaceae), *Goniothalamus* sp. (Annonaceae), *Tristaniopsis whiteana* (Griff.) Peter G.Wilson & J.T.Waterh. (Myrtaceae), *Syzygium* cf. *salictoides* (Ridl.) I.M.Turner (Myrtaceae)
5	Tree	Columnar	Intermediate	Basal, trunk	ca. 15–20	*Syzygium* sp. (Myrtaceae), *Castanopsis* sp. (Fagaceae)
6	Tree	Spreading	Codominant	Basal	ca. 20	*Dipterocarpus elongatus* Korth. (Dipterocarpaceae), *Dipterocarpus oblongifolius* Blume (Dipterocarpaceae)
7	Tree	Vase	Intermediate	Basal, trunk, branches	ca. 15	*Playmitra macrocarpa* Boetl. (Annonaceae)
8	Tree	Weeping	Overtopped	Basal, trunk, branches	ca. 15	*Hydnocarpus illicifolius* King (Achariaceae)
9	Tree	Globular	Dominant	Basal, trunk, branches	ca. 7–10	*Calophyllum wallichianum* Planch. & Triana (Calophyllaceae), *Leptospermum polygalifolium* Salisb. (Myrtaceae)
10	Tree	Globular	Intermediate	Basal	ca. 10	*Macaranga gigantea* (Rchb.f. & Zoll.) Müll.Arg. (Euphorbiaceae)
11	Tree	Round	Intermediate	Branches	ca. 20	*Goniothalamus* sp. (Annonaceae)
12	Tree	Oval	Dominant	Basal	ca. 40	*Ochanostachys amentacea* Mast.(Olacaceae)
13	Tree	Broad	Intermediate	Basal, branches	ca. 10	*Neonauclea pallida* subsp. *malaccensis* (Gand.) Ridsdale (Rubiaceae), *Saraca declinata* Miq. (Fabaceae), *Eurya* cf. *acuminata* DC (Pentaphylacaceae)
14	Liana	Leaflet wholly arranged	Intermediate	Stem	ca. 20	*Spatholobus ferrugineus* (Zoll. & Moritzi) Benth. (Fabaceae)
15	Liana	Spreading	Overtopped	Stem	ca. 6	Apocynaceae
16	Fallen tree	Spreading	Emergent	Branches, trunk	ca. 50	Dipterocarpaceae
17	Fallen tree	Round	Codominant	Branches	ca. 20–30	*Ficus* sp. (Moraceae), *Artocarpus elasticus* (Moraceae)
18	Fallen tree	Spreading	Dominant	Branches, trunk	ca. 40	*Shorea* sp. (Balau) (Dipterocarpaceae), *Hopea* sp. (Dipterocarpaceae), *Pentace eximia* (Malvaceae)
