

Assemblages of orthopteroid insects along environmental gradients in central and southern Madagascar

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Abstract

Madagascar is one of the world hotspots for endemics, and its rapidly changing habitats accelerate the need for their study and conservation. Orthopterans, mantids, phasmids, and cockroaches were sampled in five main habitats (savanna and shrubland, semiarid spiny forest, rainforest, mountain grass- and shrubland, and cultivated habitats) in central and southern Madagascar (41 sites, 0–2250 m a.s.l.) with the aim of getting the first data on their diversity and distribution along environmental gradients shortly after the rainy period. Samples were collected primarily by sweeping herb and shrub vegetation along transects 100 m long and 1–2 m wide (5–8 transects/site) and supplemented using other techniques. Altogether 117 species of orthopteroid insects were found (94 Orthoptera, 7 Mantodea, 4 Phasmida, and 12 Blattodea), among them two katydid species which had been recently described as new to science (*Mimoscudderia longicaudata* Heller & Kríštín, 2019, *Parapyrrhicia leuca* Hemp & Heller, 2019). High species diversity was documented: altogether 63 species (53.8%) were present at only one site, 14 (12%) at two sites, and 5 species (4.2%) at three sites. Nonmetric multidimensional scaling analysis on species composition did not clearly separate the assemblages of the sampled sites. Species assemblages from four habitats overlapped due to their similarity. Only assemblages from the rainforest sites were partially separated from the other sites. Cultivated habitats were characterized by the most frequent ($F > 50\%$) and abundant grasshopper species, such as *Acorypha decisa*, *Aiolopus thalassinus rodericensis*, *Oedaleus virgula*, *Gelastorrhinus edax*, *Gymnobothrus* spp., and *Acrotylus* spp. We found a significant association between habitat management and species rareness, where the number of rare species was higher in natural/unmanaged habitats. However, we found no association between habitat management and the number of endemic species. For several species we provide the first detailed data on their localities and habitat.

Keywords

altitude, biogeography, diversity, ecology, endemism, habitat

Introduction

Madagascar represents one of the most important hotspots of endemism on Earth (Myers et al. 2000, Ganzhorn et al. 2001,

Goodman and Benstead 2005, Vences et al. 2009). The contact of tropical dry and rainforests, semi-arid savannas, thorny bushes, as well as a mosaic of cultural steppes offer an excellent opportunity to study animal and plant assemblages along different environmental gradients. Rapidly changing environments are accelerating the need to study them, as well as for the identification of conservation priorities for global biodiversity stability (Goodman and Benstead 2003, Irwin et al. 2010).

Orthopteroid insects are among the most important bio-indicators of the status of integrity of natural habitats, especially habitats with small plot sizes (Gerlach et al. 2013). They are also excellent study systems, e.g., for the coevolution of native and introduced species on some of the Mascarene Islands (Boyer and Rivault 2003). Therefore, assemblages of orthopterous insects, especially brachypterous species, provide valuable information on habitat conditions and the status of sites (Marini et al. 2009). Orthopterans in Madagascar include a large percentage (ca 80–90%) of endemic species (Descamps and Wintrebert 1965, Dirsh and Descamps 1968, Descamps 1971, Wintrebert 1972, Devriese 1991, 1995, Braud et al. 2014, etc.); a similar situation is also known in the phasmids (Bradler and Buckley 2018) and mantids (Ehrmann 2002). Non-endemics show similarities with African or Indomalayan orthopteroid fauna (e.g., Hemp 2009, 2013, Braud et al. 2014, Heller et al. 2018). There are several, though mostly older, studies describing orthopteroid insects in Madagascar. The best known seem to be those on the grasshoppers Acridoidea and Pyrgomorphoidea (Rehn 1953, Dirsh 1962, 1963a, b, 1966, Descamps and Wintrebert 1966, 1967, Dirsh and Descamps 1968) and monkey hoppers (Eumastacoidea; Descamps and Wintrebert 1965, Descamps 1971), with the first identification keys, maps and notes on their biology and habitats. Groundhoppers (Tetrigidae) are also quite well-known (e.g., Günther 1974, Devriese 1991, 1995). The ensiferans are a less-known orthopteran group in Madagascar, e.g., Phaneropterinae, Pseudophyllinae, Conocephalinae (Carl 1914, Ragge 1964, Gorochoch and Llorente 2004, Ūnal and Beccaloni 2008, 2017, Gorochoch 2009, Heller et

al. 2018), Meconematinae (Hugel 2012), Gryllidae, Mogoplistidae (Gorochoy 2004, 2006, 2014), and there are still species new to science (e.g., Massa 2017a, b, c, d, Heller et al. 2019). Based on recent studies (Hemp 2009, 2013, Hemp et al. 2015, 2017), some tettigoniids (the Agraeciini/Euconchophorini-complex) are related to the studied Agraeciini from Africa, India, and Australia, but within Conocephalinae. A member of this Agraeciini/Euconchophorini-complex seems to have arrived in Madagascar relatively long ago. Hence, a comparison with East African taxa is necessary to know the evolutionary patterns of Malagasy tettigoniids.

The Malagasy mantids were described, e.g., by Mériguet (2005, 2013) and the phasmids, e.g., by Cliquennois (2003, 2008). A comprehensive study on Malagasy cockroaches is still lacking (cf. Princis 1965, 1966, 1969, Vinson 1968).

Today, only 10-15% of Madagascar's natural areas remain relatively well-preserved, while some areas and regions are managed and cultivated with high intensity and some are abandoned or seminatural (Vences et al. 2009, Irwin et al. 2010, Vieilledent et al. 2018). Forest habitats, in particular, are critically endangered by massive deforestation. In 1953, 27% of the island was under forest cover, and by 2000 only 17% was forested. Despite increased environmental awareness in recent decades, deforestation has continued (Irwin et al. 2010). This has had a serious impact, mainly on the many arboricolous and sylvicolous endemic Malagasy Orthoptera species (Braud et al. 2014, Heller et al. 2018). Such changing conditions create a challenge for studying the impact of different intensities of human management in biodiversity. Furthermore, there is a rather steep altitudinal gradient of particular regions from sea level up to nearly 2900 m a.s.l. with different habitats characterized by different moisture, geo-

morphology, and climate (Goodman and Benstead 2003, Vences et al. 2009).

It is known that the number of orthopterous species and their abundance changes with altitude (Claridge and Singhrao 1978, Grytnes and Vetaas 2002, Hemp 2009), but there is almost no data from Madagascar. Also, information on assemblages along different environmental gradients (e.g., Descamps and Wintrebert 1966) is almost completely lacking. For many endemic Malagasy species, even now the only information on 'Madagascar' exists without any further details on locality or ecology. This is true, for example, for distinctly more than half of all endemic species of phaneropterines (e.g., Heller et al. 2018). Based on these facts, we focused on 1) the diversity and distribution of orthopteroids along environmental gradients (habitat, altitude, management type) at 41 sites in central and southern Madagascar (after the rainy season, in March 2015) and 2) assemblage structure of orthopteroid insects in five different habitats and altitudes (0–2 250 m a.s.l.).

