

Congruent patterns between species richness and areas of endemism of the Greenideinae aphids (Hemiptera: Aphididae) revealed by global-scale data

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Species richness and endemism are of remarkable significance in historical and ecological biogeography. Aphids with close association with their host plants may well reveal the underlying mechanism that shaped distribution patterns from both biotic and abiotic factors. We identified patterns of species richness and endemism for Greenideinae aphids on the global scale, using 1049 records of 192 extent species/subspecies. Parsimony analysis of endemism and endemism analysis were applied to detect areas of endemism (AoEs). The parsimony analysis of endemism was performed in PAUP 4.0a152 on weighted data (down-weighting of widespread species); three different grid sizes were used in the endemism analysis. The highest species richness was located in the eastern Himalayas, Hainan Island, Taiwan Island and Java. AoEs were detected as the eastern Himalayas, western Himalayas, mountains of southwest China, south edge of China, east China mountains, Hainan Island, Taiwan Island, Honshu Island, Malay Peninsula and Java. There is noticeably a congruent pattern between species richness and AoEs. Montane areas and mountainous islands characterized by complex topography and varied habitats were beneficial for forming these hotspots of diversity and endemism, whereas intimately associated host plant distribution and diversity were more important in illuminating distribution patterns for these host-specific insects.

ADDITIONAL KEYWORDS: aphid – biodiversity – biogeography – endemism – Greenideinae – island – montane area – patterns of distribution.

INTRODUCTION

Identifying and understanding patterns of biodiversity are fundamental to biogeography and conservation biology. Both species richness and endemic species are frequently used as indices in defining biodiversity hotspots (Myers *et al.*, 2000; Mittermeier *et al.*, 2005; Orme *et al.*, 2005). The definition of area of endemism (AoE) is now generally agreed upon after a much debated past, as a distribution congruence of at least two restricted species (Cracraft, 1985; Harold & Mooi, 1994; Morrone, 1994; Linder, 2001). AoEs are entities compared in terms of ascertaining earth history based on biological patterns (Henderson, 1991; Linder, 2001).

Studies on species richness and endemism are also of remarkable significance in biogeographic regionalization (Linder & Mann, 1998; Escalante, Morrone & Rodríguez-Tapia, 2013; Morrone, 2014a). Myers & Giller (1988) considered the determination of species distribution patterns as the starting point for all biogeographic studies. Furthermore, illuminating patterns of species richness and endemism is of particular value in setting priorities for biodiversity conservation.

In an AoE, faunal or floral distributions are supposed to have been generally influenced by historical processes, such as tectonic activities or climate changes. These areas are supposed to be characterized by a stable climate, and they therefore offered considerable opportunities for past speciation and persistence (Jetz, Rahbek & Colwell, 2004). This long-term evolution may explain why AoEs often contain high

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species richness, which is less predictable by contemporary environment alone. Thus, a history is behind species richness, despite the prominent role of contemporary environmental factors on patterns of overall species richness (Jetz *et al.*, 2004; López-Pujol *et al.*, 2011; Fjeldså, Bowie & Rahbek, 2012). Although covering only a small proportion of land area, mountains account for a large proportion of biodiversity hotspots, harbouring many narrow-ranged species (Orme *et al.*, 2005; Fjeldså *et al.*, 2012; Wu *et al.*, 2017). Many mountains have been anticipated as refugia with stable climates combined with heterogeneous topography. These characteristics of montane areas facilitate both persistence (species museums) and speciation (species cradles). High rate of endemism is normally observed for island systems because of biotic isolation and oceanicity (Cronk, 1997; Myers *et al.*, 2000). The species richness and endemism of island systems are related to size, environmental complexity, climatic stability, as well as isolation from source continents.

Currently, alternative protocols and algorithms have been proposed to delimit AoEs (Shi, 1993; Linder, 2001; Szumik *et al.*, 2002; Hausdorf & Hennig, 2003; Szumik & Goloboff, 2004; Morrone, 2014b). Although different optimality criteria have been developed to compare the performance of these methods (Linder, 2001; Carine *et al.*, 2009), no consensus has emerged on the most appropriate method for detecting endemism. In some cases, a study may combine and integrate more than one method, to verify or assist each other, depending on specific purpose of the analysis (e.g. Moline & Linder, 2006; Escalante *et al.*, 2013; DaSilva, Pinto-da-Rocha & DeSouza, 2015). Morrone (1994) modified the parsimony analysis of endemism (PAE) proposed by Rosen (1988). Based on the cladistic principle, PAE hierarchically groups area units as AoEs according to their shared taxa. It is the first method proposed to formally and objectively ascertain AoEs and remains widely used (e.g. in Huang, Lei & Qiao, 2008; Escalante *et al.*, 2013; DaSilva *et al.*, 2015). Szumik *et al.* (2002) and Szumik & Goloboff (2004) proposed the endemism analysis (NDM) method, which directly incorporates spatial information into delimitation of AoEs by assessing the congruence between a given area and species distributions. Searches for AoEs are usually conducted in endemic taxa confined to islands or to specific regions on one continent. Only a few works elucidating geographical patterns on a global scale have been conducted.

Greenideinae is a subfamily of Aphidoidea. Species therein are commonly known for their long and hairy siphunculi and long body hairs with variable apices (Ghosh & Agarwala, 1993). Three tribes and 18 genera have been recognized in this subfamily, including 179 extant species, six subspecies and 10 fossil species. The extant Greenideinae are distributed worldwide,

except for in North America and the Antarctic. Many species of Greenideinae have small distribution ranges, with most of the diversity confined to south and south-east Asia, although exceptions include *Anomalaphis*, *Meringosiphon*, *Greenidea* (*Greenidea*) *ficicola* and *Schoutedenia ralumensis* distributed in Australia, *Brasilaphis* recorded in South America, and *Eonaphis* and *Paulianaphis* restricted to palaeotropical regions. Greenideinae are monoecious, with a holocyclic or anholocyclic life cycle on woody plants of more than 40 families, such as Fagaceae, Lauraceae and Euphorbiaceae etc. (Ghosh & Agarwala, 1993; Noordam, 1994; Blackman & Eastop, 2017). Some greenideine aphids are important pests or invasive species threatening agricultural, horticultural and forestry economics.

As sap sucking insects, aphids have established a close association with their host plants, and many species in Greenideinae exhibit high degrees of specialization on a small number of host plants from specific genera and families. Lacking long distance dispersal capabilities, the distribution and radiation of aphids are directly related to those of specific host plants. Additionally, host-specific aphids are apparently easily affected by geological events or climatic changes (Zhang *et al.*, 2012). These factors make aphids a unique and excellent model for investigations of the evolutionary history of species diversity and distribution patterns from multiple factors, both biotic and abiotic, rarely conducted in other organisms.

The diversity and endemism patterns of aphids in the Qinghai-Tibet Plateau-Himalayas (QTPH) and southwest mountainous range of China have been preliminarily discussed (Huang, Qiao & Lei, 2006; Huang *et al.*, 2008; Chen *et al.*, 2016). Apart from the work of Li *et al.* (2017), few efforts have been directed towards identifying and explaining distribution patterns of aphids on such a global scale with both PAE and NDM methods.

The taxonomic system of Greenideinae has been well revised in recent years (Blackman & Eastop, 1994; Remaudière & Remaudière, 1997; Zhang, 2008; Favret, 2016), and the patterns of distribution and phylogenetic relationships have been preliminarily investigated (Zhang, 2008; Zhang *et al.*, 2011, 2012; Liu, 2014). However, an understanding of biogeography remains in its infancy, and hypotheses on shaping patterns of species richness and endemism are completely absent. Because the correlations between biodiversity hotspots under different types of indices remain controversial (Jetz *et al.*, 2004; Orme *et al.*, 2005), the comparison of AoEs with centres of species richness may allow a further investigation of congruence between historical biogeographical patterns and current spatial biodiversity patterns. Therefore, the present study aimed to: (1) identify centres of species richness and AoEs; (2) probe the congruence between patterns of species richness and endemism; (3) evaluate whether distribution patterns of Greenideinae are

accordant with those of other organisms and (4) test whether Greenideinae support the hypothesis of montane system biodiversity.

MATERIAL AND METHODS

COLLECTING DISTRIBUTION DATA

In this study, we constructed a database of all Greenideinae species across the globe. Ultimately, 1049 records for 192 species/subspecies (including nine unpublished new species) with detailed collecting sites were used in the analysis (Supporting Information, Data Matrix S5). The species distribution data, particularly the records in mainland China, were primarily extracted from the sampling data set constructed by our group over the past decades. We additionally obtained distribution data from published literatures and from the online data set *Aphids on the world's plants: an online identification and information guide* (Blackman & Eastop, 2017). The species names were verified using the aphid catalogue from the online database <http://Aphid.SpeciesFile.org> (Favret, 2016). For species containing multiple subspecies, each subspecies was treated as an independent taxon. Most of the species distribution data were arranged with geographical coordinates or detailed location address. Localities without robust coordinates or that only gave concise administrative areas were standardized using Google Earth software by identifying the detailed locations and coordinates data. Imprecise distribution records only located to country, state, province were excluded, and records at city, district or county levels were represented by the locations of the local administration. Distribution information regarding species dispersal by human activity was not considered.