19	Fallen tree	Broad	Codominant	Trunk	ca. 30	*Cynometra malaccensis* Meeuwen (Fabaceae), *Parkia* sp. (Fabaceae)
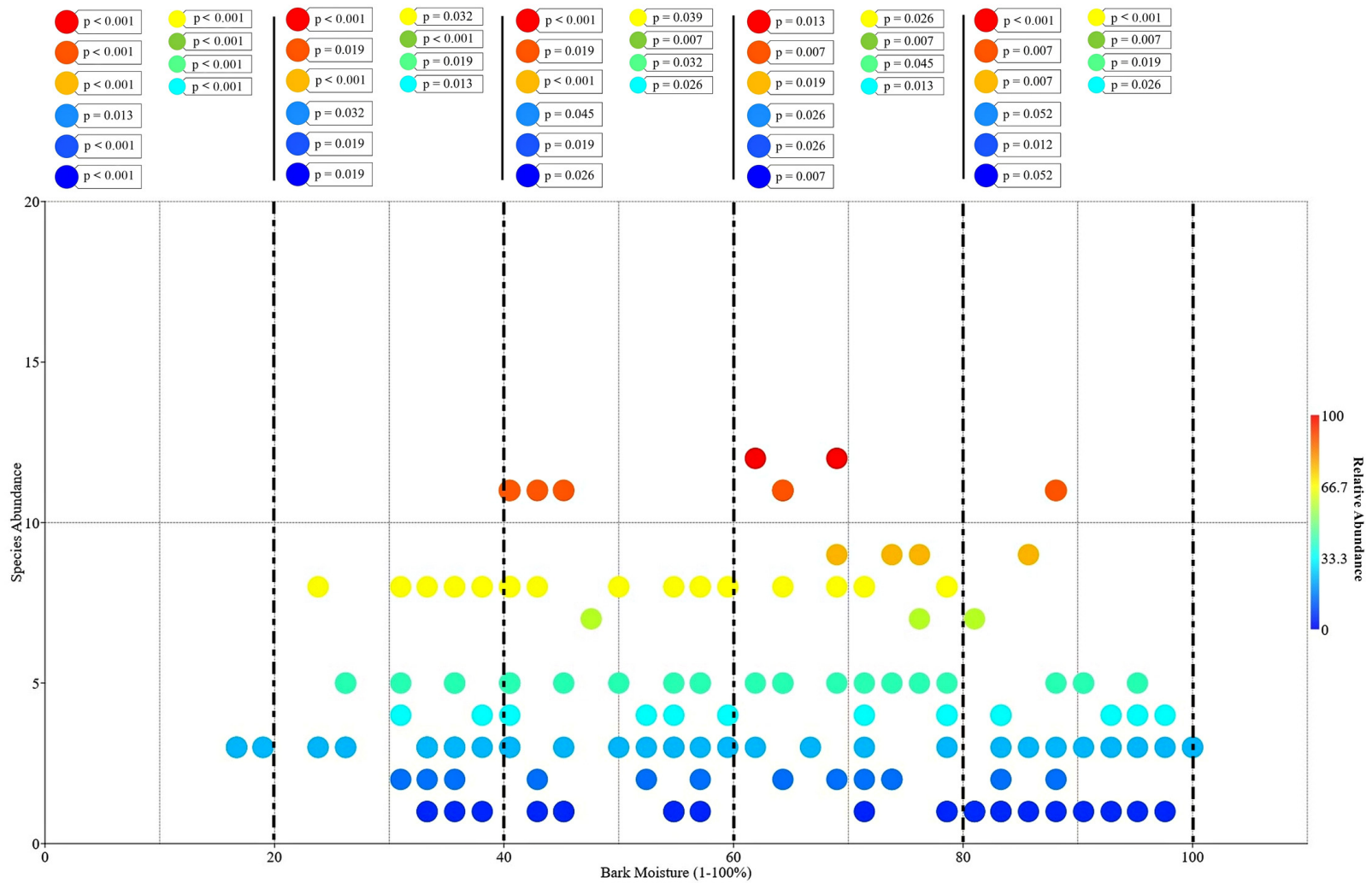
Figure 9. Relation between total epiphyte species density (species per tree) and host plants' bark moisture (bubble plot; N = 150). According to their colour, cold to hot colour, bubbles reflect multiple values.
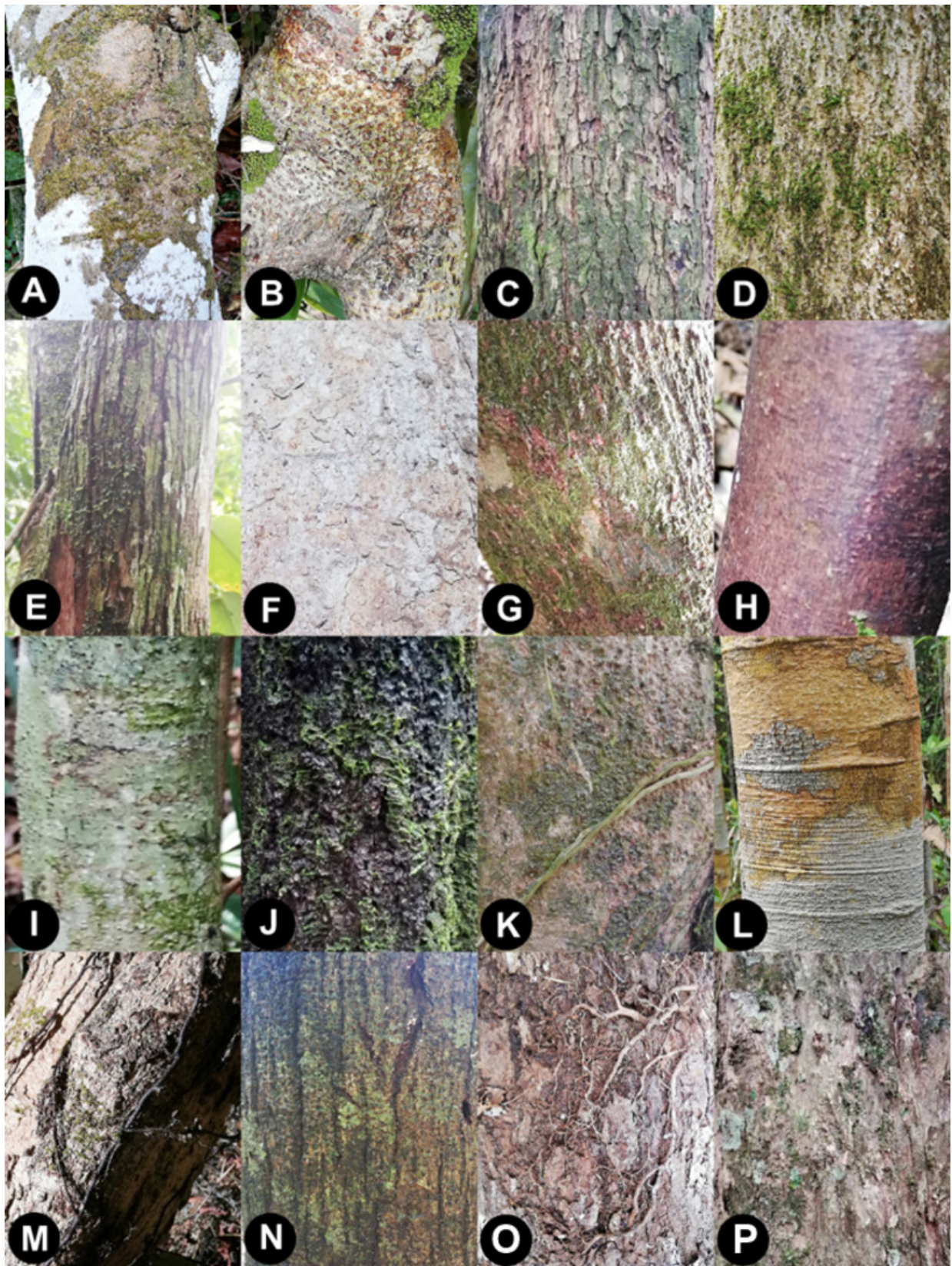
Figure 10. Types of bark texture of host plants in undisturbed and disturbed forests in Peninsular Malaysia: (**A**) Type 1, (**B**) Type 2, (**C**) Type 3, (**D**) Type 4, (**E**) Type 5, (**F**) Type 6, (**G**) Type 7, (**H**) Type 8, (**I**) Type 9, (**J**) Type 10, (**K**) Type 10, (**L**) Type 11, (**M**) Type 12, (**N**) Type 13, (**O**) Type 14, (**P**) Type 15.