Material and methods

Study area.—Orthopteroid insects were sampled (41 sites) in five main habitats in central and southern Madagascar (Fig. 1). These habitats (> 90% of the site) cover: 1) savanna and shrubland (17 sites); 2) semiarid spiny forests, characterized by dense tangles of octopus trees interspersed with baobabs (6 sites); 3) rainforests with giant forest trees festooned with vines, ferns and orchids (4 sites); 4) mountain grasslands and shrubs (6 sites); and 5) cultivated, human made habitats, such as fields, orchards, parks and gardens (8 sites) (Suppl. material 1, Fig. 2). Considering the natural/cultivated character (management status) of each site, we divided

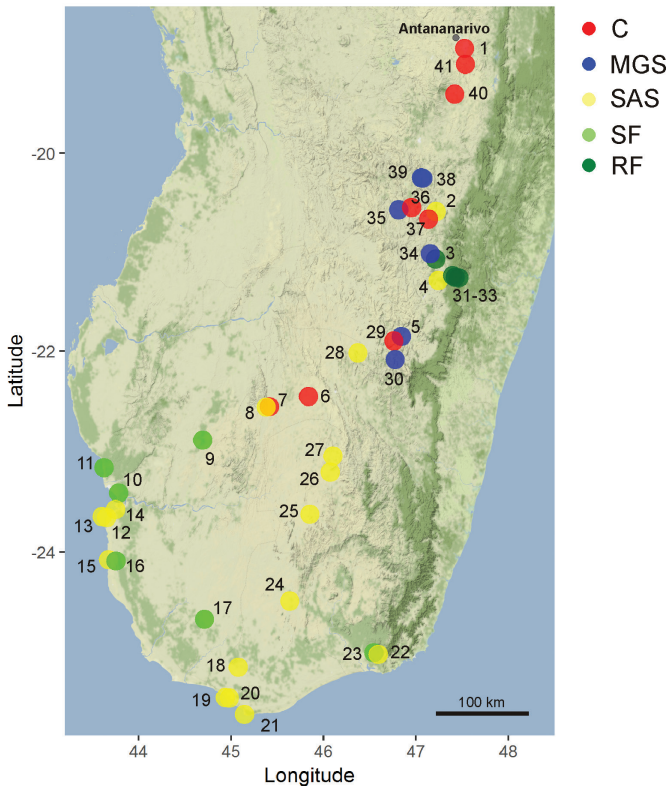


Fig. 1. Study sites (41) of orthopteroid insects in five habitats of central and southern Madagascar (C = cultivated habitats, MGS = mountain grass- and shrubland, RF = rainforest, SAS = savanna and shrubland, SF = semiarid spiny forest).



Fig. 2. Five main habitats studied in Madagascar: A. Savanna and shrubland; B. Semiarid spiny forests; C. Rainforests; D. Mountain grasslands and shrubs; E. Cultivated, human made habitats, such as fields, orchards, parks and gardens. Photos by A. Krištín.

them into three categories: 1) natural sites – not managed for > 60 years, mostly National Parks or Natural Reserves (17 sites); 2) cultivated (human-made habitats, such as fields, orchards, parks, and gardens, 8 sites); and 3) mixed character of site: natural/cultivated i.e., abandoned, formerly managed pastures and fields with a savanna, and spiny bush character (16 sites). The vertical and horizontal structure of characteristic vegetation with the main plant taxa were described for each study site. Altitudes, GPS coordinates, and all necessary environmental data were recorded (Brower et al. 1990) and the main habitat types were categorized (Moat and Smith 2007).

Study sites.—For each site we list: **management type:** C = managed cultivated habitats, as fields, gardens, orchards, N = nature near, unmanaged habitats, NC = abandoned site, formerly cultivated, with mostly natural vegetation; **GPS coordinates** and **altitude** of the site center.

1. **Antananarivo, ZOO Tsimbazaza** (C; 18.92924S, 47.52587E, 1277 m a.s.l.): managed grassland and bush in ZOO park, with riparian vegetation along the lakes, within the city.
2. **Ambositra South** (NC; 20.590497S, 47.215015E, 1325 m a.s.l.): pastures and abandoned fields with scattered bush, in herbal layer with naturalized plants, e.g., *Gladiolus dalenii*, *Lilium* cf. *formosanum*, *Lantana camara*.
3. **Lalatsara Lemur forest** (N; 21.07206S, 47.21173E, 1412 m a.s.l.): rainforest with diverse tree and bushy hygrophilous vegetation, such as bamboo, ferns, palms, endemic orchids (e.g., *Cynorkis lilacina*, *Gastrorchis francoisii*), several introduced plants like ginger (e.g., *Hedychium coronarium*) and *Pe-reskia* at the forest edges.
4. **Fiarantsoa, 31 km N** (NC; 21.286989S, 47.240574E, 1275 m a.s.l.): old abandoned fields, bush and pine forest edges with introduced *Lantana camara*.
5. **Anja Community Reserve** (NC; 21.850766S, 46.841926E, 980 m a.s.l.): well-preserved xeric and rocky habitats with succulent flora and evergreen forest (e.g., *Ravenala madagascariensis*). Several of them are endemics (e.g., *Aloe deltoideodonta*, *A. divaricata*, *Euphorbia alluaudii*, *E. bongolavensis*, *E. duranii*, *E. enterophora*, *Kalanchoe beharensis*, *Pachypodium densiflorum*, *Sobennikoffia humbertiana*, *Xerophyta dasylirioides*). On the foot of the Reserve are ruderalized fields with grasslands, lake, and bushy vegetation.
6. **Ihoso (Horombe plateau)** (C; 22.453546S, 45.838313E, 1050 m a.s.l.): grassland and pastures on plateau, covered mostly by grasses *Heteropogon* sp., on rocky fields spiny bush.
7. **Ranohira (park, hotel)** (C; 22.556500S, 45.415430E, 840 m a.s.l.): grasslands and park within the village with ruderalized vegetation.
8. **Isalo National Park** (N; 22.559474S, 45.379970E, 920–950 m a.s.l.): well-preserved xeric rocky formations and bushy grasslands with endemic succulents *Aloe isaloensis*, *A. imalotensis*, *Cynanchum*, *Euphorbia*, *Kalanchoe*, *Pachypodium rosulatum*, *Xerophyta dasylirioides*, and bush along the creeks with *Pandanus pulcher*.
9. **Zombitse-Vohibasia National Park** (N; 22.886195S, 44.691791E, 810 m a.s.l.): dry forests and their edges with bushy and grassland vegetation. Within endemic plants are represented families Euphorbiaceae, Acanthaceae (*Crossandra stenandrium*), Apocynaceae, Didieraceae, orchids (just flowering e.g., *Aeranthes* sp., *Habenaria tianae*, *Polystachya* cf. *aurantiaca*), in tree layer are, characteristically, the baobabs *Adansonia* za, *A. grandidieri*, *A. rubrostipa*. Naturalized plant species are e.g., genera *Acacia*, *Aloe*, *Ficus*, *Pandanus*.
10. **Toliara east** (NC; 23.412236S, 43.782506E, 85 m a.s.l.): xeric spiny bush and tree habitat with succulent endemics (*Euphorbia fiherenensis*, *Mimosa* sp.).
11. **Réniala Reserve, Ifaty** (N; 23.163993S, 43.624652E, 20 m a.s.l.): dry spiny bush and forest with > 2000 plant species, with very old baobabs (*Adansonia rubrostipa*) and several species of *Didiereaceae*. Among endemics are succulent species (e.g., *Adenia olaboensis*, *Commiphora mahafaliensis*, *Delonix decaryi*, *Didierea madagascariensis*, *Euphorbia pervilleana*, *Givotia madagascariensis*, *Pachypodium geayi*, *Zanthoxylum decaryi*).
12. **Soalara northeast** (NC; 23.578168S, 43.750159E, 5–40 m a.s.l.): dry spiny bush on steep rocky slopes and sandy habitats in coastal area with many endemic plants (e.g., *Aloe viguieri*, *Commiphora* sp., *Euphorbia leucodendron*, *E. capuronii*).
13. **Anakao** (NC; 23.655606S, 43.651012E, 5–10 m a.s.l.): sandy dunes and coastal habitats with *Euphorbia stenoclada* in tree layer, with some endemic *Aloe* (*A. divaricata*, *A. vaombe*), *Psidium altissima*, introduced *Euphorbia pulcherrima*, *Agave sisalana*, *Sansevieria*.
14. **Nosy Ve** (N; 23.649328S, 43.605091E, 0–5 m a.s.l.): sandy dunes and coastal habitats on small island near Anakao with breeding population of *Phaeton rubricauda* with *Euphorbia stenoclada* and *Didierea madagascariensis* in tree layer, scattered bush (e.g., *Psidium altissima*, *Scaevola plumieri*, *Commiphora* sp.), and herbal layer with *Ipomoea pes-caprae*.
15. **Ambola** (N; 24.076576S, 43.674658E, 5–10 m a.s.l.): dry sandy dunes and coastal habitats in the vicinity of Vaombe hotel with *Aloe vaombe*, *E. stenoclada*, *Commiphora* sp., *Uncarina* sp., *Acacia* sp., *Psidium altissima* in bush and tree layer.
16. **Tsimanampetosa National Park** (N; 24.086643S, 43.754726E, 5–50 m a.s.l.): limestone plateau with xeric bush and tree vegetation, mostly endemic (e.g., *Acacia bellula*, *Aloe divaricata*, *A. vaombe*, *Alluaudia comosa*, *Alluaudiopsis fiherenensis*, *Commiphora lamii*, *Delonix floribunda*, *E. leucodendron*, *E. mainty*, *E. plagiantha*, *Givotia madagascariensis*, *Operculicarya hyphaenoides*, *Uncarina stellulifera*), with old trees (*Adansonia rubrostipa*, *Pachypodium geayi*) and riparian vegetation along the Tsimanampetsotsa Lake.
17. **Ampanihy, 6 km northwest** (NC; 24.661890S, 44.710957E, 250 m a.s.l.): spiny dry bush and forest with endemic *Alluaudia dumosa*, *A. humbertii*, *Commiphora* sp., *Dombeya* sp., and *Euphorbia arahaka* and introduced plants, e.g., *Euphorbia tirucalli*, *Opuntia dillenii*.
18. **Beloha, 16 km N** (NC; 25.131933S, 45.075445E, 300 m a.s.l.): spiny dry bush with endemic *Acacia sakalava*, *Alluaudia dumosa*, *A. humbertii*, *Baudouinia rouxvillei*, *Barleria alluaudii*, and *Operculicarya decaryi*, with small wetland and abandoned pastures and fields.
19. **Lavanono coastal area** (NC; 25.429579S, 44.939260E, 5–10 m a.s.l.): sandy dunes with dry spiny bush and scattered xeric grassland with endemic *Aloe divaricata* and introduced *Agave sisalana*, *A. americana*, *E. stenoclada*, *Opuntia dillenii*, and *O. linguiformis*.
20. **Lavanono N (rocky area)** (N; 25.433282S, 44.978812E, 150 m a.s.l.): dry xeric bushy habitats with endemic *Alluaudia comosa*, *Megistostegium microphylla*, *Operculicarya decaryi*, in shaded sites *Kalanchoe linearifolia*, *Aloe antandroi*, at open plots are typical *Aloe vaotsanda* and introduced *Opuntia dillenii*.
21. **Cape Sainte Marie Reserve** (N; 25.593645S, 45.141987E, 0–165 m a.s.l.): low (< 120 cm) dry spiny bush covers 90% of this windy site, located on the southernmost point of