MAPPING SPECIES RICHNESS

The processed distributional data were imported into ArcMap 10.2 (ESRI, Inc., Redlands, CA, USA) for mapping the point occurrence pattern. To map species richness patterns, a fishnet with latitude–longitude grid size of 2° was created to subdivide the distribution area of Greenideinae, and the number of species in each grid was calculated and ranked, shown with different colours on the map.

We used a species accumulation curve to detect potential under-collection, following Moline & Linder (2006). The log-transformed number of collections per cell was plotted against the log-transformed number of species per cell. Potential under-collection in any cell will be evident in the lower than expected number of species as predicted from the number of collections.

DETECTING AOES

We applied two protocols to identify AoEs, using distribution maps constructed with different grains of grids and the presence–absence matrices as input data. The performance of different protocols can be compared by the number of AoEs they delimit, as well as by the number of species restricted to these AoEs.

Parsimony analysis of endemicity (PAE)

In PAE, the distribution map was divided into 2° grids, and the grids were treated as terminals (Morrone, 1994). We chose the 2° grid size to avoid fragmentation of the distribution, and set the grid origin at 65°N and 52°E to encompass the entire study area. Three hundred and two grids had distributional records. Among them, 169 grids containing two or more taxa were included in our final analysis. Grids with only one species or subspecies and grids with no records were excluded from the analysis because they were not informative. To reduce the influence of widespread species, we down-weighted those species by the inverse of the range for each species. The resulting values were transformed to integers between 0 and 9 to suit the parsimony analysis in PAUP 4.0a152 (Swofford, 2017).

A matrix of 170 grids × 192 taxa was constructed (Supporting Information, Data Matrix S5). An out-group comprising all zeros was added to the resulting matrix to root the trees (Morrone, 1994; Morrone & Escalante, 2002). The PAE was conducted in PAUP 4.0a152. Then, a 50% majority consensus tree of the equally parsimonious trees was obtained. During the search, we evaluated relative support for each branch using bootstraps with 1000 replicates. Branches with relatively high bootstrap values (50% or greater) were chosen as candidates for AoEs. Finally, AoEs (clades of grids), defined by two or more species restricted to these areas, were delimited and mapped.

Endemicity analysis (NDM)

All endemicity analyses (Szumik & Goloboff, 2004) were performed in NDM/VNDM v. 3.1 (Goloboff, 2016) using geographical coordinates of 192 greenideine species (Supporting Information, Data Matrix S5) under latitude–longitude grid sizes of 1°, 2° and 3°, respectively. These three different grains were set to examine the effect of this parameter on inferred endemic patterns. The analyses were conducted by saving temporary sets within 0.99 of current score, in sets with two or more endemic species and scores above 2.0. Subsets were considered overlapping if 50% of the species were unique, and the search was repeated 100 times. From the subsets obtained, species with a minimum score of 0.4 were selected (Escalante *et al.*, 2013; do Prado *et al.*, 2015).

Additionally, we calculated the consensus areas using the strict consensus, at a cut-off of 100% similarity in species (Szumik *et al.*, 2002).

To generate maps of AoEs, three outputs of different grid sizes obtained using the program NDM/VNDM v. 3.1 were converted into shape files by employing DIVAGIS 7.5 (Hijmans, Guarino & Mathur, 2012). These grid shape files were then plotted together using ARCGIS 10.2.

ABBREVIATIONS

The following abbreviations are used in the text and illustrations.

AoEs: ECM, east China mountains; EH, eastern Himalayas; HDM, Hengduan Mountains; HN, Hainan Island; HS, Honshu Island; JV, Java; MP, Malay Peninsula; TW, Taiwan Island; WH, western Himalayas; SEC, south edge of China. Genus names: *An.*, *Anomalosiphum*; *Al.*, *Allotrichosiphum*; *E.*, *Eutrichosiphum*; *Gr.*, *Greenidea*; *Gd.*, *Greenideoida*; *Mo.*, *Mollitrichosiphum*; *Me.*, *Mesotrichosiphum*; *Ma.*, *Metatrichosiphon*; *T.*, *Trichosiphum*; *Pa.*, *Paragreenidea*; *Pe.*, *Pentatrichosiphum*.

RESULTS

SPECIES RICHNESS PATTERNS

Although the subfamily Greenideinae is taxonomically well studied and documented, under-collecting remains a potential problem in biogeographical research. The species accumulation curves for 1° grid size did not indicate under-collection, with the coefficient of determination (r^2) above 85% (Fig. 3). The variation in numbers of species was explained well by the variation in numbers of collections.

High species richness was located in the Oriental and Palaearctic regions, with few species recorded in Australian, Ethiopian and Neotropical regions (Fig. 1). The richness pattern among localities was clearly asymmetric, with most species marginally distributed in east Asia, JV and Japan (Fig. 2). Within the zoogeographical regionalization of China, the highest species richness was in the south China region, but richness decreased rapidly northward. Based on the criterion of high species richness, four centres of species richness were discovered: (1) EH, (2) HN, (3) TW and (4) JV. These four areas represented centres with high species diversity for the subfamily Greenideinae (Fig. 2).

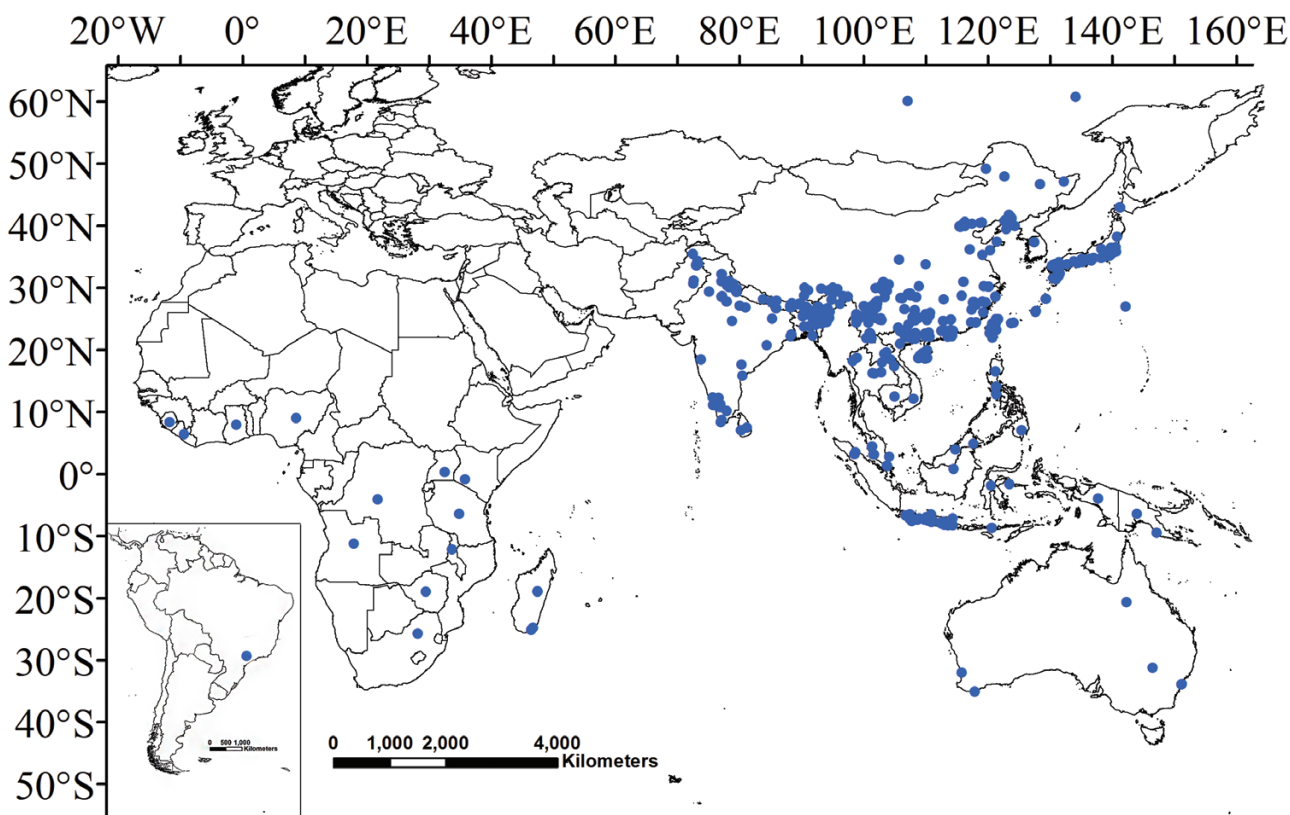


Figure 1. All records of Greenideinae aphids.

