The floristic position of Java

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ABSTRACT. Floristically, Java was always considered to be west of Wallace's line together with the Malay Peninsula, Sumatra, Borneo, the Philippines and Sulawesi. Recently, statistical analyses of rough geographic data per species (presence or absence on islands or island groups) showed that Java is part of the central Wallacean area in Malesia (together with also the Philippines, Sulawesi, the Lesser Sunda Islands, and the Moluccas) rather than of Sundaland (restricted to the Malay Peninsula, Sumatra, and Borneo). More precise distribution maps for Java with collecting localities show that most species are widespread over Java or show a (more) western distribution; few species show an eastern distribution. The distributions show strong correlations with altitude (mountain species) and with precipitation (roughly wet in the west, dry in the east). The expectation was to find mainly species with a drought preference (Wallacean). However, most species show a preference for a wet distribution, which is related to a Sunda distribution. The fact that the statistical tests used for the first database show a Wallacean connection for Java probably is the result of the relative values these test use instead of absolute numbers, e.g., the resemblance between, especially, the flora of the Lesser Sunda Islands with Java is very high.

Keywords. Flora Malesiana, floristics, Java, Malesia

Introduction

In 1859 Wallacea introduced his famous zoological boundary, Wallace's line (Huxley 1868), that divided the Malay Archipelago (or Malesia: Steenis 1950; Raes & Welzen 2009) into an eastern and western part. Wallace's line runs east of the Philippines, then either west (Wallace 1859, 1863–1876) or east (Wallace 1860, 1910) of Sulawesi (also known as Celebes), and ends between Bali and Lombok in the Lesser Sunda Islands. Wallace discussed the position of Sulawesi in his book 'Island life' (Wallace 1880), in which he calls Sulawesi an 'anomalous island' with no continental connections as Sulawesi lacks Sundaic groups and contains (old) endemic and Australasian species. A more complete historical overview is presented in Simpson (1977) and George (1981), who both show that a number of variants of Wallace's line have been proposed based on the study of different groups of organisms (Fig. 1). The area encompassed by these lines is often called Wallacea, a term coined by Dickerson (1928), for an area already delimited by Wallace in 1863. The areas to the west (Malay Peninsula, Sumatra, Java, Borneo) and to the east (New Guinea) are referred to as the Sunda Shelf and the Sahul Shelf, respectively.

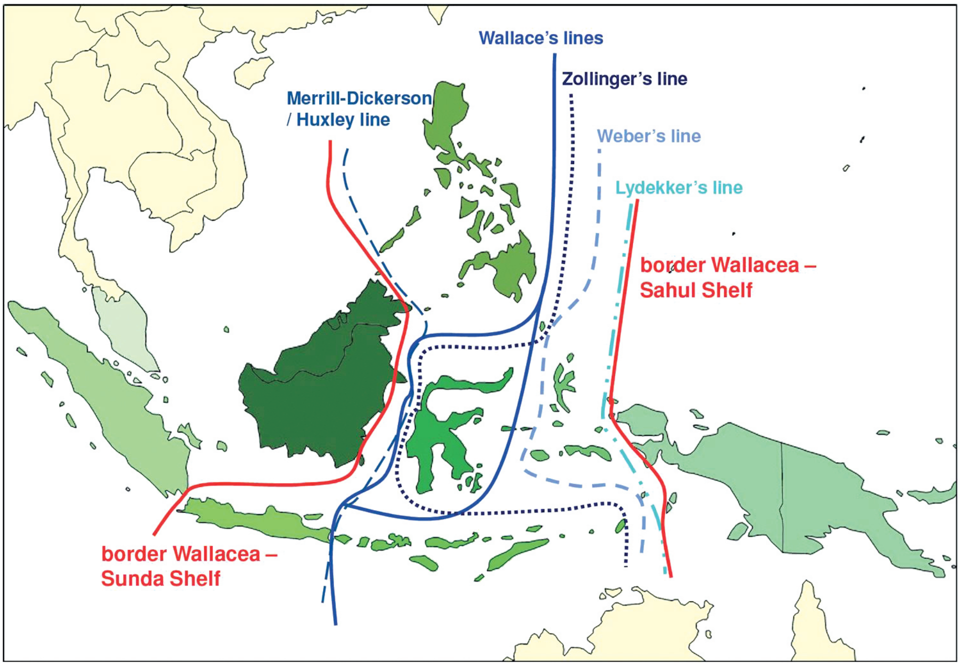

Fig. 1. Interpretations of Wallace's lines around Sulawesi and various alternatives are depicted in shades of blue. Red lines show the borders between the Sunda Shelf, Wallacea and the Sahul Shelf resulting from analyses discussed in the text.