- Madagascar. The most common plants are endemic species of genera *Commiphora*, *Salvadora*, *Megistostegium*, *Operculicarya*, *Alluaudia*, *Aloe* and *Euphorbia*, *Catharantus roseus*, *Tephrosia vohimenaensis*, and introduced *Opuntia* spp.
22. **Andohahela National Park – Mangatsiaka** (N; 24.988649S, 46.545776E, 50–70 m a.s.l.): dry spiny forest and bush on limestones with many old and big endemic plants (e.g., *Alluaudia ascendens*, *A. procera*, *Cedrelopsis grevei*, *Commiphora humbertii*, *C. brevicalyx*, *C. simplicifolia*, *Decarya madagascariensis*, *Euphorbia cylindrifolia*, *E. plagiantha*, *Grewia androyensis*, *Kosteletzkya reflexiflora*, *Pachypodium geayi*, *P. lamerei*, *Senecio cedrorum*, and *Uncarina grandidieri* (for more detailed info see Andriaharimalala et al. 2012).
 23. **Andohahela – Tsimelahy River** (NC; 25.005266S, 46.590382E, 70 m a.s.l.): riparian vegetation and ruderalized bushy grassland along the river with some introduced (*Agave sisalana*, *Arundo donax*, *Opuntia monacantha*, *Salvadora angustifolia*) and endemic plants (*Abrahamia grandidieri*, *Alluaudia ascendens*, *A. procera*).
 24. **Betroka 174 km S Ampanaha** (NC; 24.484383S, 45.633321E, 455 m a.s.l.): old abandoned fields with wetland and bush containing endemic plants (*Aloe divaricata*, *Mimosa* sp.) and ruderalized pastures with invasive *Opuntia monacantha*.
 25. **Betroka 51 km S Hasofotsy S** (NC; 23.626795S, 45.850270E, 760 m a.s.l.): ruderalized grasslands, introduced plants (e.g., *Leonotis nepetaefolia*) and pastures with bush.
 26. **Betroka 10 km N** (NC; 23.206678S, 46.071662E, 850 m a.s.l.): grassland and bush along the dry riverbed with endemic *Aloe macroclada* and several introduced plants (*Agave sisalana*, *Opuntia linguiformis*, *O. monacantha*).
 27. **Betroka 30 km N – Befangitra Horombe plateau** (N; 23.047154S, 46.098617E, 1000 m a.s.l.): isolated well-preserved granite plateau with xeric vegetation and rare endemics, e.g., *Pachypodium horombense*, *Euphorbia horombensis*, *Aloe acutissima*, *Kalanchoe integrifolia*, *K. orgyalis*, *K. synsepala*, *Xerophyta dasyliroides*, surrounded by grasslands.
 28. **Ambalavao W 80 km Zazafotsy N 20 km** (NC; 22.017146S, 46.372121E, 900 m a.s.l.): granite cliffs with xeric succulent flora (e.g., *Aloe acutissima*, *A. deltoideodonta*, *Euphorbia enterophora*, *Kalanchoe hildebrandtii*, *K. synsepala*, *Pachypodium densiflorum*), surrounded by rocky grasslands.
 29. **Ambalavao W 25 km Besoa NW** (C; 21.896802S, 46.760451E, 1100 m a.s.l.): pastures and old fields with scattered *Eucalyptus* trees and endemic plants of *Aloe macroclada*.
 30. **Andringitra Catta camp S** (N; 22.084026S, 46.772666E, 950 1050 m a.s.l.): rocky alpine grasslands and pastures with endemic plants (e.g., *Adenia* sp., *Aloe acutissima*, *A. macroclada*, *Cynanchum* sp., *Dombeya* sp., *Kalanchoe beharensis*, *Pachypodium densiflorum*, *Uapaca bojeri*, *Xerophyta andringitrensis*) and introduced *Pandanus* and pine trees.
 31. **Ranomafana Manja** (N; 21.261799S, 47.460840E, 680 m a.s.l.): wet grasslands, bush on the ecotone of village and rainforest with some endemic trees (e.g., *Ravenala madagascariensis*) and cultivated and introduced plants, e.g., *Zingiber* sp., *Hedychium coronarium*, *Musa* sp.
 32. **Ranomafana Soarana/Varibolomena trail** (N; 21.256813S, 47.422720E, 920 m a.s.l.): high tropical rainforest with lemur with few open sites, with many palm species, several orchid species (e.g., endemic *Aerangis citrata*), ferns such as *Asplenium nidus*, and tree form *Cyathea* sp.
 33. **Ranomafana Vohiparara trail** (N; 21.238889S, 47.393682E, 1120–1200 m a.s.l.): mountain rainforest in ridge position of the National Park with many orchids (e.g., genera *Bulbophyllum*, *Polytachya*, *Microcoelia*), palms (e.g., *Dypsis*) and some introduced species (*Pandanus*, *Peperomia*, *Tristemma mauritanium*).
 34. **Ambositra 70 km S Vohiposa S** (NC; 21.019383S, 47.151838E, 1430 m a.s.l.): diverse rocky grasslands and bush within old, narrow, and managed fields (peanut *Arachis hypogea*, maize) on slopes and terraces, with scattered pine plantations.
 35. **Ambatofinandrahana Itremo Mts** (NC; 20.575811S, 46.811050E, 1360 m a.s.l.): xeric rocky grasslands on limestone near marmore quarry Ambatofinandrahana. There are several characteristic endemic succulents (*Aloe capitata*, *A. calcairophila*, *Euphorbia alluaudii*, *Kalanchoe tomentosa*, *Pachypodium densiflorum*, *Xerophyta dasyliroides*), orchids (*Habenaria ambositrana*) surrounded by tapia (*Uapaca bojeri*) and introduced pine stands.
 36. **Ambositra W 50 km** (C; 20.553153S, 46.951285E, 1370 m a.s.l.): ruderalized grassland and bush along the river surrounded by rice and maize fields.
 37. **Ambositra W 30 km Tsarafandry W** (C; 20.669935S, 47.135434E, 1550 m a.s.l.): rocky habitat (with endemic succulents *Aloe conifera*, *Dombeya macrantha*, *Helichrysum benthamii*, *Kalanchoe tomentosa*, and orchids *Benthamia flavida*, *Cyanotis speciosa*) with pine plantations and fields in surroundings.
 38. **Ibity, alpine grasslands** (N; 20.254053S, 47.071768E, 1700 m a.s.l.): alpine rocky grasslands with scattered bush and pine, palm (*Dypsis decipiens*) and tapia trees (*Uapaca bojeri*). On rocky sites there are characteristic endemic succulents *Pachypodium brevicaulis*.
 39. **Ibity Mts. Ridge** (N; 20.248007S, 47.056952E, 1950–2250 m a.s.l.): alpine scattered bush with *Uapaca bojeri*, *Xerochlamys bojeriana*, in rocky sites with succulent, frequently endemic plants (e.g., *Aloe capitata* var. *quarziticola*, *A. trachyticola*, *Kalanchoe integrifolia*, *Pachypodium brevicaulis*, *Tetradenia goudotii*), stapelia (*Cynanchum compactum*), and orchids (*Angraecum*, *Benthamia*, *Bulbophyllum*, *Cynorkis sacculata*, *Habenaria monadenioides*).
 40. **Ambatolampy S 77 km S of Tana** (C; 19.401214S, 47.420855E, 1500 m a.s.l.): pastures and managed fields surrounded by scattered bush, eucalyptus, and pine trees.
 41. **Tsiafahy S Tana 37 km S** (C; 19.093084N, 47.532912E, 1350 m a.s.l.): edges of ruderalized rice and maize fields, bushy landscape, near pine and eucalyptus plantations with *Mimosa* sp., *Albisia* sp.
- Data collection.*—Concerning the assemblage structure, orthopteroïd species (Orthoptera, Mantodea, Phasmida, and Blattodea) were surveyed shortly after the rainy period, in March (6–30) 2015, almost always during sunny weather. The material was sampled mostly by sweeping (net diameter 40 cm, depth 60 cm) herb and shrub vegetation along transects 100 m long and 1–2 m wide (5–8/ site, ca 2000 sweeps per site) (Gardiner et al. 2005). This method was supplemented with acoustical localization, beating of the lower part of trees (when present) and individual collection of specimens. We spent at least three hours of collection at each site. No special sampling techniques were used for ground dwelling species, tetrigids, cockroaches, mantids, and phasmids that could influence the lower species number and their abundance found. Species abundance was estimated on the basis of individuals sampled at the studied sites and expressed using the following semi-quantitative classification scale: 1 – very rare (fewer than 3 adult specimens), 2 – rare (3–10 specimens), 3 – abundant (11–100 specimens), 4 – very abundant (more than 100 specimens). These values for abundance, listed in the results, represent the highest recorded values of adults corresponding to one site (Suppl. material 1).