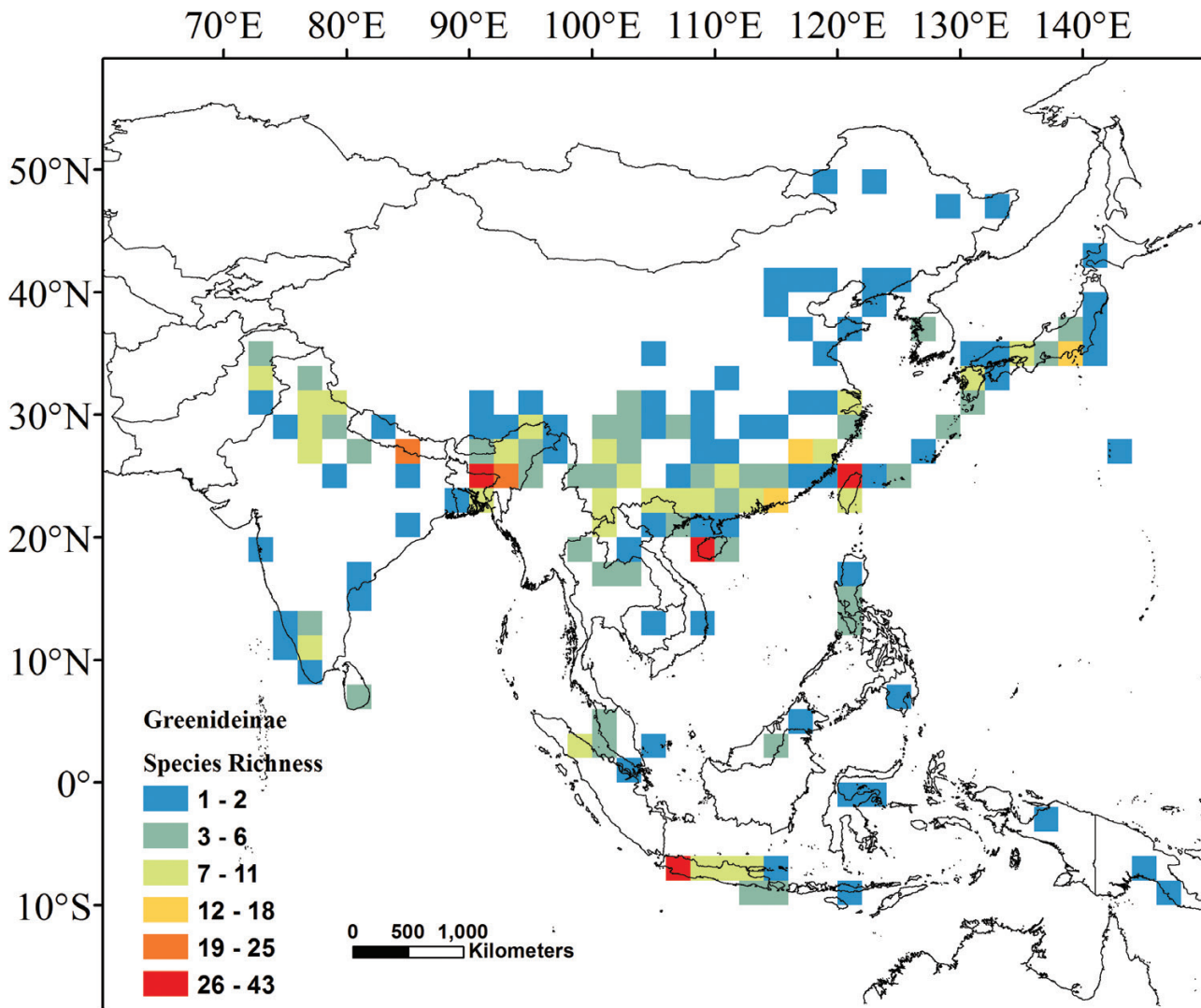


Figure 2. The species richness pattern of Greenideinae aphids under 2° grid size. The bars in the lower left show the corresponding colour scale, which is linear in terms of numbers of species.

AREAS OF ENDEMISM

Parsimony analysis of endemism

Among 192 taxa examined, 167 were parsimony-informative. Twenty-eight branches with relatively high bootstrap values (above 50%) were selected as candidates for AoEs; therefore, a group of cells was defined as an AoE when at least two species were restricted to the region. Clades defining South Africa and Madagascar were excluded for under-collection. Finally, nine AoEs were identified: EH that shared 15 species: *Al. assamense*, *An. indigoferae*, *E. manipurense*, *E. quercifoliae*, *E. sikkimense*, *E. subinoyi*, *Gd. (Pe.) lambersi*, *Gr. (T.) gigantea*, *Gr. himansui*, *Gr. longisetosa*, *Gr. photiniphaga*, *Gr. querciphaga*, *Gr. (T.) manii*, *Gr. (T.) quercicola* and *Gr. (T.) spinotibium*;

HDM which shared three species: *E. dubium yulongshanense*, *E. izas* and *E. russellae*; SEC that shared two species: *An. scleroticum* and *Gr. sp5.*; HN that shared five species: *E. sp1.*, *Gd. (Pe.) longirostrum*, *Gr. sp1.*, *Gr. sp4.* and *Me. Pentaiarticulatum*; TW that shared five species: *Gr. brideliae*, *Gr. mangiferae*, *Gr. quercifoliae* and *Gr. (Pa.) viticola* and *Gr. (T.) nigra kanzanensis*; ECM which shared five species: *E. sclerophyllum*, *E. parvulum*, *E. arunachali jianglense*, *Gr. (Pa.) cayratiae* and *Mo. (Ma.) luchuanum*; HS that shared five species: *Al. kashicola*, *E. shiicola*, *E. nigrisiphon*, *Gr. (T.) isensis* and *Gr. (T.) carpini*; MP that shared two species: *An. murphyi* and *E. roepkei* and JV which shared four species: *E. pullum*, *Gr. magna*, *Gr. rappardi* and *Gr. (T.) flacourtiae* (Fig. 4).

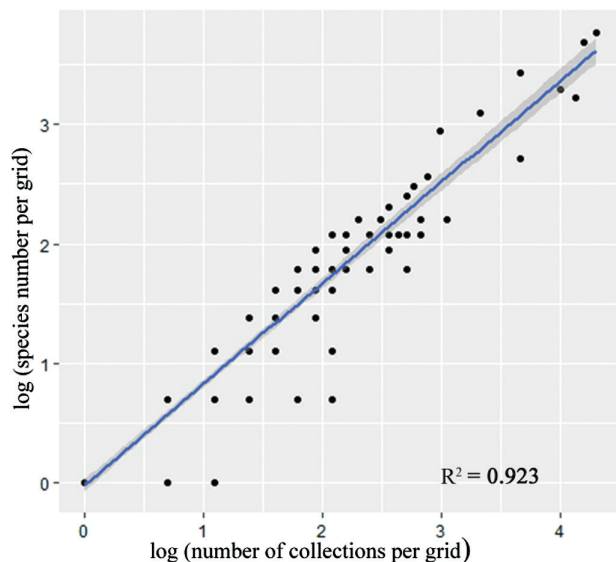


Figure 3. Species accumulation curves.

Endemicity analysis

The analysis using the 1° grid identified 11 sets. The consensus analysis identified seven consensus areas. These areas are associated with the EH, southwest of Guangxi Province, north of TW, and west of JV (Table 1; Supporting Information, Fig. S1). The search using the 2° grid yielded 18 sets and 14 consensus areas, which were primarily associated with the northwest India, northeast of India, Nepal, Bangladesh, and Burma, the junction of Yunnan and Guangxi provinces and Vietnam, Fujian Province, TW, and JV (Table 1; Supporting Information, Figs S2, S3). The analysis with the 3° grid produced 11 sets and 10 consensus areas, covering the EH, south China, Fujian Province, TW, HS, and JV (Table 1; Supporting Information, Fig. S4).

High degrees of overlap and proximity of consensus areas among different grid sizes provided consistent evidence of a high degree of endemicity (do Prado *et al.*, 2015). The overlapping patterns of the aforementioned consensus areas (Fig. 5) uncovered four main AoEs with great congruence among different grid sizes: (1) EH, which consisted of areas 2, 3, 5, 7, 8, 10, 11, 15, 17, 21, 27 and 30; (2) SEC, which included areas 1, 12, 16, 23, 24, 26 and 28; (3) TW, which was formed by areas 4, 9, 20 and 23 and (4) JV, which comprised areas 6, 14, 19, 22 and 31; in addition, four peripheral AoEs were defined only in one or two grid sizes: (5) HN, which included areas 16, 24 and 28; (6) ECM, which comprised areas 20 and 23; (7) WH, which included areas 13 and 18 and (8) HS of Japan, which comprised 25 and 29.