Almost only zoological data were used to distinguish the lines (George 1981), and unsurprisingly, most botanist did not use the various boundaries. Steenis (1950) used distributions of plant genera when he contemplated the limits of the Malesian region, and based on the same data Wallace's line did not appear to be a distinct boundary in plant distributions. Welzen et al. (2005) used a limited floristic species database to show that all lines do form distinctive boundaries in plant distributions, each line stopping at least twice as many taxa as passing. Welzen & Slik (2009) even indicated which families are mainly responsible for the distribution patterns in Malesia. Only 20 families determine the patterns. Dipterocarpaceae, Fagaceae, and Nepenthaceae have their centre of diversity on the Sunda Shelf; Ericaceae, Monimiaceae, and Sapindaceae are typical for the Sahul Shelf; Araliaceae, Boraginaceae, Convolvulaceae, Cyperaceae, Dioscoreaceae, Lamiaceae, Loranthaceae, Mimosaceae, and Moraceae are predominantly Wallacean, and Burseraceae, Caesalpiniaceae, Flacourtiaceae, Meliaceae, and Myristicaceae show no distinct centre.

Recently, Welzen et al. (2011) analysed the distribution data per island group of all species published in Flora Malesiana series 1 (Angiosperms) and the Malesian orchids in Orchids Monograph (for island groups see Fig. 1). Various phenetic techniques were used: Principal Components Analysis, Fig. 2A; Non-metric Multidimensional Scaling analysis, Fig. 2B; a cluster analysis, Unweighted Pair Group Method with Arithmetic mean, Fig. 2C; and Kroeber's coefficient, the mean floral similarity between pairs of areas, Fig. 2D. All results show that Java is not west of Wallace's line, but east of it (Fig. 2). The tests were repeated for 100 randomly drawn matrices with equal contributions of all areas (500 species per area), which should nullify the effect of different island sizes (large islands like Borneo and New Guinea harbour far more (endemic) species than other areas and are then automatically separated from the rest in the analyses). Also, the analyses of the 100 matrices showed the same result for Java, not a part of the Sunda Shelf areas, but part of Wallacea. Thus, the borders between the three areas, Sunda Land/Shelf, Wallacea and Sahul Land/Shelf, have to be redrawn a bit (red lines in Fig. 1).

The Kroeber's Coefficient (Fig. 2D) nicely shows that in fact the botanical relationship between Java and Wallacea just wins in the other three analyses (PCA, NMS, UPGMA) from a Sunda relationship, because Java has a high floral mean resemblance (Fig. 3) with on the one hand Sumatra and the Malay Peninsula (Sunda Land) and on the other hand a slightly higher mean resemblance with the Lesser Sunda Islands and Sulawesi (Wallacea). The floral resemblance with Borneo (Sunda) and the Philippines and Moluccas (Wallacea) is somewhat less. Welzen et al. (2011)