Table 7. Types of bark texture of the host plants harbouring epiphytic orchids in the undisturbed and disturbed forests in Peninsular Malaysia.

Types	Bark Textures	Sites	Forest Types
1	Fissured	1, 2, 3, 5, 8, 9, 10, 11, 12, 13, 14, 17, 18	Undisturbed, disturbed
2	Fissured, lenticeled	1	Disturbed
3	Fissured, peeled off	5, 6	Disturbed
4	Fissured, peeled off, soft	8	Undisturbed
5	Fissured, shedding	3	Disturbed
6	Peeled off, dry	1, 5, 13, 15, 16	Disturbed
7	Ridged, warty	5	Disturbed
8	Smooth	2, 4, 14	Undisturbed, disturbed
9	Smooth to fissured, moist	2, 3, 7, 17, 18	Disturbed
10	Smooth to fissured, warty	9, 12	Undisturbed
11	Smooth, lenticeled	2, 4, 8	Undisturbed
12	Soft, small fissured, warty	3, 5	Disturbed
13	Strongly fissured	9, 10, 11	Undisturbed
14	Strongly fissured, shedding	6, 13, 15, 16	Disturbed
15	Strongly fissured, soft, dry	1, 13	Disturbed
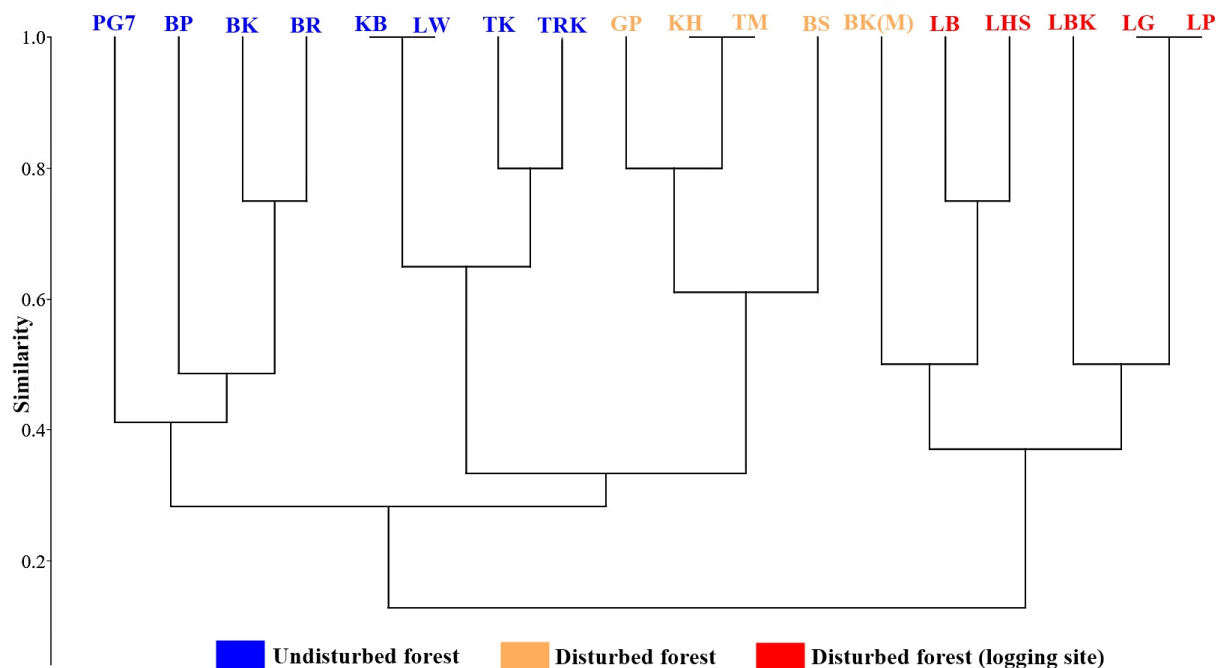
Figure 11. Similarity of host plants (bark textures) amongst the studied vegetation alliances using Bray–Curtis Similarity Coefficient.