Eastern Himalayas: The EH included areas that were obtained from all grid sizes (Supporting Information,

Figs S1–S4). *Eutrichosiphum makii*, *E. sankari*, *E. subinoyi*, *Greenidea himansui*, *Gr. longicornis*, *Gr. (Paragreenidea) symplocosis*, *Gr. (Trichosiphum) manii* and *Greenideoida (Neogreenideoida) bengalensis* support the consensus areas for the three grid sizes (areas 2, 3, 5, 8, 10, 15, 17, 21, 27 and 30; Supporting Information, Figs S1b–d, S2a, c, h, S3a, e, S4f, i, respectively). *Greenidea (T.) heterotricha* supports one 1° consensus area (area 3; Supporting Information, Fig. S1c), whereas *E. blackmani* supports one consensus area in 1° grid (area 3; Supporting Information, Fig. S1c) and two in 3° grid (areas 27 and 30; Supporting Information, Fig. S4f, i, respectively).

In the 2° grid, both *Cervaphis rappardi indica* (areas 8 and 17; Supporting Information, Figs S2a, S3a, respectively) and *Gr. photiniphaga* (areas 15 and 21; Supporting Information, Figs S2h, S3e, respectively) support two consensus areas, whereas *Anomalosiphum indigoferae*, *Gr. longisetosa* and *Gr. (T.) spinotibium* provide support for three consensus areas (areas 11, 15 and 21; Supporting Information, Figs S2d, h, S3e, respectively). *Eutrichosiphum rameshi* and *Gr. (T.) camelliae* support two consensus areas only in the 3° grid (areas 27 and 30; Supporting Information, Figs S4f, i, respectively). *Eutrichosiphum quercifoliae*, *Gr. querciphaga*, *Gr. (T.) gigantean* and *Gd. (Pentatrichosiphum) lambersi* provide support for one 1° consensus area and three 2° consensus areas (areas 7, 11, 15 and 21; Supporting Information, Figs S1g, S2d, h, S3e, respectively). *Eutrichosiphum sensoriatum*, *Gr. (T.) quercicola* and *Gd. bhalukpongensis* support two consensus areas in both the 2° and 3° grid sizes (areas 8, 10, 27 and 30; Supporting Information, Figs S2a, c, S4f, i, respectively); the first two species also provide support for an additional 2° consensus area (area 17; Supporting Information, Fig. S3a).

The areas with the greatest values were located in northeast India, eastern Nepal to Bhutan and Bangladesh and were found in the 2° and 3° grid sizes (Table 1, area 15, score = 10.16568; area 27, score = 11.75000; area 30, score = 10.33333). Fourteen species are restricted to this area; additional details regarding the supporting species of these areas are listed in Table 1.

South edge of China: This area consists of areas detected under all three grid sizes in VNDM/NDM. Three species, *Gr. sp2.*, *Gr. sp5.* and *Gr. sp6.*, support the consensus areas from three grid sizes (areas 1, 12, 24 and 26; Supporting Information, Figs S1a, S2e, S4c, e, respectively). Additionally, three species, *E. sp1.*, *Gr. sp4.* and *Mesotrichosiphum pentaiarticulatum*, support three consensus areas in the 2° and 3° grid sizes (areas 16, 24 and 28; Supporting Information, Figs S2i, S4c, g, respectively). *Greenideoida (Pe.) longirostrum* supports one 2° consensus area (area 16;

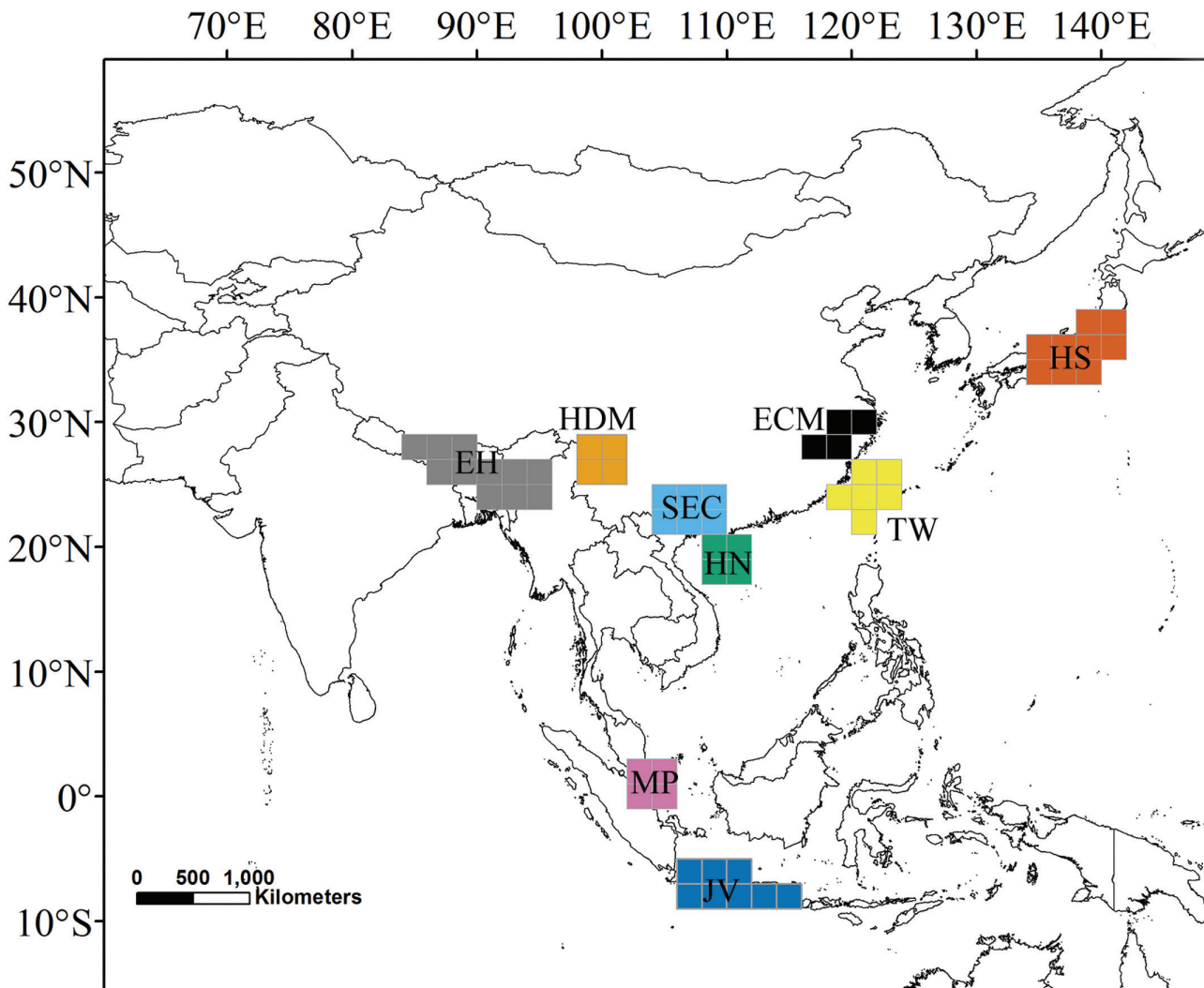


Figure 4. Areas of endemism detected for Greenideinae by parsimony analysis of endemism using 2° grid size.

Supporting Information, Fig. S2i); three species, *An. pithecolobii*, *E. parvulum* and *Gr. brideliae*, support one 3° consensus area (area 23; Supporting Information, Fig. S4b); two species, *Allotrichosiphum castanopse* and *Gr. sp3.*, support one 3° consensus area (area 24; Supporting Information, Fig. S4c).

The areas with the greatest endemism values were located in the south of China and were found in the 2° and 3° grid sizes (Table 1, area 16, score = 3.75000; area 24, score = 4.98571). Twelve species are confined to the areas, additional details of the supporting species of these areas are provided in Table 1.

Taiwan Island: AoEs were identified in all three grid sizes. Three species, *Gr. quercifoliae*, *Gr. (Pa.) viticola* and *Gr. (T.) nigra*, support one consensus area in the 1° grid and one consensus area in the 2° grid (areas 4 and 9; Supporting Information, Figs S1d, S2b,

respectively). Two species, *E. arunachali* and *Gr. (Pa.) cayratiae*, support one 2° consensus area (area 20; Supporting Information, Fig. S2d); and three species, *An. pithecolobii*, *E. parvulum* and *Gr. brideliae*, only provide support for area 23 in the 3° grid (Supporting Information, Fig. S4b), which is disjunctive, and also covers with SEC. In total, eight species are responsible for delimitating this area.