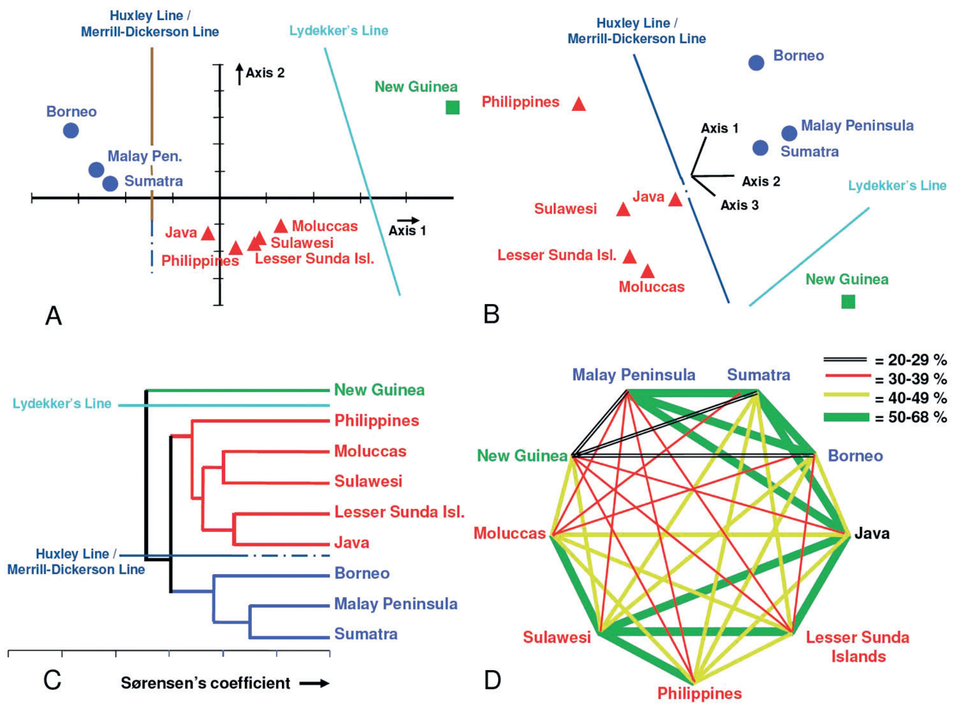

Fig. 2. The results of various phenetic tests on a database with presence/absence data per island group for indigenous species revised in Flora Malesiana and Orchid Monographs. All tests place Java together with Wallacean areas. **A.** Principle Components Analysis (PCA). **B.** Non-metric Multidimensional Scaling analysis (NMS). **C.** Unweighted Pair Group Method with Arithmetic mean (UPGMA). **D.** Kroeber's coefficients with a mean floral similarity between pairs of areas indicated by various thicknesses of the lines connecting the pairs.

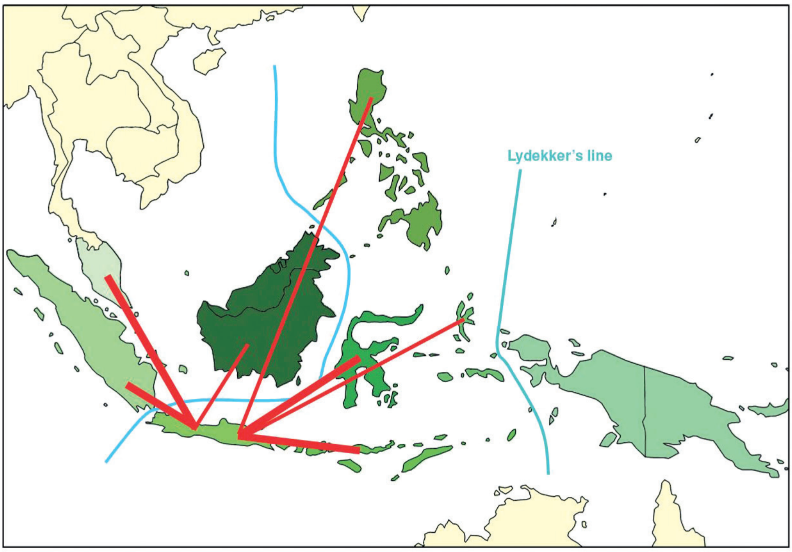

Fig. 3. Kroeber's coefficients between Java and the Sunda and Wallacean areas showing a high resemblance, on the one hand, with Sumatra and the Malay Peninsula on the Sunda Shelf; and, on the other hand, with the Lesser Sunda Islands and Sulawesi within Wallacea. Blue lines depict the borders of Wallacea.

discuss that the floral resemblances can largely be explained by the supposed savannah corridors running from the Malay Peninsula along and over Sumatra to Java during glacial periods. Via this corridor species that prefer a yearly dry period could disperse and are now still found in areas with a yearly dry monsoon.

The purpose of this paper is threefold: - establish why plant distributions more strongly point to a Wallacean relationship for Java; - check which kind of phenetic distribution patterns exist witin Java; and - explain these.