4. Discussion

4.1. Ecological Implications of Current Findings on Orchid Diversity

Species richness, diversity, and abundance of the wild orchids differed in the different localities. It is known that orchid species richness differs across a land-use intensity gradient [3,63]. Generally, increment in the number of orchid individuals at each locality is corresponding to the classical species-area relationship where larger areas tend to contain larger numbers of species [64,65]. Moreover, in certain occasions, in extremely disturbed and dry forests, orchids do not decrease in species diversity and density with increasing disturbance, suggesting that orchids may indeed be comparatively disturbance-resilient [41,50]. In the current study, high abundance of orchids in disturbed forests was majorly comprised of epiphytic orchids whose occurrence was highly influenced by number of fallen trees, accessibility, and ease of human access for collections in the logged forest areas [50,66,67].

The problem of greater access to fallen trees in logged areas seems to be a methodological problem that appears to invalidate the 'higher diversity' found in the disturbed forests. Despite the vast area, the number and distribution of wild orchids in the deforested area were influenced by the number of host plants for epiphytic orchids and the microclimate conditions. Additionally, in some logging sites, especially the ones that have been neglected for many years, only one or two fallen trees are found over such a large area. Moreover, since most of the ground vegetation has been cleared for skid trails, ground orchids are rarely seen in the clearing zone and therefore have a low density. As in this study, species density decreased with increased disturbance level. The microclimate of disturbed forests was markedly altered from that of undisturbed forests, similarly, reported in [68] (also cited in [41]). Temperature, air humidity, and light intensity in the undisturbed forests and the extremely disturbed forests (logging sites) were significantly different proving that opening up of the forest canopy resulted in significant microclimate changes, which in turn affected the wild orchids [50,69].

Impoverishment of the logging sites was eminent, greatly contrasting with the non-logging disturbed forests and the undisturbed forests. Logging sites were reported with extremely high temperature and low relative air humidity and host plants' bark moisture. The abundance of epiphytes usually decreases in sites with lower precipitation [14,41,70]. The smaller number of orchids' taxa and terrestrial orchids in the non-logging disturbed forests (excluding logging sites) than the undisturbed forests indicates that the study area with extreme microclimate condition is a marginal habitat for wild orchids and seems to confirm the importance of temperature and humidity [41,70–72], light intensity, and the ground conditions [50] as a driver of wild orchids' species richness. Dry microclimate in the secondary forest, caused by the more open canopy of the secondary forest and the stronger radiation drove impoverishment [69]. The authors of [69] report that high temperature, low humidity, and lack of a dense bryophyte cover affected the bark moisture, and apparently had cascading effects on the diversity of epiphytic orchids in these forests. Epiphyte species should show stronger host specificity in habitats where climatic conditions are suboptimal for their performance because the modulating effect of tree traits is stronger under such conditions [73].

Presumably, drier sites featured only the dominant, robust, and drought-tolerant species [41,50,74] such as of *Bulbophyllum* and *Dendrobium* species. This explains the dominance of these genera in both undisturbed and disturbed forests. The drought-tolerant orchids tolerate drought instead of avoiding it [75]. They may be limited in their ecological distribution by their inability to maintain a positive carbon balance during repeated cycles of wetting and drying [76]. The lack of broad, thick leaves (thick cuticles) and trichomes (which protect against radiation and reduce water loss by protecting against wind and heat) are associated with their drought avoidance phenology. The plants produce roots at the beginning of the wet season and shed them as the dry season approaches [77,78]. Some plants possess storage organs such as pseudobulbs or pseudobulbous stem and rhizome to store water [79].

The results also show that sites with little anthropogenic influence have higher species densities than those with high anthropogenic influence. Primary or undisturbed forest areas have more natural vegetation and a protected microclimate, are less polluted, less disturbed by humans, including collecting pressures, and have more abundant host tree species with suitable characteristics [80,81]. The contradicting results of orchid diversity between undisturbed and disturbed forests from this study may also have been influenced by the unseen (unmeasured) drivers such as microbiomes [82,83] and soil properties [18,84].