Java: AoEs were found in all three grid sizes, and these areas almost overlap entirely. Three species, *Gr. (T.) pallidipes*, *Gd. fransseni* and *Mollitrichosiphum (Metatrichosiphon) syzygii*, provide support for the three grid sizes (areas 6, 14, 22 and 31; Supporting Information, Figs S1e, S2g, S4a, j, respectively). *Greenidea maculata* supports one 1° consensus area and one in the 2° grid size (areas 6 and 14; Supporting Information, Figs S1f, S2g, respectively). Two species,

Table 1. Summary of information on the consensus areas of Greenideinae, with information on species composition with their respective score, number of cells for each area, the maximum scores and the grid size of each consensus areas

Consensus areas	Endemic species (score)	Number of cells	Maximum score	Grid size
1	<i>Greenidea</i> sp2. (0.688); <i>Greenidea</i> sp5. (0.889); <i>Greenidea</i> sp6. (0.875)	9	2.38996	1
2	<i>Eutrichosiphum makii</i> (0.875); <i>Eutrichosiphum sankari</i> (0.875); <i>Greenidea</i> (<i>Greenidea</i>) <i>longicornis</i> (1.000); <i>Greenidea</i> (<i>Paragreenidea</i>) <i>symplocosis</i> (0.938); <i>Greenideoida</i> (<i>Neogreenideoida</i>) <i>bengalensis</i> (0.875)	4	4.46429	1
3	<i>Eutrichosiphum blackmani</i> (0.813); <i>Eutrichosiphum subinoyi</i> (0.600); <i>Greenidea</i> (<i>Greenidea</i>) <i>himansui</i> (0.600); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>heterotracha</i> (0.750); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>manii</i> (0.750)	4	3.76250	1
4	<i>Greenidea</i> (<i>Greenidea</i>) <i>quercifoliae</i> (1.000); <i>Greenidea</i> (<i>Paragreenidea</i>) <i>viticola</i> (1.000); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>nigra kanzanensis</i> (1.000)	2	3.25000	1
5	<i>Eutrichosiphum subinoyi</i> (0.667); <i>Greenidea</i> (<i>Greenidea</i>) <i>himansui</i> (0.667); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>manii</i> (1.000)	2	2.58333	1
6	<i>Greenidea</i> (<i>Greenidea</i>) <i>maculate</i> (0.833); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>pallidipes</i> (1.000); <i>Greenideoida</i> (<i>Greenideoida</i>) <i>fransseni</i> (0.833); <i>Mollitrichosiphum</i> (<i>Metatrichosiphon</i>) <i>syzygii</i> (0.833)	3	3.75000	1
7	<i>Eutrichosiphum quercifoliae</i> (1.000); <i>Greenidea</i> (<i>Greenidea</i>) <i>querciphaga</i> (1.000); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>gigantea</i> (1.000); <i>Greenideoida</i> (<i>Pentatrichosiphum</i>) <i>lambersi</i> (1.000)	2	4.25000	1
8	<i>Cervaphis rappardi indica</i> (0.750); <i>Eutrichosiphum sensoriatum</i> (0.875); <i>Eutrichosiphum subinoyi</i> (0.800); <i>Greenidea</i> (<i>Greenidea</i>) <i>himansui</i> (0.800); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>manii</i> (0.750); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>quercicola</i> (0.875); <i>Greenideoida</i> (<i>Greenideoida</i>) <i>bhalukpongensis</i> (0.500)	6	5.41818	2
9	<i>Greenidea</i> (<i>Greenidea</i>) <i>quercifoliae</i> (0.875); <i>Greenidea</i> (<i>Paragreenidea</i>) <i>viticola</i> (0.875); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>nigra kanzanensis</i> (0.875)	4	2.75000	2
10	<i>Eutrichosiphum sensoriatum</i> (0.538); <i>Eutrichosiphum subinoyi</i> (0.875); <i>Greenidea</i> (<i>Greenidea</i>) <i>himansui</i> (0.875); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>manii</i> (0.813); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>quercicola</i> (0.538); <i>Greenideoida</i> (<i>Greenideoida</i>) <i>bhalukpongensis</i> (0.500)	4	4.38942	2
11	<i>Anomalosiphum indigoferae</i> (0.667); <i>Eutrichosiphum quercifoliae</i> (0.667); <i>Greenidea</i> (<i>Greenidea</i>) <i>longisetosa</i> (0.667); <i>Greenidea</i> (<i>Greenidea</i>) <i>querciphaga</i> (0.667); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>gigantea</i> (0.667); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>spinotibium</i> (0.667); <i>Greenideoida</i> (<i>Pentatrichosiphum</i>) <i>lambersi</i> (0.667)	2	4.91667	2
12	<i>Greenidea</i> sp2. (0.833); <i>Greenidea</i> sp5. (0.900); <i>Greenidea</i> sp6. (1.000)	5	2.58333	2
13	<i>Eutrichosiphum betulae</i> (0.833); <i>Eutrichosiphum querciphaga</i> (0.833); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>kumaoni</i> (0.556)	3	2.47222	2
14	<i>Eutrichosiphum pullum</i> (0.700); <i>Greenidea</i> (<i>Greenidea</i>) <i>magna</i> (0.750); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>pallidipes</i> (0.750)	4	2.45000	2

Table 1. Continued

Consensus areas	Endemic species (score)	Number of cells	Maximum score	Grid size
15	<i>Anomalosiphum indigoferae</i> (0.800); <i>Eutrichosiphum makii</i> (0.818); <i>Eutrichosiphum quercifoliae</i> (0.800); <i>Eutrichosiphum sankari</i> (0.818); <i>Greenidea (Greenidea) longicornis</i> (0.692); <i>Greenidea (Greenidea) longisetosa</i> (0.800); <i>Greenidea (Greenidea) photiniphaga</i> (0.571); <i>Greenidea (Greenidea) querciphaga</i> (0.800); <i>Greenidea (Paragreenidea) symplocosis</i> (0.643); <i>Greenidea (Trichosiphum) gigantea</i> (0.800); <i>Greenidea (Trichosiphum) spinotibium</i> (0.800); <i>Greenideoida (Neogreenideoida) bengalensis</i> (0.773); <i>Greenideoida (Pentatrichosiphum) lambersi</i> (0.800)	5	10.16568	2
16	<i>Eutrichosiphum</i> sp1. (0.875); <i>Greenidea</i> sp4. (0.875); <i>Greenideoida (Pentatrichosiphum) longirostrum</i> (0.875); <i>Mesotrichosiphum pentaiarticulatum</i> (0.875)	4	3.75000	2
17	<i>Cervaphis rappardi indica</i> (0.800); <i>Eutrichosiphum sensoriatum</i> (0.818); <i>Eutrichosiphum subinoyi</i> (0.682); <i>Greenidea (Greenidea) himansui</i> (0.682); <i>Greenidea (Trichosiphum) manii</i> (0.636); <i>Greenidea (Trichosiphum) quercicola</i> (0.950)	5	4.81818	2
18	<i>Eutrichosiphum betulae</i> (1.000); <i>Eutrichosiphum querciphaga</i> (1.000)	2	2.25000	2
19	<i>Eutrichosiphum pullum</i> (0.833); <i>Greenidea (Greenidea) magna</i> (0.875); <i>Greenidea (Greenidea) rappardi</i> (0.500)	6	2.45833	2
20	<i>Eutrichosiphum arunachali</i> (1.000); <i>Greenidea (Paragreenidea) cayratiae</i> (1.000)	2	2.25000	2
21	<i>Anomalosiphum indigoferae</i> (0.875); <i>Eutrichosiphum makii</i> (0.438); <i>Eutrichosiphum quercifoliae</i> (0.875); <i>Eutrichosiphum sankari</i> (0.438); <i>Greenidea (Greenidea) longisetosa</i> (0.875); <i>Greenidea (Greenidea) photiniphaga</i> (0.583); <i>Greenidea (Greenidea) querciphaga</i> (0.875); <i>Greenidea (Trichosiphum) gigantea</i> (0.875); <i>Greenidea (Trichosiphum) spinotibium</i> (0.875); <i>Greenideoida (Pentatrichosiphum) lambersi</i> (0.875)	4	7.83333	2
22	<i>Eutrichosiphum pullum</i> (0.875); <i>Greenidea (Greenidea) maculata</i> (0.800); <i>Greenidea (Greenidea) magna</i> (0.917); <i>Greenidea (Greenidea) rappardi</i> (0.625); <i>Greenidea (Trichosiphum) pallidipes</i> (0.850); <i>Greenideoida (Greenideoida) fransseni</i> (0.800); <i>Mollitrichosiphum (Metatrichosiphon) syzygii</i> (0.800)	6	5.70833	3
23	<i>Anomalosiphum pithecolobii</i> (0.781); <i>Eutrichosiphum parvulum</i> (0.543); <i>Greenidea (Greenidea) brideliae</i> (0.688)	8	2.26223	3
24	<i>Allotrichosiphum castanopse</i> (0.700); <i>Eutrichosiphum</i> sp1. (0.700); <i>Greenidea</i> sp2. (0.467); <i>Greenidea</i> sp3. (0.536); <i>Greenidea</i> sp4. (0.700); <i>Greenidea</i> sp5. (0.467); <i>Greenidea</i> sp6. (0.467); <i>Mesotrichosiphum pentaiarticulatum</i> (0.700)	5	4.98571	3
25	<i>Allotrichosiphum kashicola</i> (0.477); <i>Eutrichosiphum shiicola</i> (0.750); <i>Greenidea (Trichosiphum) carpini</i> (0.714); <i>Greenidea (Trichosiphum) prinicola</i> (0.639)	7	2.83045	3
26	<i>Greenidea</i> sp2. (0.938); <i>Greenidea</i> sp5. (0.938); <i>Greenidea</i> sp6. (0.938)	4	3.06250	3