All the sampled taxa were measured; morphological data were analyzed and documented by photos using a dissecting microscope (OLYMPUS SZ Binocular Stereo Zoom Microscope) and digital cameras (SONY Cyber-shot DSC-P120 and Nikon Coolpix P520) for further identification and comparison and then archived. The insects that were difficult to identify were collected and preserved in 75% alcohol or ethyl acetate for further identification (maximum of 2-3 specimens per species). Phenotypic data were compared with the literature, and the specimens were identified using keys, e.g., in Descamps and Wintrebert (1965), Dirsh and Descamps (1968), Descamps (1971), Wintrebert (1972), Ůnal and Beccaloni (2017), Heller et al. (2018), and particular group species files. Some specimens could not be identified to species level (females of cryptic species, crickets, and cockroaches). For assemblage analysis, we numbered them or identified them to genus or higher taxon level (Suppl. material 1).

Systematic nomenclature and endemism status were listed according to the Orthoptera Species File (Cigliano et al. 2019) and the mantid (Otte et al. 2019), phasmid (Brock et al. 2019), and cockroach species files (Beccaloni 2019). The full names of taxa with the author(s) names and their endemism status are given in Appendix 1.

Collection of specimens was done with a permit from the Malagasy government, No. 042/15/MEEF/SG/DGF/DCB.SAP/SCB from 13 February, 2015. The collections are located at the Institute of Forest Ecology SAS and in the collection of K.-G. Heller.

Data analysis.—Ordination analysis was performed using CANOCO 5.0 (Šmilauer and Lepš 2014) to assess the association between species composition and environmental factors. We analyzed 117 species sampled at 41 sites. The environmental variables considered were altitude, latitude (to assess effect of spatial autocorrelation), and habitat type. Nonmetric multidimensional scaling (NMDS) analysis was used to classify the sampled sites based on the species composition. Variation in species composition was assessed using Detrended Correspondence Analysis (DCA) (the length of the gradient was 3.5 SD units); the environmental variables were passively projected onto the ordination to interpret the pattern. As species abundance was assessed using a log-like ordinal scale, no transformation was used for response data; rare species were downweighted, and detrending by segments was performed. To partition variation in species composition by the three environmental factors, Detrended Canonical Correspondence Analysis (DCCA) with an unrestricted Monte Carlo permutation test was used. Again, no transformation was used for the response data; rare species were downweighted, and detrending by segments was performed, with 999 permutations used for testing the significance of the pure and joint effect of the explanatory variables. Association between type of landscape management category (C, C/N, N; see above) and species rareness (% frequency) and endemism, respectively, was assessed using the χ^2 test.

Results

Diversity and distribution of orthopteroid insects.—Altogether 117 species of orthopteroid insects were found (94 Orthoptera, 7 Mantodea, 4 Phasmida, and 12 Blattodea). High species diversity was documented. Altogether 63 species were found only at one site (53.8%), 13 at two sites (11%), and 6 species (5%) at three sites, several of them only as single specimen (Suppl. material 1).

Orthoptera: Altogether we found 94 species (Ensifera 26, Caelifera 68) from 8 families (Ensifera 4, Caelifera 4) and 22 subfamilies

(Ensifera 5, Caelifera 17). Within 19 precisely identified Ensifera species, 13 are endemics (68.5%), while four show relations to African fauna and the other two are widespread. A higher endemism rate is shown by Caelifera, in which 58 of the 68 identified species are endemic to Madagascar (85.3%), two species are related to African fauna, two species to Indomalaya, and six are widely distributed, e.g., migratory species *Cyrtacanthacris tatarica*, *Acrotylus patruelis*, *Locusta migratoria*, and *Gastrimargus africanus* (Suppl. material 1). In some caeliferan families, we found only endemic species (e.g., Tetrigidae 6, Pyrgomorphidae 16).

Considering the 50% frequency limit (occurrence > 20 sites), the grasshoppers *Acorypha decisa* (frequency = 76%), *Aiolopus thalassinus rodericensis*, and *Oedaleus virgula* (68%), *Gymnobothrus malagassus* (66%), *Acrotylus patruelis* (59%), *A. aberrans*, *Duronion chloronota*, *Gastrimargus africanus*, and *Gymnobothrus variabilis* (54%) are habitat generalists and widespread species. The frequency and abundance of katydids were lower, with the most frequent species being *Ruspolia differens* (37%) and species of the genera *Tylopsis* (26.8%) and *Conocephalus* (22%). All of these species were found in both natural and cultivated (human made) habitats.

Habitat specialists seem to be species found only in nature and near well-preserved habitats, and most of them were found only at one site, sometimes as only one specimen (Suppl. material 1). Among them found only in the rainforests were: e.g., *Plangia segooides*, *Ruspolia abrupta*, *Arexion saavis*, *Oxytettix lathraeospanius*, *O. arius*, *Chlorophlaeobella tananarive*, *Schulthessia biplagiata*, three mantid, and two phasmid species; in dry spiny forests: *Mimosculderia longicaudata*, *Trigonocorypha maxima*, *Amblylakis* sp., *Colossopus grandidieri*, and *Pamphagella stenoptera*; in dry spiny bush *Eurycorypha prasinata*, *Parapyrrhicia leuca*, *Geloius nasutus*, *Gymnohippus marmoratus*, and the mantid *Chopardempusa neglecta*; in savannas and shrubland the grasshoppers *Caprorhinus ranohirae*, *C. zolotarevskiyi*, and the phasmid *Achrioptera impennis*; and in open coastal sandy habitats with savanna and shrubland, the grasshopper *Conipoda calcarata* (Suppl. material 1).