Based on the genera abundance, the orchid flora of disturbed forests was not distinct from the canopy-protected and undisturbed forests, but still, the species richness and density were reduced. Forests that were either regenerating after clear-cutting or surrounded by plantations generally show considerably reduced species number compared to the matured and primary ones. Similar observations have been made in several studies, in which secondary moist forests regenerating after clear-cutting generally have

significantly reduced epiphyte species abundance compared to mature forests (vascular plants [14,85,86], bryophytes [2,87–89], epiphyte [41]). Three sites we studied, BS, GP, KH, which were regenerated and secondary forests, showed a similar pattern. The authors of [63,81] reported that species richness and abundance of epiphytic orchids gradually declined significantly with increasing habitat modification from unmanaged via remnant forest patches, agricultural land to very strong land-use intensity. This could indicate the regeneration of wild orchid communities in the disturbed forests following disturbance is very slow. However, this depends on how the forests are managed after cutting. For instance, one of our studied sites, PG7, is a regenerated forest that has now gazetted as a High Conservation Value Forest (HCVF) area, showing a considerably high diversity and density of orchids compared to the other studied undisturbed and disturbed sites. Different management practices influenced the orchid species and their composition and density.

4.2. Applications of the Current Findings for Informing Conservation and Restoration of Orchids

This investigation also gives prominence to the importance of the adjacent forests or the remaining natural forests for restoration as the forests constitute biological sources that enable succession from species-poor systems to highly diverse ones [90,91]. However, the disturbance projected by the forest clearing affected the ecological conditions and environment of the canopy-covered adjacent area. Forest clearing created forest margin or forest edge, where a large area of the forests was opened and disturbed, and a number of fallen trees cut during logging fell into the adjacent area. The adjacent area experienced increased temperature and light intensity. Consequently, it had lower diversity and density, too, if compared to the adjacent undisturbed forest. Similarly reported in studies [41,92,93], edge habitats experienced increased solar radiation, air temperature, vapour pressure deficit, and wind speed compared to the forest interior. Edge habitat fostered lower total species richness than any other habitat, but was similar in composition to closed forest [41]. Projected warming threatens the persistence of a population unless these populations possess a high micro-evolutionary potential that aid them in tolerating the environmental changes [94]. This includes species or certain species from genera *Bulbophyllum*, *Coelogyne*, *Cymbidium*, *Eria*, *Liparis*, *Oberonia*, *Paphiopedilum*, *Panisea*, *Pholidota*, and *Vanilla* [95]. Based on the comparative study on ecological and forest structure in Bukit Batu Kapal, Terengganu, a lowland to hill forest area, the undisturbed patches were home to abundant orchids and mature tree species, whereas the adjacent logged and secondary forest was composed of *Bulbophyllum* and *Coelogyne* species, and invasive and pioneer 'non-orchid' plant species. *Bulbophyllum* and *Coelogyne* species employed 'drought escape' adaptive strategy by shedding leaves and roots in dry conditions and leaving dormant pseudobulbs or stems to minimise transpiration.

The species composition of epiphytic orchids depends on several factors other than temperature, humidity, and light intensity, such as host plant species and bark characteristics as shown in [15,63]. Associations between epiphytic orchids and host characteristics are among the main factors affecting the diversity and distribution of epiphytes [3]. Along with altered microclimate, this has been attributed to reduced surface area for colonisation, and the lack of late successional substrates on young, small, and fast-growing host trees. In comparison with study [87], an analysis of tree-wide cortical moss diversity in primary rainforests, specialists recovered more slowly than generalists. In addition to this, the dominance of invasive tree and shrub species may restrict colonisation by epiphytic species. Exotic species such *Acacia*, invasive species such as *Bambusa*, and native pioneer species such as *Macaranga* have smooth bark texture, less favourable for the epiphyte colonisation, including the mosses and lichens. In forest areas that have been subjected to disturbance, *Acacia*, *Macaranga*, bamboos, and several species of early successional woody shrubs, such as Melastomataceae are common. Other than that, *Macaranga*, *Arenga*, and *Acacia* have a dominant presence in the secondary or converted forests. Epiphytic orchid specificity towards certain or single species of host plants was rather weak, in fact, their preference was more on the host characteristics regardless of species. According to studies [54,96], host