Materials and methods

In previous studies (Welzen et al. 2005, Welzen & Slik 2009, Welzen et al. 2011), a database was used whereby the presence and absence of indigenous species revised in Flora Malesiana series 1 and Orchid Monographs was noted for the Malay Peninsula, Sumatra, Java, Borneo, the Philippines, Sulawesi, Lesser Sunda Islands, Moluccas, and New Guinea. The areas used necessitated two alterations for two lines. The Merrill-Dickerson variant of the Huxley line runs officially between Palawan and the rest of the Philippines. This line is now considered to run between Palawan and Borneo (Fig. 1). Also, Wallace's line ends between Bali and Lombok in the Lesser Sunda Islands; this is redrawn between Java and Bali (Fig. 1). These redrawn lines are used in this study.

For this study, a database was created with collecting localities of species that are represented by digitised herbarium specimens from Java. Up to now, the database contains 97 families and 447 genera. The families starting with A or B are fully digitised, plus a part of C (26 families), some of the other families have also been digitised (e.g., Euphorbiaceae, Rhamnaceae, Sapindaceae, Vitaceae), but most other families are only partly digitised. The localities were georeferenced with the websites http://earth-info.nga.mil/gns/html/index.html and http://www.fallingrain.com/world/. Only the species with five or more different localities were included in the analysis, fewer localities were considered too incomplete to infer a distribution pattern. In total 808 species were sorted visually into different distribution patterns. This appeared to be rather straightforward. Four patterns were discriminated: 1) widespread over the island; 2) a western distribution (subdivided into 2a purely west, 2b west plus a few dots in central Java, and 2c west up to central Java; these three were not always distinctive); 3) a (central to) eastern distribution; and 4) a west-and-east-only distribution. All distributions were divided into low and high (above 1000 m) altitude.

The dot maps were produced with MapInfo Professional 7.0 (© MapInfo Corporation), the altitudinal and precipitation maps were made with Manifold GIS (Manifold.net), for which the datasets were obtained from the WorldClim 30 arc-second dataset (www.worldclim.org).

Results

Table 1 shows how many species were found per pattern. A large part, 49%, of the sampled plant species is widespread over Java (Fig. 4A). This group was not used in further analyses as they did not convey any information concerning a possible split of Java into the Sunda or Wallacean realms. It is possible to split off from this group plants typical for mangroves and beaches/dunes. A total of 273 species (Table 1) show a predominantly western distribution (Fig. 4B–D), some only in the extreme west (123 species, Fig. 4B), others with a few specimens in central Java (97 species, Fig. 4C)

Table 1. Numbers of species per pattern, divided for low, high or all altitudes. The western pattern is subdivided into three sub-patterns (shown in italics). The percentage is the percentage of 808 species.

Pattern	< 1000 m alt.	> 1000 m alt.	All altitudes	Total	%	Fig.
Widespread	288	36	72	396	49%	4a
West – Central	175	64	34	273	34%	
West	*76*	*37*	*10*	*123*	*15%*	4b
West (- Central)	*61*	*18*	*18*	*97*	*12%*	4c
West – Central	*38*	*9*	*6*	*53*	*7%*	4d
West and East	57	14	17	88	11%	4e
Central – East	36	10	5	51	6%	4f

or spread from west up to central Java (53 species, Fig. 4D). The opposite pattern, (central to) east Java also exists (51 species, Fig. 4F). The most curious distribution is perhaps the west and east distribution (88 species, Fig. 4E), whereby the species are absent in central Java.

Fig. 5A shows the mean amounts of yearly precipitation; western Java up to the central part, with the exception of the northern rim, plus the areas around the mountains in east Java are relatively wet, whereas the northern rim and the eastern