Table 1. Continued

Consensus areas	Endemic species (score)	Number of cells	Maximum score	Grid size
27	<i>Eutrichosiphum blackmani</i> (0.800); <i>Eutrichosiphum makii</i> (0.900); <i>Eutrichosiphum rameshi</i> (0.800); <i>Eutrichosiphum sankari</i> (0.900); <i>Eutrichosiphum sensoriatum</i> (0.800); <i>Eutrichosiphum subinoyi</i> (0.800); <i>Greenidea</i> (<i>Greenidea</i>) <i>himansui</i> (0.700); <i>Greenidea</i> (<i>Greenidea</i>) <i>longicornis</i> (0.800); <i>Greenidea</i> (<i>Paragreenidea</i>) <i>symplocosis</i> (0.900); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>camelliae</i> (0.800); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>manii</i> (0.800); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>quercicola</i> (0.800); <i>Greenideoida</i> (<i>Greenideoida</i>) <i>bhalukpongensis</i> (0.800); <i>Greenideoida</i> (<i>Neogreenideoida</i>) <i>bengalensis</i> (0.900)	5	11.75000	3
28	<i>Eutrichosiphum</i> sp1. (1.000); <i>Greenidea</i> sp4. (1.000); <i>Mesotrichosiphum pentaiarticulatum</i> (1.000)	2	3.25000	3
29	<i>Allotrichosiphum kashicola</i> (0.472); <i>Eutrichosiphum shiicola</i> (0.850); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>carpini</i> (0.682)	5	2.25404	3
30	<i>Eutrichosiphum blackmani</i> (0.875); <i>Eutrichosiphum makii</i> (0.583); <i>Eutrichosiphum rameshi</i> (0.875); <i>Eutrichosiphum sankari</i> (0.583); <i>Eutrichosiphum sensoriatum</i> (0.875); <i>Eutrichosiphum subinoyi</i> (0.875); <i>Greenidea</i> (<i>Greenidea</i>) <i>himansui</i> (0.750); <i>Greenidea</i> (<i>Paragreenidea</i>) <i>symplocosis</i> (0.583); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>camelliae</i> (0.875); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>manii</i> (0.875); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>quercicola</i> (0.875); <i>Greenideoida</i> (<i>Greenideoida</i>) <i>bhalukpongensis</i> (0.875); <i>Greenideoida</i> (<i>Neogreenideoida</i>) <i>bengalensis</i> (0.583)	4	10.33333	3
31	<i>Eutrichosiphum pullum</i> (0.538); <i>Greenidea</i> (<i>Greenidea</i>) <i>maculata</i> (0.875); <i>Greenidea</i> (<i>Greenidea</i>) <i>magna</i> (0.577); <i>Greenidea</i> (<i>Trichosiphum</i>) <i>pallidipes</i> (0.938); <i>Greenideoida</i> (<i>Greenideoida</i>) <i>fransseni</i> (0.875); <i>Mollitrichosiphum</i> (<i>Metatrichosiphon</i>) <i>syzygii</i> (0.875)	4	4.92788	3

E. pullum and *Gr. magna*, support one 2° consensus area and two 3° consensus areas (areas 19, 22 and 31; Supporting Information, Figs S3c, S4a, j, respectively). Areas 19 and 22 are also supported by *Gr. rappardi*. In the 3° grid size, *E. pullum* and *Gr. maculata* support areas 22 and 31 (Supporting Information, Fig. S4a, j).

AoEs with the greatest endemicity values were found in the 3° grid size and covered almost the whole JV and southern Sumatra. Nine species are confined to this area. Additional details regarding the supporting species of these areas are listed in Table 1.

Western Himalayas: In the 2° grid size, consensus areas 13 (Supporting Information, Fig. S2f) and 18 (Supporting Information, Fig. S3b) were identified with *E. betulae* and *E. querciphaga* supporting both areas, and *Gr. (T.) kumaoni* supporting only area 13. The two areas almost overlapped entirely and were located in the northwest of India. This area is supported by three species totally.

Hainan Island: In total, nine species are restricted to this area. Three species, *E. sp1.*, *Gr. sp4.* and *Me. pentaiarticulatum*, support three consensus areas in the 2° and 3° grid sizes (areas 16, 24 and 28; Supporting Information, Figs S2i, S4c, g, respectively). *Greenideoida* (*Pe.*) *longirostrum* supports one 2° consensus areas (area 16; Supporting Information, Fig. S2i); three species, *An. pithecolobii*, *E. parvulum* and *Gr. brideliae*, support one 3° consensus area (area 23; Supporting Information, Fig. S4b); and two species, *Al. castanopse* and *Gr. sp3.*, support one 3° consensus area (area 24; Supporting Information, Fig. S4c).

East China mountains: This area is supported by five species. Two species, *E. arunachali* and *Gr. (Pa.) cayratiae*, support one 2° consensus area (area 20; Supporting Information, Fig. S3d); and three species, *An. pithecolobii*, *E. parvulum* and *Gr. brideliae*, only provide support for area 23 in the 3° grid (Supporting Information, Fig. S4b).

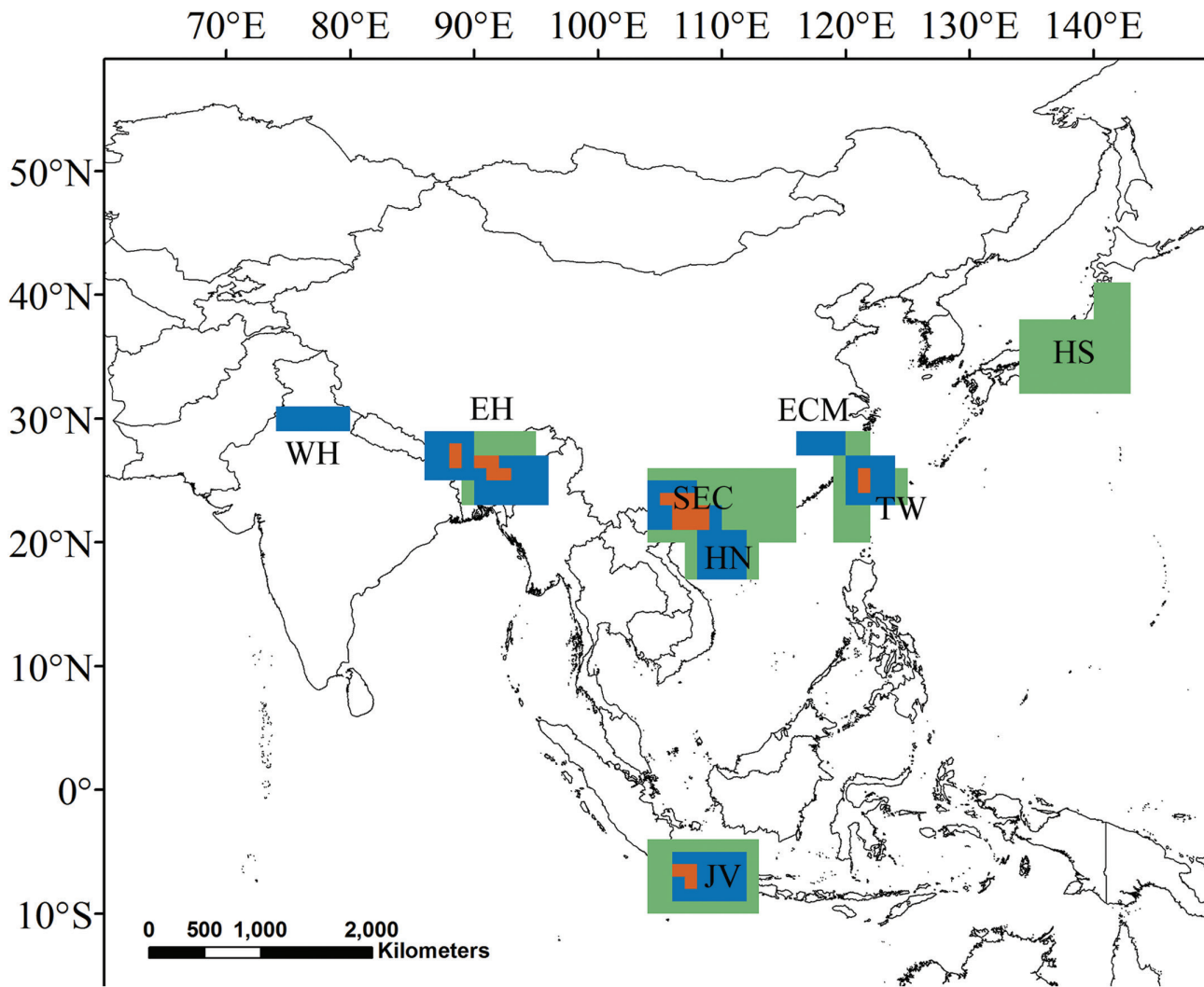


Figure 5. Overlap of the consensus areas of endemism detected for Greenideinae by NDM using 1° (green squares), 2° (blue) and 3° (orange) grid size.