The mean species number per site was 14.4, ranging between 6 species (two sites: cultivated and degraded ruderal grassland near Ambositra and a dry spiny bush site in isolated island Nosy Vê) and 26 (mosaic of preserved xeric rocky habitats and edges of evergreen forest and grasslands with bush in the Anja reserve), or 25 species (dry spiny bush in Cape Saint Marie).

Mantodea and Phasmida: We found altogether seven mantid species (six of them endemic to Madagascar) belonging to four families and five subfamilies, and four phasmid species (three of them endemic to Madagascar) from three families and three subfamilies (Suppl. material 1, Appendix 1). All mantid and phasmid species were found mostly as single individuals. The species *Popa spurca crassa* was known till now only from eastern and southern Africa (Patel and Singh 2016). Six of seven mantid species and three of four phasmids were found in natural or well-preserved habitats with low impact of human management, confirming their significance for site conservation. Three species of the genus *Tarachomantis* could be not identified to the species level because the identification key is still being prepared (Meriguet B., in litt.)

Blattodea: Altogether we found 12 cockroach species from three families and five subfamilies. Ten species belong to the family Blaberidae and five blaberid species from the subfamily Oxylaloinae. We found at least two species endemic to Madagascar (*Aeluropoda insignis*, *Gromphadorhina portentosa*), one species (*Blattella lobiventris*) has an Afro-Malagasy range, and the other species/specimens

were identified only to the genus or higher taxon level (Vidlička L., in litt). All the species were found at single sites and in low abundance, mostly as single individuals.

Assemblages of orthopteroid insect in different habitats and altitudes.— NMDS analysis on species composition did not clearly separate the assemblages of the sampled sites (Fig. 3). Assemblages from four habitats overlapped due to their similarity in species composition and their relative abundance. Only assemblages from rainforest sites were partially separated from the other sites, despite the rainforest sites being geographically nearby (Fig. 1).

Rainforest sites had a higher abundance of the species *Phaneroptera sparsa*, *Tylopsis bilineolata* (Ensifera), *Oxytettix arius*, *Duronia chloronota*, and *Finotina radana* and a very high abundance of *Oxya hyla* (Caelifera) (Fig. 4). However, these mostly openland species have colonized forest clearings from adjacent open habitats. Ten of 94 orthopteran species (e.g., three tetrigid species, and *Chlorophlaeobella tananarive*, *Schulthessia biplagiata*), two of four phasmid, and three of seven mantid species were found only in rainforest sites (Suppl. material 1). The cultivated habitats and mountain grass- and shrubland sites and their assemblages were clustered mostly at higher altitudes in the central part of Madagascar. The cultivated habitats were characterized by widespread and abundant grasshoppers, such as *Acrida subtilis*, *Acorypha decisa*, *Gelastorrhinus edax*, *Gymnbothrus madagassus*, and *Oedaleus virgula*, and the katydid *Ruspolia differens*; in savanna and shrubland sites, strong-flying grasshoppers e.g., *Acrotylus aberrans*, *A. patruelis*, *Aiolopus thalassinus rodericensis*, and *Nomadacris septempunctata* were dominant; in the mountain grass- and shrubland habitats the species *Pycnocrania grandidieri*, *Heteracris zolotarevskyi*, *Gelastorhinus edax*, and *Dyscolorhinus squalinus* were characteristic, and we found e.g., *Parahysiella betsileana*, *Heteracris antennata*, *Eyrepocnemis brachyptera*, *Ambositracris ornata*, and *Pyrgomorphella madegassa* only in high mountains. We found the katydid *Mimoscudderia longicaudata*,

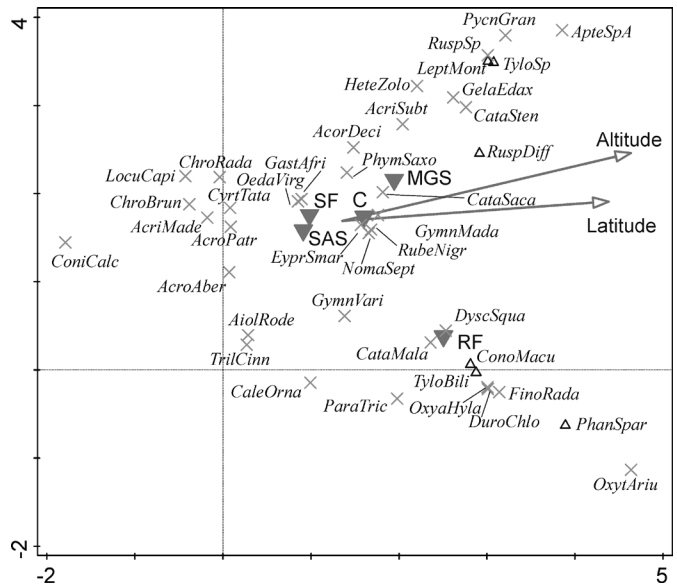


Fig. 4. DCA ordination plot summarizing the differences in orthopteran assemblages along altitudinal and latitudinal gradients in five habitats in central and southern Madagascar. Displayed are 41 species with a weight of more than 2% (6 Ensifera: triangle, 35 Caelifera: x-mark) and no Mantodea, Phasmida, and Blattodea). Abbreviations for the taxa are composed of the first four letters of their genus and species names when taxa were identified to the species level; otherwise the first four letters of the higher taxonomic unit is used. For the full species names, see Appendix 1. Environmental variables are only passively projected into the ordination. C = cultivated habitats, MGS = mountain grassland and shrubland, RF = rainforest, SAS = savanna and shrubland, SF = semiarid spiny forest.

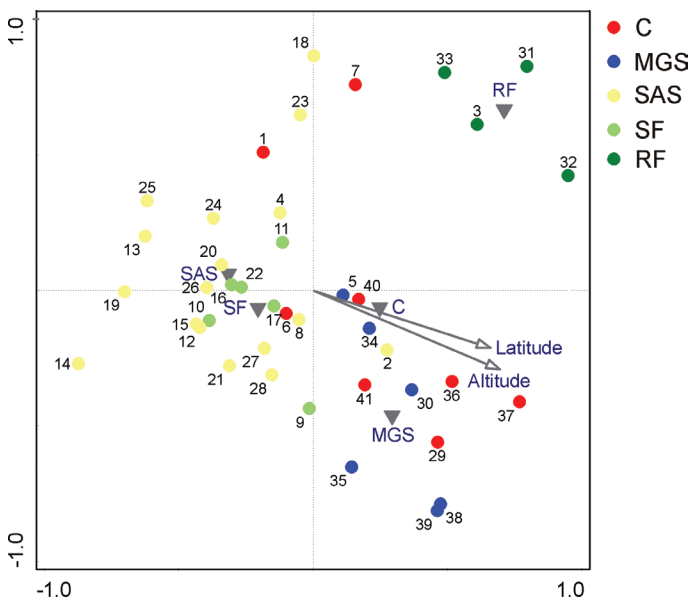


Fig. 3. Classification of 41 sites (central and southern Madagascar, 0–2250 m a.s.l.) based on orthopteran insect species composition by nonmetric multidimensional scaling (NMDS). C = cultivated habitats, MGS = mountain grass- and shrubland, RF = rainforest, SAS = savanna and shrubland, SF = semiarid spiny forest.