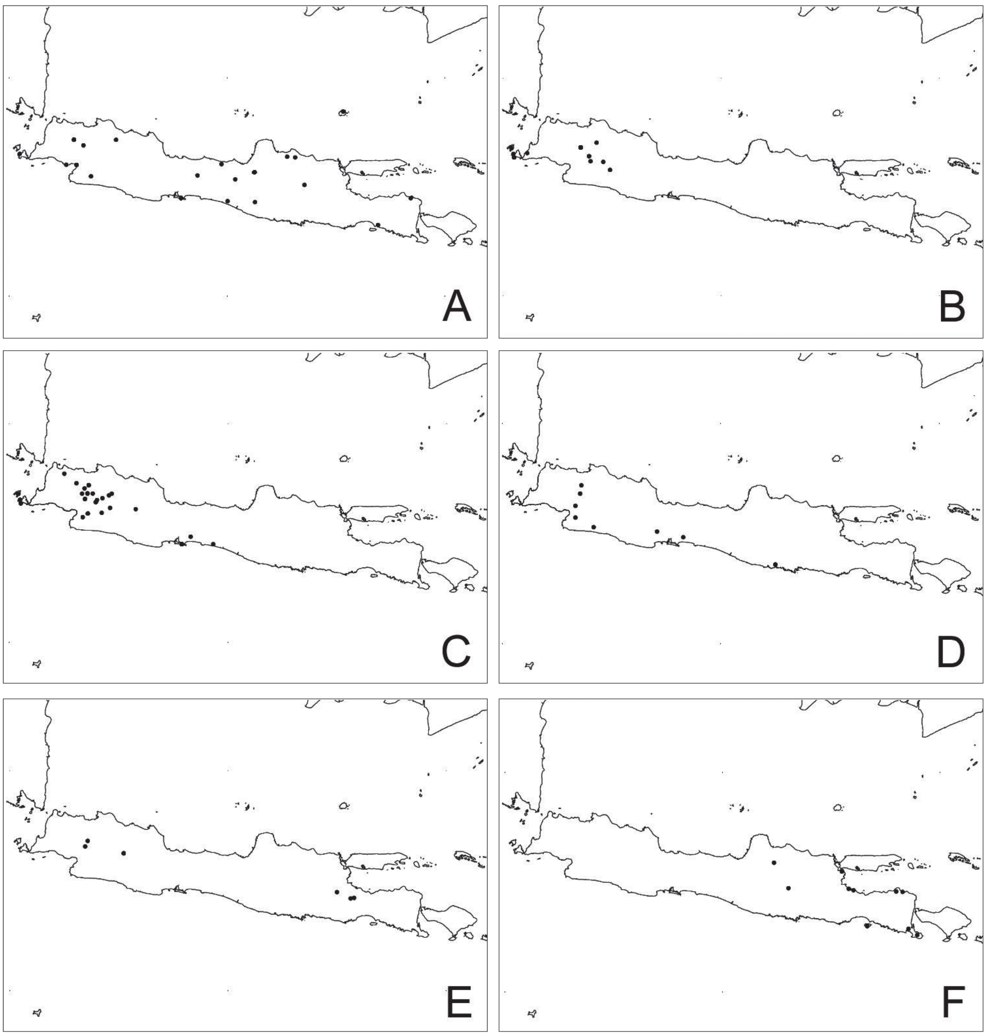

Fig. 4. Examples of the different distribution patterns, all low altitude. — **A.** *Maranthes corymbosa* Blume (Chrysobalanaceae/Rosaceae): widespread. **B.** *Pometia pinnata* J.R.Forst. & G.Forst. (Sapindaceae): west. **C.** *Kibara coriacea* (Blume) Tul. (Monimiaceae): West (– Central). **D.** *Cayratia japonica* (Thunb.) Gagnep. (Vitaceae): West – Central. **E.** *Epipogium roseum* (D.Don) Lindl. (Orchidaceae): West and East. **F.** *Capparis pubiflora* DC. (Capparaceae): Central – East.

half are much drier. Fig. 5B shows the mountains on Java. There is a row of volcanoes along the central axis of the island with a concentration of mountains in especially the western part. The low-altitude distributions correlate very well with the precipitation map (Fig. 5A). The western distributions are present in the wetter areas (demonstrated by the red dots of *Kibara coriacea*; Fig. 5A). The same correlation with wet areas is shown by the west and east distributions (grey dots of *Epipogium roseum*; Fig. 5A), in the west they are in the wet areas, in the east in the wet areas around the mountains. The eastern patterns show a correlation with low amounts of rain (blue dots of *Capparis pubiflora*; Fig. 5A).

The high-altitude distributions show a good correlation with the altitudinal map. Fig. 5B shows with red dots the distribution of the widespread *Sarcococca pruniformis* Lindl., and with blue dots the west and east distribution of *Dendrobium tetraedre* (Blume) Lindl. These species are present on the slopes of the mountains and thus also in areas with a higher precipitation.