specificity exists when mutual trade-offs prevent a host-dependent species from adapting equally well to the full range of conditions found in different host species. The same species of orchids found on a variety of host plant species have similar characteristics in undisturbed lowland forests. This is a 'parallel host-specific scenario', a term coined in [54], in which all epiphyte species exhibit the same low or high performance on a particular tree species. Moreover, previous studies of few and small populations of an epiphytic orchid species increases the likelihood that limitation to a single tree species was simply due to randomness in combination with host biases [8,97]. For instance, the epiphytic orchids preferred host plant species, such as *Tristaniopsis*, *Syzygium*, and *Eurya* species growing along the riparian area, but not in the dry habitat as in the heath vegetation and belukar (bushes). In the riparian area, overtopped and intermediate trees were canopy-protected and constantly moist with thick substrate covering the trunk and branches. Host plants with smooth and dry bark texture, such as *Leptospermum javanica*, *Calophyllum* species, and *Tristaniopsis merguensis*, were abundant in Padang 7 which is peaked with coastal heath vegetation. Fewer epiphytes growing on these trees was not just because of the unsuitable bark texture, but was also highly affected by the extreme hot and dry environment of the heath vegetation. In fact, epiphytic orchids' associations with many host bark textures varied between localities indicating that some of the bark textures are locality-specific. Moreover, certain host traits may change during ontogeny which, in turn, may lead to differential 'life stage biases' [54]. These traits include leaf size and deciduousness [98] and bark properties [99].

Although species specificity (host-orchid species specificity) was not proved here in the current study, previous works have shown that epiphytes depend to some degree on potential host species [40] and some orchid species are restricted to certain host tree species [63,100,101]. In the protected forests, tall and large trees with Type 6 bark texture (soft, small fissured, peeled off, warty) were common, but rare in the secondary and intensively used forests. Tall and large trees in disturbed forests are often isolated. The crowns of such isolated large trees are also isolated from each other, meaning that large parts of the crowns are exposed to sun, favouring the orchids which use pseudobulbs as a water reservoir [4]. This was also observed in the current study where only the *Bulbophyllum* and *Coelogyne* were commonly dominating the isolated trees. Thus, large and old host tree individuals and host plants with rough or fissured bark are essential for the protection of epiphytic biodiversity.

However, not only the tree size but also the suitability of the stand to provide a microhabitat for the epiphytes is important. Some epiphytic orchids are more common in smaller trees and shrubs, similar to what was observed in [81,102]. Small trees with spreading crown along the riparian areas would accumulate as much as the tall trees. High abundance of species was not only observed on tall trees but also on smaller trees with spreading crown along the riparian area because, similarly, they are exposed to light and moisture. Host plants growing in the riparian area offer epiphytes specific microclimatic conditions. Similarly, the authors of [103–106] observed that the most preferred tree species occupied riparian areas, lower slopes, and valleys near swamps. These type of host plants were observed with very low abundance in disturbed forests. As reported in study [54], there are numerous instances of extreme basic host specificity that are not the typical 'tree' growth morphology. A notable example here is liana. Lianas such as *Spatholobus* species also accumulate epiphytic orchids, but the orchids were not recorded as being abundant as on trees.