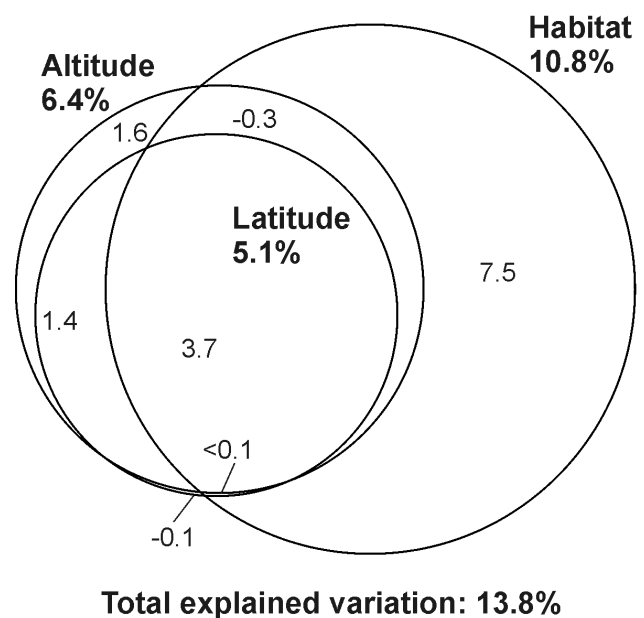


Fig. 5. Variation partitioning (%) in orthopteran insect assemblages was explained by three variables—habitat, altitude and latitude—using CCA. A unique effect of habitat type and altitude were statistically significant ($P < 0.01$).

Trigonocorypha maxima, *Amblylakis* sp., and *Collossopus grandidieri* only in spiny forests (Suppl. material 1, Fig. 4).

Eigenvalues for the first and second DCA axes were 0.33 and 0.26, respectively, and the first two axes of the ordination explained 20.7% of the variation in the species data. Altitude and latitude strongly correlated to each other and with the first axis (Fig. 4). The DCA biplot (Fig. 3) indicated that altitude (latitude) was positively correlated with species e.g., *Apteropoeodes* sp., *Oxytettix arius*, *Tylopsis* sp., *Pyncocrania grandidieri*, and *Leptacris monteiroi*, when e.g., *Conipoda calcarata* was found only in lowland sites under 100 m a.s.l. (six sites) and the grasshoppers *Chromacrida brunneriana*, *Pamphagella stenoptera*, *Gelious* and *Gymnohippus* species, as well as the mantid *Chopardempusa neglecta*, only under 150 m a.s.l.

Variation partitioning indicated that a large part of the variation in the composition of the orthopteroid insect assemblages explained by habitat type (10.8%) was shared with altitude and latitude (3.7%). Due to the uneven distribution of habitats along an altitudinal and/or latitudinal gradient (Fig. 1), the unique contribution of habitat was larger than the contribution of the other two variables (Fig. 5).

Landscape management, endemics and species frequency.—When we divided the studied sites into three management categories, we found significantly higher numbers of the most frequent species (25%), 24 vs. 45% ($n = 37$ vs. 89 species) and significantly lower numbers of species with the lowest frequency (2%), 25 vs. 54% in managed habitats than in natural habitats ($\chi^2 = 17.81$, $P = 0.007$, Fig. 6A). However, we found no statistically significant differences in the number of endemic species among the management levels ($\chi^2 = 2.53$, $P = 0.28$, Fig. 6B), although there was a lower number of endemic species in the managed habitats than in the natural habitats (64 vs 78 %). It is known that species' reactions to anthropogenic disturbance in Madagascar are generally negative, but they still re-

main poorly known (Irwin et al. 2010, Vieilledent et al. 2018). Our results have confirmed the negative effect of the management practice of deforestation and burning.

Discussion

Diversity of orthopteroid insects in Madagascar.—In Madagascar, the fourth largest island in the world, there are a total of 15 Orthoptera families with 713 species (Cigliano et al. 2019), 21 mantid species from three families (Otte et al. 2019), 77 phasmid species from six families (Brock et al. 2019), and 121 cockroach species from five families (Beccaloni, 2019). These show a high rate of endemism, some having an Afro-Malagasy range. Nonetheless, several Malagasy insect groups are taxonomically more similar to Africa than Asia or Australia (e.g., Goodman and Benstead 2003). This suggests that geographical proximity and trans-oceanic dispersal may be an important determinant of the Malagasy insect fauna. In our study, performed shortly after the rainy period, we found altogether 94 orthopteran species (13.2% of those known in Madagascar) from eight families. They show a high endemism rate within the identified species (83.5%) and a bit more relation to African (7% of species) than to Indomalayan orthoptero-fauna (4.7% of species) (cf. Cigliano et al. 2019, l.c.) (Appendix 1). Hence, this endemism rate is similar to other insect groups (Goodman and Benstead 2003, Vences et al. 2009).

Two katydid species (*Mimoscudderia longicaudata*, *Parapyrrhicia leuca*) were recently described as new to science, and the latter shows a relation to African fauna (Heller et al. 2019), while two other species (*Plangia segonoides*, *Trigonocorypha maxima*) were found for the first time after their description more than 100 years ago (Carl 1914, Heller et al. 2019). Altogether the 94 orthopteran species found certainly do not represent the final species number in the 41 studied sites, and one could expect a higher number of species during a long-term study in different seasons there. In March, after the rainy season, a relatively high proportion of unidentifiable nymphs (e.g., in Ensifera, Eumastacoidea) and females (*Ruspolia*, *Conocephalus*) was also found. Furthermore, several species groups (mainly crickets Gryllidae, monkey hoppers Eumastacoidea, and katydids of genera *Conocephalus*, *Ruspolia*, and *Tylopsis*) could not be identified to the species level, because the adequate keys for females are still missing and we have no sound recordings of males.

The mantid fauna in Madagascar is insufficiently known, and new species for science are frequently described (e.g., Mériquet 2005, 2013, in prep.). All seven species we found are still not included in the current Mantodea species file (Otte et al. 2019) On the other hand, all four phasmid species we found were already known in Madagascar (Brock et al. 2019).

The relatively low number of cockroach, phasmid, and mantid species we found can be explained by the methods used, with no special sampling techniques (use of light traps, night sampling) applied.

Assemblages of orthopteroid insect in different habitats and altitudes.—Here we present the first information on orthopteroid assemblages in five characteristic habitats and at different altitudes of Madagascar (e.g., Dirsh and Descamps 1968, Braud et al. 2014, Heller et al. 2018). We found habitat to be the most important variable explaining the variation among the particular species assemblages (7.5%, Fig. 5). When we look at the species diversity of these habitats, the highest number of species (51%) was found in savanna and shrubland sites and the lowest (29%) in cultivated sites/habitats. As savanna and shrubland are the most widely distributed

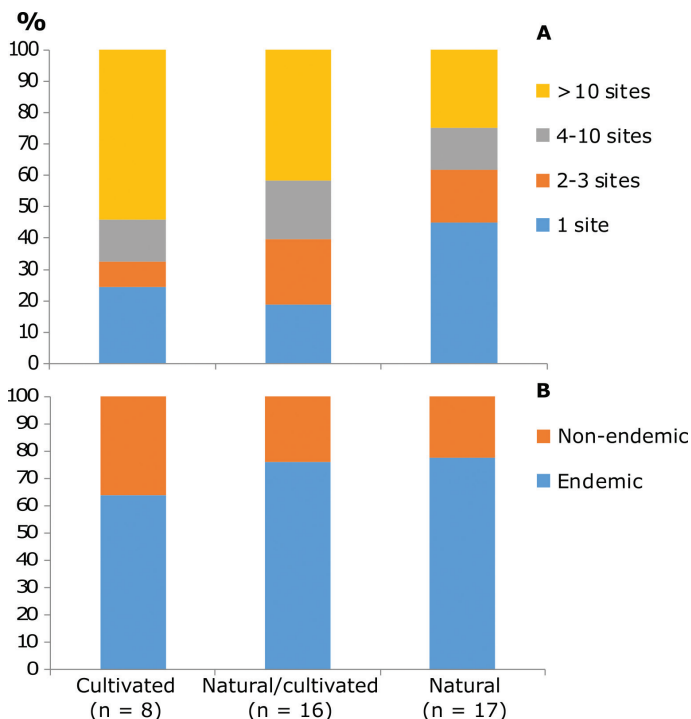


Fig. 6. A. Species frequency and B. Endemics in three categories of management (n = number of sites in each category).

habitat types in Madagascar (Moat and Smith 2007), and we sampled 17 such sites (41% of 41 sites), this percentage corresponds to 60 species, including the newly described *Parapyrrhicia leuca* Hemp & Heller, 2019 (Heller et al. 2019). We also found a high number of species (52) also at six high mountain sites (mountain grass- and shrubland), supporting their importance for conservation. Thanks to higher altitude (> 1000 m a.s.l.), this habitat is still less influenced than the lowland sites and habitats, similar to other countries where agriculture dominates (e.g., Grytnes and Vetaas 2002, Hodkinson 2005).