Honshu Island: In the 3° grid size, areas 25 (Supporting Information, Fig. S4d) and 29 (Supporting Information, Fig. S4h) are found, covering almost the entire HS of Japan. Three species, *Al. kashicola*, *E. shiicola* and *Gr. (T.) carpini*, provide support for both consensus areas, whereas *Gr. (T.) prinicola* supports only area 25 (Supporting Information, Fig. S4d). In total, four species are confined to this area.

DISCUSSION

CONGRUENCE OF SPECIES RICHNESS AND ENDEMISM

In this study, species richness patterns for Greenideinae and patterns of endemism were generally consistent. Congruence between species richness and endemism patterns has also been discovered

in other groups, for example, aphids in the QTPH (Huang *et al.*, 2006, 2008), leafhoppers (Yuan *et al.*, 2014), birds (Jetz *et al.*, 2004; Lei *et al.*, 2007), mammals (Tang *et al.*, 2006) and plants (López-Pujol *et al.*, 2011). This congruence confirmed the hypotheses that AoEs have acted as centres of speciation in the past (Terborgh, 1992). This is frequently related to areas characterized by diverse habitats and stable climates, which maintain long-term speciation and persistence. Both centres of species richness and endemism uncovered in this study are located along the southern edge of the QTPH, the south margin of the Asia mainland, and on mountainous islands in the Pacific Ocean. Each area supposedly experienced a specific geological history (geological event or climate change), that contributed to its rich and often unique biota.

AOES IN MONTANE AREAS

Tectonic events generate high mountain–valley–river systems, which act as sky islands preventing organisms from dispersing to adjacent regions (McCormack *et al.*, 2009; Ye, Chen & Bu, 2016). Montane areas characterized by complex topography and heterogeneous environments provide varied habitats for aphid speciation and maintenance of diversity, as proposed in total insects (Tojo *et al.*, 2017), leafhoppers (Yuan *et al.*, 2014), *Pseudovelia* (Ye *et al.*, 2016), Auchenorrhyncha (Ramsay, 2016) and birds (Fjeldså *et al.*, 2012; Wu *et al.*, 2017). Complex topography of montane systems interact with thermally stable tropical oceans and thereby generate high climatic stability, which ensures long-term evolution and underpins specialization and diversification (Fjeldså *et al.*, 2012). Moreover, mountains with steep elevation gradients are more likely to serve as refugia accommodating up and down shifts of organisms responding to palaeoclimate oscillations (Wu *et al.*, 2017).

Five AoEs were concentrated in montane areas, three of them are located on the south edge of QTPH, as WH, EH and HDM. The uplift of the QTPH system exerted strong evolutionary pressures on the regional biota and promoted a high diversity and endemism of aphid species (Huang *et al.*, 2006, 2008). Phylogenetic study indicates that divergence and distribution of *Mollitrichosiphum* were greatly attributed to geographical isolation generated by the QTPH uplift (Zhang *et al.*, 2012); a similar mechanism is also revealed in other Hemiptera groups (see Ye *et al.*, 2016). The other two AoEs are along the southern margin of the Asia mainland, at the SEC and in the ECM.

Eastern Himalayas: This area exhibits the greatest number of consensus areas in the NDM analysis, and the highest number of endemic species (14 spp.). The area includes eastern Nepal, northeast India, northwest Burma and the southern fringe of Tibet. In this area, the diverse climate and vegetation zones across elevational gradient due to the uplift of the QTPH promoted adaption and differentiation of aphids (Huang *et al.*, 2008). Several gorges in the EH may have been important corridors for dispersal of plants and consequently aphids between different biogeographical regions, which, combined with the diversity of habitats, may facilitate accumulation and differentiation of endemic and nonendemic taxa (Huang *et al.*, 2006). Stable climate during glacial periods might have maintained high regional endemism, such as occurred in local birds (Lei *et al.* 2015). The dominant subtropical trees in the EH, generally species of Lauraceae, Betulaceae and Fagaceae (Behera, Kushwaha & Roy, 2002), partially account for the diversity of Greenideinae because of their host-specific life histories.

Western Himalayas: This area was recognized as an AoE only in the 2° NDM analysis, corresponding roughly

to Himachal Pradesh and western Uttar Pradesh of India. Three species delimit this AoE: *E. betulae*, *E. querciphaga* and *G. (T.) kumaoni*. Diversity of elevation, climatic conditions and vegetation types characterized this region. The endemic aphids are associated with the developed Oak-Rhododendron forests (at an altitude above 1500 m) and the dominant *Quercus semicarpifolia* and *Q. floribunda* at altitude above 2800 m.

Hengduan Mountains: This AoE was recovered only in the PAE and consists of northwestern Yunnan and western Sichuan provinces. The HDM are parallel, north-south oriented mountain ranges characterized by steep elevational gradient. This dramatic topography combined with the subtropical monsoon influence has generated highly varied climates and habitats across both planimetric and elevational gradients. The area is a biodiversity corridor geographically located at the junction of Palearctic and Oriental regions, bridging the faunal exchange between these regions (Lei *et al.*, 2003, 2007). A diversity of habitats that scatter this transition zone thus created favourable conditions for maintaining and promoting endemic and regional diversity (Wu *et al.*, 2017). The environment of this region remained stable during the Pleistocene glaciations and, consequently, offered refugia for aphids and other biota (Huang *et al.*, 2006; Qu *et al.* 2014).

South edge of China and east China mountains: The SEC borders Vietnam and contains the southeastern Yunnan, most of Guangxi, and southwestern Guizhou. The area is surrounded by the southeastern fringe of the Yungui Plateau, Wumeng Mountains, Shiwang Mountains and Nanling Mountains. Twelve endemic species delimit this AoE. López-Pujol *et al.* (2011) reported four small centres of plant endemism in the same region. The relatively high fringe may isolate the fauna of this area from surrounding areas. This region is influenced by a subtropical monsoon climate with warm temperatures and abundant precipitation that result in varied vegetation (Wen *et al.*, 2014). The dominant trees in the subtropical broad-leaved forest, such as the Fagaceae, are the main host plants of the Greenideinae. The ECM largely correspond to Fujian Province, encompassing the Wuyi Mountains, Jiufeng Mountains, Daiyun Mountains and Bopingling Mountains. The long geologic history and complicated topography resulted in the abundant plant species in this region, particularly the pantropic element (Jiang & Zhang, 2000). Many dominant plant families and genera are the main hosts of Greenideinae aphids, such as Fagaceae, Lauraceae, Sapindaceae and Anacardiaceae. Greenideini is postulated to have coevolved with ancestral host plants in the family Fagaceae (Liu *et al.*, 2015). Host shift and expansion of host range that

occurred among genera also contributed to species differentiation (Zhang *et al.*, 2012; Liu *et al.*, 2015). High host plant diversity (Jiang & Zhang, 2000) in this area may have promoted aphid diversification.

AOES ON ISLANDS

Four AoEs are mountainous islands isolated from the Asia continent by vast tracts of sea: HN, TW, HS and JV. These islands were reported to once interrelate with Asia mainland when sea level retreated. Islands are relatively isolated regions that are vulnerable to fluctuating sea level, and punctuational connections with the source continent and adaptive radiation may promote species accumulation and speciation. For these species, geographical isolation might have limited dispersal back to the mainland and consequently promoted the present distribution pattern. The endemic levels of islands are affected by the area, distance and period of isolation from the mainland, historical events, multiple source pools, as well as island ecology and structure. Oceanic islands have been postulated as refugia for relict endemics because of thermal stability and slow biotic turnover (Cronk, 1997; Fjeldså *et al.*, 2012).

Hainan Island and Taiwan Island: These two AoEs are typical mountainous islands influenced by tropical/subtropical climates. Mountains in Taiwan are relatively high, for example, Mt. Yushan (alt. 3952 m) is the highest mountain in southeastern China. Thus, Taiwan exhibits diversified habitats, with extensive altitudinal gradients and complex climates. Vegetation types in Taiwan are similar to those in southern China. The dominant plant families (Fagaceae, Lauraceae and Theaceae) in montane areas are hosted by greenideine aphids. Some species from those plant families even form endemic ecosystem types (Cai & Xu, 2002). For these two AoEs, especially Taiwan, diversification after isolation from the mainland might be responsible for the current endemic species. High levels of biodiversity on these two islands have been extensively reported, for example, in Hormaphidinae aphids (Li *et al.*, 2017), leafhoppers (Yuan *et al.*, 2014), scale insects (Wei, Niu & Feng, 2016) and birds (Lei *et al.*, 2003; Huang, Qiao & Lei, 2010). During the Quaternary period, TW and HN have repeatedly been connected to the mainland, which may have promoted speciation and gene flow between island and mainland. The two islands have high endemism for plants, birds, mammals and many other organisms (Lei *et al.*, 2003; Tang *et al.*, 2006; López-Pujol *et al.*, 2011). The fact that Taiwan was isolated from the mainland earlier than Hainan, by a wider Taiwan Strait may partially explain a higher level of endemism in Taiwan than that in Hainan.