Previous studies indicate that host species with rough bark are more frequently colonised by epiphytes [15,63,107,108]. The reasons for more epiphytes occurring on rough and fissured bark are that they retain moisture for longer and seedling recruitment is better as seed lodges more easily in the crevices in bark than on smooth bark [109,110]. Host plants with either flaking, large peeling or smooth bark, and low substrate cover are observed as poor hosts. The colonisation of bryophytes and lichens may influence substrate suitability for vascular epiphytes [8,71,111,112]. However, quantitative evidence

is lacking to support this claim. Rarity of the epiphytic orchids in young secondary forests was influenced by bark characteristics and tree architecture such as having little-branched crowns with oblique instead of horizontal branches [69]. This type of crown architecture is unfavourable for the establishment of epiphytes ([113]; cited in [69]). In secondary forests in Peninsular Malaysia, trees with round and overtopped crowns with a height of 6 m to 10 m are common. The hosts' bark texture significantly increased towards higher human impact, showing significant differences between all intensities [63]. Previous studies indicate that the diversity of epiphytes is positively correlated with host characteristics of bark texture [15,63], type of host (deciduous or evergreen) [114], pH of bark, light, wind, and tree diameter [115]. Unfortunately, in this study, the hosts' ages and sizes (diameter at breast height, tree height, and canopy volume) were not fully accounted for, as the age and size of some individuals of the fallen trees and lianas are difficult to verify. Additionally, the substrate cover was recorded only based on their general distribution on the hosts.

Terrestrial and mycoheterotroph orchids were found to be sensitive indicators of microclimate and human disturbance in the disturbed forests. Since most of the terrestrial and mycoheterotroph orchid species lack water storage organs and leaf cuticles, they are highly dependent on the soil conditions, more sensitive to forest disturbance, and favoured in forests with a dense tree canopy. Based on the findings, the terrestrial orchid species were underrepresented in disturbed forests. Additionally, the predominance of lithophytic orchids growing in rocky outcrop habitats, such as conglomerate hill and limestone hill forests, is significant. Some orchid species in the rocky outcrops are capable of living in two growth forms, growing as epiphytic and lithophytic. Many orchids, such as *Bulbophyllum*, *Coelogyne*, and *Dendrobium* species, which are normally epiphytic, but also grow on the ground or on limestone cliffs, similar to those reported in [116], are on the summit areas with high light levels. Their adaptation increases the likelihood that the rocky outcrop is lacking alternative hosts [54]. As reported in study [117], some shrubby or arborescent, mat-forming monocots have been found as alternative hosts on rocky outcrops in Africa and South America, including several Velloziaceae [118–121] and one Cyperaceae [117]. In this study, the alternative hosts could be bamboos (Poaceae) and *Eugeissona* or bertam (Arecaceae) growing at the bottom of rocky outcrops, but wild orchids were not seen growing there. Bases of limestone hills and ravines are usually shaded and have high humidity, which often creates a microhabitat that is suitable for terrestrial orchids [18,116], including *Paphiopedilum niveum* (Rchb.f.) Stein, *Nervilia concolor* (Blume) Schltr., and a *Crepidium* species.

5. Conclusions

Conclusively, microclimatic changes, anthropogenic disturbance, and low abundance of suitable host plants were key determinants of wild orchid composition and colonisation. We suggest these criteria should be considered in forest restoration to reduce disturbance impact on the associated orchid community. The study reported high diversity of epiphytic orchids and big differences in species richness, abundance, and species composition of orchid communities in different localities across disturbance gradients in Peninsular Malaysia. Wild orchids showed sensitivity to habitat quality and disturbance. Generally, wild orchid species density was decreasing with increasing human impact, especially with removal of host plants and extreme high temperature and light, and low humidity and bark moisture. Occurrence of terrestrial and mycoheteretroph orchids are indicators of microclimatic conditions and human disturbance. In non-logging forests, orchid abundance changes along the disturbance gradient. Epiphytic assemblages exhibit correlation to the type, bark texture, and bark moisture of the host plants. Conservation values of the suitable host plants for epiphytic orchids' diversification is worth further study. The significant difference in microclimate of the adjacent undisturbed and disturbed forests appears to underline the extreme effect of the disturbance which happened in the disturbed area towards the intact adjacent area. Forest and ecological alterations caused a shift in patterns of orchid species composition, where the robust and sun-loving species are dominating the

forests. However, the considerable effect of the disturbance towards the community in the specific vegetation types requires further research because our current study was limited to the pre-created trails only.

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