Rainforests are highly endangered habitats (Moat and Smith 2007, Vences et al. 2009, Irwin et al. 2010), and we were only able to sample orthopteroids at four sites. However, we found a relatively high number of species there (38; mainly in protected Ranomafana National Park). Most of these species are habitat specialists (tetrigids, katyids, *Chlorophaeobella tananarive*, and mantids).

We found the same number of species (38) in semiarid spiny forests, another very characteristic and highly endangered habitat, occurring mostly in SW Madagascar (six sites surveyed), as in rainforests. However, this was the only site at which we found the katydid *Mimoscudderia longicaudata* Heller & Krištín, 2019 (Heller et al. 2019).

As expected, we found the lowest number of species (34) at the eight cultivated habitats sites (fields, orchards, and gardens). Within the most characteristic species, we found the grasshopper species *Aiolopus thalassinus rodericensis*, *Gastrimargus africanus*, *Oedaleus virgula*, *Acrida subtilis*, and *Acrotylus* spp. to be widespread. In more humid sites and rice field ecotones the species *Oxya hyla*, *Paracrinema tricolor*, and *Duronia chloronota* were abundant, thus confirming the findings of Descamps and Wintrebert (1966). These habitats are the most changed and disturbed habitats of Madagascar, and most species live in ecotones with shrubland, pastures, and savannas. But the species number found there is still relatively high in comparison to other relatively undisturbed habitats. In this regard, it is important to mention that "disturbed habitats" have evolved differently in different Malagasy regions due to abiotic differences, but also differences in human pressure and land use, invasive and anthropogenic species, and the biotic contrasts between natural and anthropogenic habitat. For example, in southern areas the species might face gentler environmental contrasts between open spiny thicket and grazing lands used by livestock, whereas on the eastern part of the island species might face sharper contrasts between closed rainforest and open rice fields (cf. Irwin et al. 2010).

Altitudinal distribution.—The number of heterometabolous insect species and their abundance changes with altitude. The number of species mostly increases steeply with altitude up to a certain level, giving the maximum species richness at mid-altitudes. Within these mid-altitudes (e.g., some hundreds of metres a.s.l.), only a small change in the number of species is observed, but later, above a critical altitude (specific for each area), a decrease in species richness is evident (e.g., Claridge and Singhrao 1978, Grytnes and Vetaas 2002, Hodkinson 2005, Bidau 2014). In Orthoptera, for example, in East Africa, at the altitudinal gradient of Mt Kilimanjaro, Hemp (2009) found altogether 139 Caelifera species, while the majority of species (76) had their main occurrence in the lower altitudes, in the colline zone (700–1100 m a.s.l.) around the mountain, and 23 species were adapted to mountainous habitats, inhabiting sub-montane and lower montane zones. Only eight of these 23 species showed a clear preference for montane habi-

tats (Hemp 2009). In our study, we could not find the altitudinal preferences of species, because several species were found only in small number of individuals and the material was sampled only during one month. But when we divided our 41 sites into three altitudinal zones, altogether 49 species were found at lower altitudes (< 455 m a.s.l., 15 sites), 73 species at middle altitudes (680–1050 m a.s.l., 13 sites) and 63 species at higher altitudes (1120–2250 m a.s.l., 13 sites). The relatively low number of species at lower altitudes can be explained by human disturbance at these sites, when more habitat changes occurred in frequently managed agricultural areas at lower altitudes and thus more species can survive at higher altitudes that are still less affected by human impact.

In Ensifera, we found more species only at lower altitudes (< 300 m a.s.l.), e.g., *Eurycorypha prasinata*, *Parapyrrhicia leuca*, *Trigonocorypha maxima*, *Colossopus grandidieri*, and *Amblylakis* sp., while at higher altitudes (> 1500 m a.s.l.) we found only species of the genera *Tylopsis* sp., *Conocephalus* sp., and *Ruspolia differens*. In Caelifera, we found more species at higher altitudes (> 1350 m a.s.l.), e.g., *Pycnocrania grandidieri*, and the following species were found only at high altitudes: *Parahysiella betsileana*, *Eyprepocnemis brachyptera*, *Heteracris antennata*, *Spathosternum malagassum*, *Pyrgomorphella madecassa*, and *Ambositracris* spp. At lower sites (< 300 m a.s.l.), we found only e.g., *Conipoda calcarata* (6 sites, mostly up to 50 m a.s.l.), *Chromacrida brunneriana* (4 sites up to 50 m a.s.l.), *Pamphagella stenoptera*, *Geloius* sp., *Gymnohippus* sp., and *Lavanonia* sp., which supports a few present findings (Dirsh 1963a, b, Descamps and Wintrebert 1965, 1966, Dirsh and Descamps 1968). Comparing our data on altitudinal distribution of Caelifera species with the literature, most of the species have a wide altitudinal distribution from sea level up to 1500 m a.s.l. (Braud et al. 2014). However, we could confirm the occurrence at higher altitudes of several species, e.g., *Eyprepocnemis brachyptera* (Wintrebert 1972, Braud et al. 2014), *Ambositracris* spp., *P. betsileana* (Wintrebert 1972), and *P. madecassa* (Dirsh 1963b, Descamps and Wintrebert 1966), but some species were also found at higher altitudes than previously described (e.g., *H. zolotarevskyi*, *P. grandidieri* now up to 2250 m a.s.l., formerly only up to 300 m and 1200 m a.s.l., respectively).

Notes on distribution and ecology of some species.—*Pamphagella stenoptera*: We found this cryptic colored and endemic species in the gravel bank of a dry river bed in a dry spiny forest of Andohahela Mangatsiaka National Park (20 March 2015, 2 adult females and a subadult female); this species had been found previously only at four sites of southern and south-western Madagascar (Descamps and Wintrebert 1966, Dirsh and Descamps 1968).

Heteracris antennata: Only limited and outdated data are available on the distribution of this endemic species (Dirsh 1962, Dirsh and Descamps 1968). We found one male in Ibity Mts. (1950 m a.s.l., 29 March 2015) within the mountain grass- and shrubland assemblage together with the mountainous species *E. brachyptera*, *Parahysiella betsileana*, *Pyrgomorphella madecassa*, and *Dyscolorrhinus vittatus* (cf. Dirsh and Descamps 1968).

Rubellia nigrosignata: This normally brachypterous and endemic species was the most frequent (27% of sites) and abundant pyrgomorphid species in our material, occurring from the sea level up to 1550 m a.s.l. Moreover, we regularly found two color forms (mostly yellow-black, less green) and three macropterous individuals (one male and two females) in the coastal shrubland of the south and southwest (Ambola and Cape Saint Marie). Macroptery is rather rare, but known in this species (e.g., Descamps and Wintrebert 1966).