Malay Peninsula and Java: During the Pleistocene sea level fluctuation, the Indonesian Archipelago was

connected with Southeast Asia (Voris, 2000). Aphid migrations from the Asia mainland to the archipelago might have occurred during this period. The MP and JV are part of Sundaland, a globally important hotspot (Myers *et al.*, 2000). Java is composed of extensive volcanic mountain chains, and Western JV is influenced by constant temperature and wet weather for almost all the year round (MacKinnon, 1988). Separate volcanic mountains, together with climate contrasts directly influence the vegetation and therefore are conducive to diversification and speciation. The species richness and endemism of aphids are predominantly related to the dominant plants families on the island, such as Fagaceae, Loranthaceae, Moraceae and Convolvulaceae. Given the small land mass, JV is reported with high species richness and endemism for birds, bats, psocids and butterflies (Whitten, Soeriaatmadja & Afiff, 1996; Stattersfield *et al.*, 1998; Kentjonowati, Thornton & New, 2002; Jones *et al.*, 2009; Matsumoto, Noerdjito & Fukuyama, 2015; Prawiradilaga, 2016).

Honshu Island: This is the largest island of Japan, with mountain ranges running north-south through the island chain. The montane regions play an important role in geographical climate variation on this island. High species richness of Greenideinae was delimited in this area, particularly in the central mountain region. Greenideinae species likely immigrated into Hondu (the unit of Honshu, Shikoku and Kyushu) during the Pleistocene through a land bridge connected to the Indo-Malayan region in South China. Some of the species have since undergone vicariant speciation after the isolation caused by marine straits, and a high degree of endemism is the result.

HOST PLANTS AND THE FORMATION OF AOES OF GREENIDEINAE

Aphids in Greenideinae have established relatively strong host fidelity, typically colonizing plants in Fagaceae, Fabaceae, Euphorbiaceae, Lauraceae, Betulaceae and other families, with most species feeding on plants of Fagaceae (Blackman & Eastop, 1994). The geographical ranges of aphids are closely associated with host plant distributions and diversity. In China, the diversity centre of Fagaceae is Yungui Plateau, and this area together with the HDM, HN and TW also had high endemism (Liu & Hong, 1998). These distribution patterns of Fagaceae correspond to those of Greenideinae detected from our analyses. Host plants are commonly assumed to have greatly influenced the diversification of aphids. Co-speciation with host plant mainly occurred during the early stage of aphid diversification and among higher taxa. For example, the radiation of angiosperms most likely

contributed to the major Tertiary diversification of aphids; the tribal diversifications of Hormaphidinae were coincident with the appearance of their primary host plants (Huang *et al.*, 2012). By contrast, more aphid speciation is attributed to host shift and adaptation to new hosts. In *Mollitrichosiphum* (Greenideinae), the first acquired host plant is likely in Fagaceae, and the subsequent acquisition of new hosts and expansion in host range may have promoted species differentiation within this genus (Zhang *et al.*, 2012).

A number of Greenideinae species are economically important pests in agriculture, horticulture and forestry and can injure plants by sucking their sap. Some aphids have been reported as invasive species outside their original regions, for example, *Greenidea* (*Trichosiphum*) *psidii* has been introduced to North America (Hidalgo, Muller & Durante, 2009), *Greenidea ficicola* to Africa, North and South America (Remaudière, Autrique & Ntahimpera, 1992; Halbert, 2004; Sousa-Silva, Brombal & Ilharco, 2005). Although most extant Greenideinae are located to the south and southeast of Asia, fossil representatives have been recorded in Europe, which indicate a markedly wider range of this group in the Miocene, extending to the northern coasts of the Tethys Sea (Wegierek & Peñalver, 2002). In the Miocene, southern Europe was influenced by a hot subtropical climate (Peñalver, Santisteban & Barrón, 1999), and many of the dominant terrestrial plants, such as Betulaceae, Fagaceae, Juglandaceae and Lauraceae, are host plants of recent Greenideinae (Wegierek & Peñalver, 2002). Later geological events changed the climatic conditions and thereafter the composition of flora in southern Europe. This contributed to a narrower range of Greenideinae, in southeast Asia, where climate remained relatively stable (van Andel, 1994). Similarly, the disjunct distributions of Hormaphidini in eastern Asia and eastern North America are likely related to host plant fragmentation (von Dohlen, Kurosu & Aoki, 2002). Thereby, the adaptable Greenideinae seem to have the capacity to colonize the broad temperate zone as potential pest. Pest detection and management are essential to prevent anthropochory due to human activities.

ASSESSMENT OF PERFORMANCE OF THE TWO DIFFERENT TECHNIQUES

In general, PAE and NDM achieved similar results in numbers of AoEs and endemic species. The consensus tree obtained in PAE resulted in more AoEs but fewer endemic species. This result might be explained to some extent by the disparate algorithms under these two methods. NDM tends to encompass more species into one AoE, whereas PAE arbitrarily clusters clades depending on shared taxa. As a consequence, one final AoE from PAE is often assembled by multiple

clades in the consensus tree. Even though two grids in Madagascar clustered into one clade in the PAE and the monotypic genus *Paulianaphis* is endemic to this area, the validity of this as an AoE remains uncertain due to insufficient collecting effort.

The results of NDM will inevitably be affected by grid size, both in constitution and coverage of AoEs (Szumik *et al.*, 2002; 2012). Use of grids that are too small makes all distributions entirely discontinuous, with the consequence that only very small AoEs are recognized. By contrast, large grid cells will delimit very large AoEs. Moreover, the grid size is correlated with the number and dispersion of the localities. In concordance with the above expectations, our analysis employing the 1° grid generated the lowest number of consensus areas. The use of the 2° grid detected more consensus areas than using the 3° grid, because the 3° grid analysis merged some consensus areas, which were exclusive among results of the other two analyses. In the 3° grid analysis, Fujian Province, Guangdong Province and TW constituted one disjunct area (area 23; Supporting Information, Fig. S3b); and the SEC and HN were assembled into an area, possibly reflecting close affinities between these AoEs (area 24; Supporting Information, Fig. S3c). Although the 3° grid appears to be too large, particularly for regions of continent margins and peninsulas, this grid size recovered an exclusive and relatively larger AoE, HS. In general, 2° is the most preferred grid size in our study. As AoEs resulting from different grid size analyses slightly varied in location, area and boundary, it is reasonable to combine results from three grid scales to delimit AoEs. In addition, the use of different grid sizes will minimize the artefacts of collecting biases, since DaSilva *et al.* (2015) declared that small cells are more sensitive to well-sampled regions, and larger cells will locate areas in poorly sampled regions.

CONCLUSIONS

We studied the biogeographical patterns of Greenideinae species richness and endemism based on different methods. Our results indicate that biodiversity centres are generally located in montane areas and on mountainous islands. The EH, Mt. Shiwandashan, TW and western JV are the major centres of endemism.

The coincident patterns of overall species richness and endemism confirmed the speculation that areas with high endemism (AoEs) often exhibit high capacity to promote speciation, species persistence, or both (Fjeldså & Lovett, 1997; Herkt *et al.*, 2016). However, spatial incongruence between biodiversity and endemism may be induced by immigration, migration and extinction in response to changing environmental condition (Herkt *et al.*, 2016). Our results highlight the importance of montane areas and mountainous islands

in conservation and historical biology. Stability and habitat mosaics in these areas underpinned specialization, differentiation and accumulation. Additionally, the distributions of the host plants much further limit the distribution patterns of the Greenideinae. Further research is required to address the underlying mechanisms and evolutionary histories that contribute to the present patterns of distribution.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. Consensus areas detected for Greenideinae by NDM using 1° grid size. Areas of endemism: EH, eastern Himalayas; JV, Java; SEC, south edge of China; TW, Taiwan Island.

Figure S2. Consensus areas 8–16 detected for Greenideinae by NDM using 2° grid size. Areas of endemism: EH, eastern Himalayas; HN, Hainan Island; JV, Java; SEC, south edge of China; TW, Taiwan Island; WH, western Himalayas.

Figure S3. Consensus areas 17–21 detected for Greenideinae by NDM using 2° grid size. Areas of endemism: ECM, east China mountains; EH, eastern Himalayas; JV, Java; WH, western Himalayas.

Figure S4. Consensus areas detected for Greenideinae by NDM using 3° grid size. Areas of endemism: ECM, east China mountains; EH, eastern Himalayas; HN, Hainan Island; HS, Honshu Island; JV, Java; SEC, south edge of China; TW, Taiwan Island.

Data Matrix S5. Data matrix used in species richness and endemism analysis.