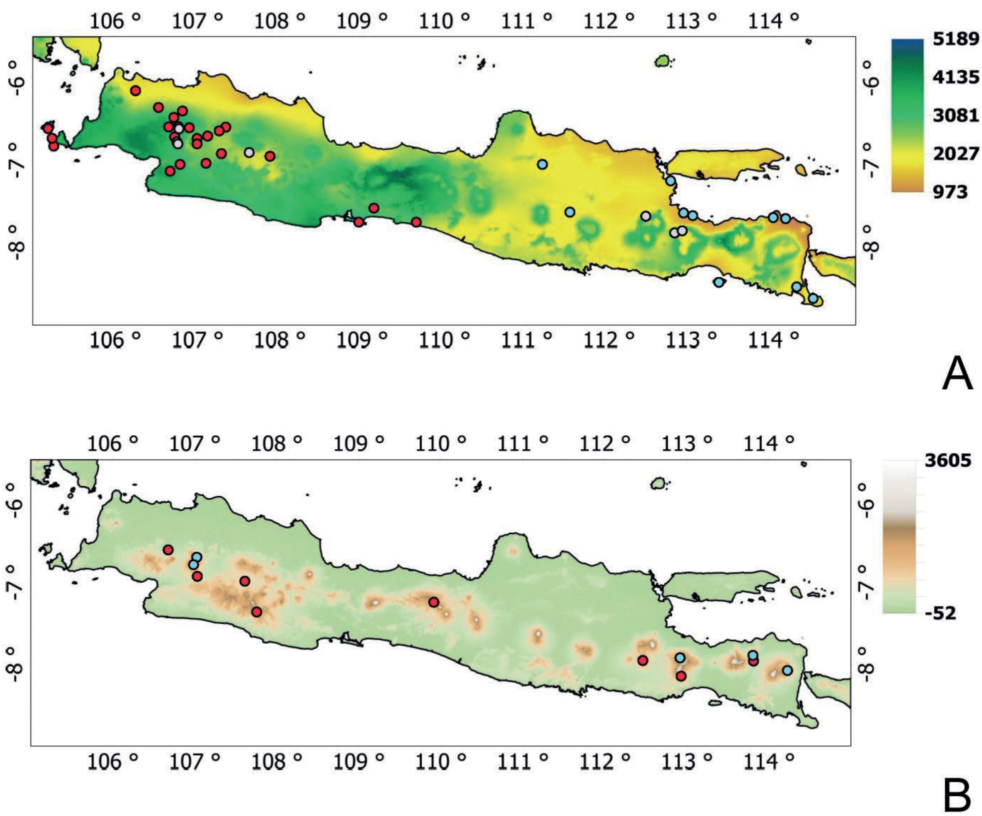

Fig. 5. A. Map of Java showing the mean annual precipitation in mm, ranging from 973 mm per year (brownish yellow) to 5189 mm (dark green). Red dots represent the distribution of *Kibara coriacea* (Blume) Tul. (Fig. 4C), green dots are *Capparis pubiflora* DC. (Fig. 4F); and grey dots are *Epipogium roseum* (D.Don) Lindl. (Fig. 4E). **B.** Map of Java showing altitude in m; red dots: *Sarcococca pruniformis* Lindl. (Buxaceae); blue dots: *Dendrobium tetraedre* (Blume) Lindl. (Orchidaceae); both are species of higher altitudes.

Discussion

The Sunda Shelf is characterised by an everwet climate, while most areas in Wallacea have a dry monsoon during part of the year (Steenis 1979). Thus, the distributions correlating with high(er) precipitation, the western (Fig. 4B–D; 5A: red dots), west and east (Fig. 4E, 5A: grey dots) and higher altitudinal distributions (Fig. 5B) point at a Sunda element in the flora of Java, while the distributions correlated with a dry monsoon, the eastern distributions (Fig. 4F, 5A: red dots), show the Wallacean influence. From Table 1 it follows that most species show a Sunda distribution pattern, while in the introduction it was explained that the highest floristic bonds are with the Wallacean areas (Fig. 2). How can we explain this apparent discrepancy?

The sample used might be too small. Up to now only the Javanese collections of the families starting with "A" or "B" have been fully digitised and georeferenced. These families might be biased towards a western distribution. The database will be extended in the future to cover all Javanese collections. The bias is probably absent, because Araliaceae and Boraginaceae, representing typical Wallacean elements (Welzen & Slik 2009; see introduction), are already included in the sample.

Dot maps only show places that were visited by collectors. All distributions are incomplete, because many places have never been visited or sampled. This problem can be overcome by applying species distribution or ecological niche modelling (e.g., Raes 2009), whereby environmental variables are correlated with the conditions present at the collecting localities and these are extrapolated to possibly suitable, non-sampled areas. These models may perhaps show a more Wallacean correlation. However, this is not expected as the dot maps already infer such a high correlation with precipitation and altitude.

One might argue that redrawing Wallace's line between Java and Bali, instead of between Bali and Lombok, caused the close floristic bonds between Java and the Lesser Sunda Islands. A possible high floral resemblance between Java and Bali may obscure the gap in floral elements between Bali and the rests of the Lesser Sunda Islands. However, this is not the case, because Bali is (as far as plants are concerned) much under-sampled in comparison to Java and the two other provinces in the Lesser Sunda Islands. The specimen database in the Leiden herbarium (L) shows 44,038 specimens for Java, only 728 for Bali, and 6,180 for the rest of the Lesser Sunda Islands.

Table 2 provides another explanation. Java shares a very high percentage of its flora with Sumatra and the Malay Peninsula (74% with each), but from the viewpoint of Sumatra and the Malay Peninsula this is far less (48% and 39%, respectively). For the Lesser Sunda Islands and Sulawesi this is different, they share 78% and 56% of their flora, respectively, with Java, while slightly more than 50% of the Javanese flora is present in the Lesser Sunda Islands and Sulawesi. Thus, based on percentages the shared flora between Java and the Wallacean areas is higher than with Sunda Land. However, when total numbers of species are compared (first column of Table 2), then Java shares more species with Sumatra and the Malay Peninsula than with Wallacea. The statistical tests discussed in the introduction (Welzen et al. 2011; Fig. 2) use

Table 2. Floristic overlap between Java and the various other islands: the first column shows the number of shared species between Java and one of the other regions; the second column the percentage overlap from the perspective of the other region; and the third column the percentage overlap from the perspective of Java. Thus Java and Sumatra share 999 species, which is 48% of Sumatra's flora and 74% of Java's flora. The numbers of species were obtained from a database with presence/absence data per island group for all Malesian indigenous species published in Flora Malesiana ser. I and in Orchid Monographs.

Region	No. Spp.	% Region	% Java
Sumatra	999	48	$\boxed{74}$
Malay Peninsula	831	39	$\boxed{74}$
Borneo	773	28	57
Lesser Sunda Islands	702	$\boxed{78}$	52
Sulawesi	683	$\boxed{56}$	51
Philippines	762	41	57
Moluccas	490	52	36
New Guinea	581	20	43

relative numbers in their analyses. Therefore, it is not surprising that the tests placed Java in the Wallacean realm, while total numbers point at a Sunda connection.

The West and East disjunct distributions are not easily explained. They may be a result of glacial–interglacial cycles. During glacial periods the sea levels dropped and altitudinal floral zones on mountains became much lower, probably providing continuous ranges or stepping stones for dispersal and as a result, continuous, non-disjunct distributions. During interglacial periods, like present day, sea levels are much higher, just like the altitudinal floral zones on mountains. Seemingly, especially in central Java, species have disappeared, perhaps due to adverse conditions on the central mountains. This may also have happened to species now only restricted to higher altitudes in west Java: these may have been widespread during glacial periods, but disappeared in central and east Java during interglacial periods. An alternative explanation might be that the human influence in especially central Java was much higher than in east and west (probably not realistic as most people live in west Java) or that there has been less sampling in especially central Java.

Conclusions

Java shows a kind of floristic Janus head. On the one hand, based on total numbers of shared species, Java clearly has a Sunda Shelf relationship with especially Sumatra and the Malay Peninsula (Table 2, column 1). On the other hand, when relative numbers are used, then the higher resemblance with especially the flora of the Lesser Sunda

Islands and, to a lesser extent, that of Sulawesi, places Java in the Wallacean realm.

The distributions in Java mainly show a western or eastern component. The western distributions correlate with a high(er) amount of rainfall, the eastern distributions with a preference or tolerance for a drier climate. The higher altitudinal distributions correlate with the presence of volcanoes on Java.

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