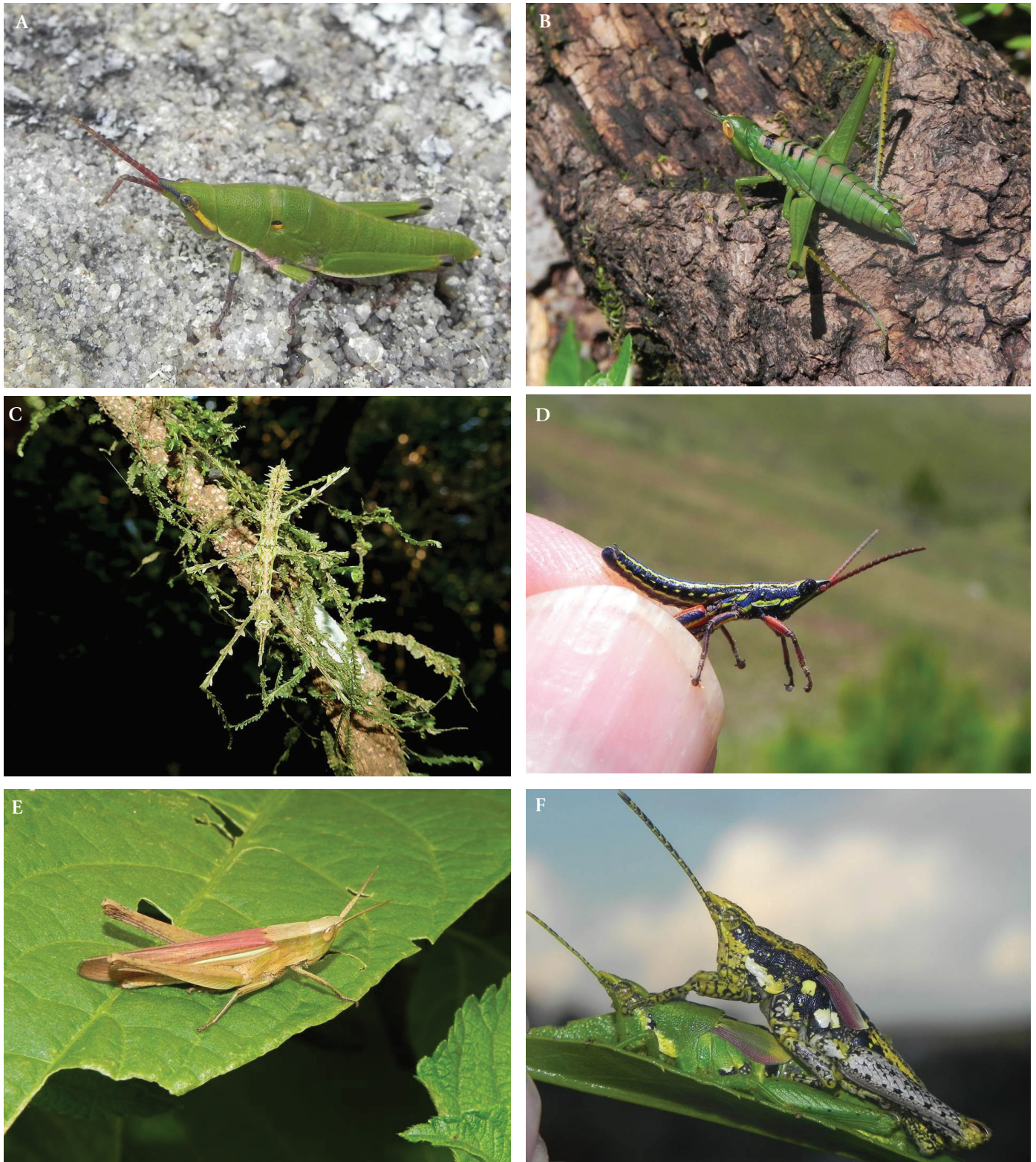


Fig. 7. A. Endemic species *Caprorhinus ranohirae* in savanna and shrubland of Isalo National Park; B. Monkey hopper *Apteropeodes nigroplagiatus* female in semiarid spiny forest of Zombitse National Park; C. Cryptic and endemic mantid *Antongilia laciniata* in Ranomafana rainforest; D. Endemic *Ambositracris ornata* male in mountain grasslands and shrubs of Ibity Mts.; E. Afro-Malagasy species *Duronia chloronota* (yellow pink form) in cultivated habitats near Ambositra, and; F. eurytopic and color dimorphic endemic *Rubellia nigrosignata* in copula (shrubland in Anakao). Photos by A. Krištín.

The genus *Caprorhinus* is endemic to Madagascar and adjacent islands, and, in species number, it is the richest grasshopper genus (28 species). We found a few specimens of three species, *C. ranohira* (savanna and shrubland in Isalo National Park), *C. zolotarevskiyi* (shrubland near Fianarantsoa), and *C. kevani* (cultural steppe with bush near Ambatolahy), expanding the present knowledge on their distribution (Wintrebert 1972).

A few specimens of the endemic genera *Gymnohippus* and *Geloius* were found only in coastal shrubland (March 18, 2015) in south western Madagascar, similarly to Descamps and Wintrebert (1966).

Conspicuous aposematic species of the genus *Phymateus* were found in March only in the nymph stage at six sites, when clusters of nymphs were found in the second instar (one site with 81 individuals), the fourth instar (3 sites with 25–60 individuals), and the sixth instar (two sites with 20–22 individuals). All the nymph clusters were found on toxic host plants from the family Apocynaceae (*Pervillaea venenata*, *Leptadenia madagascariensis*, *Gomphocarpus fruticosus*), similarly to that mentioned by Descamps and Wintrebert (1966) and Braud et al. (2014).

Chlorophaeobella tananarive: This small endemic species (syn. *Paralobopoma*) was previously found only in eight forested sites of C and E Madagascar (Dirsh and Descamps 1968). We found it in the rainforest of Ranomafana National Park (1150 m a.s.l.).

The most conspicuous eumastacid species, *Apteropeodes nigroplagiatus*, was found at two sites (forest edge in Andringitra National Park and in a dry spiny forest of Zombitse National Park), which has expanded our knowledge on species distribution (Descamps and Wintrebert 1965). This species and some characteristic orthopteroid species found in particular in five habitats are shown in Fig. 7.

Remarks on data sampling.—Short-term (lasting one month) research has both advantages and disadvantages. The advantage is that in the same phenological aspect we can sample and compare species assemblages from different sites and habitats, but the disadvantage is that there are many species or life stages (e.g., adult males) that could not be found over such a short time or in a specific season. Hence, further research is needed to improve identification keys in some orthopteroid groups and the use of different sampling techniques. We could expect many more species, perhaps several new to science, to be found during systematic surveys over several seasons at the studied sites. In spite of all these methodological problems, we believe that these results can be used in the identification of conservation priorities at the studied sites and in Madagascar's endangered habitats.

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Appendix 1

List of all orthopteroid insect taxa with abbreviations used in the analyses and figures); * species endemic to Madagascar, ** Afro-Malagasy distribution, *** Indomalaya- Malagasy distribution, **** widespread species.

Eurycorypha prasinata Stål, 1874* – EuryPras; *Mimoscudderia longicauda* Heller & Krištín, 2019* – MimoLongi; *Parapyrrhicia leuca* Hemp & Heller, 2019* – ParaLeuc; *Phaneroptera sparsa* Stål, 1857**** – PhanSpar; *Xenodoxus* sp.* – XenoSp; *Plangia segonoides* (Butler, 1878)* – PlanSego; *Trigonocorypha maxima* Carl, 1914* – TrigMaxi; *Tylopsis bilineolata* Karsch, 1893** – TyloBili; *Tylopsis* sp. – TyloSp; *Amblylakis* sp.* – AmbLSp; *Colossopus grandidieri* Saussure, 1899* – ColoGran; *Conocephalus (Anisoptera) iris* (Serville, 1838)** – ConoIris; *Conocephalus (Anisoptera) cf. maculatus* (Le Guillou, 1841)**** – ConoMacu; *Conocephalus (Megalotheca) cf. marcello* Gorochov & Llorente, 2004* – ConoMarc; *Conocephalus (Megalotheca) cf. xiphidioides* (Karny, 1907)* – ConoXiph; *Conocephalus* sp1. – ConoSpA; *Conocephalus* sp2. – ConoSpB; *Ruspolia differens* (Serville, 1838)** – RuspDiff; *Ruspolia cf. abrupta* (Walker, 1869)* – RuspAbr; *Ruspolia cf. madagassa* (Redtenbacher, 1891)* – RuspMada; *Ruspolia* sp. – RuspSp; *Gryllotalpa madecassa* (Chopard, 1920)* – GryllMada; *Gryllidae* g.sp.1 – GryllSp; *Podoscirtinae* g.sp.1. – PodoSpA; *Podoscirtinae* g.sp.2. – PodoSpB; *Oecanthus cf. brevicauda* Saussure, 1878** – OecaBrev; *Arexion suavis* Rehn, 1929* – ArexSuav; *Cryptotettix* sp.* – CrypSp; *Oxytettix arius* (Rehn, 1929)* – OxytAriu; *Oxytettix lathraeospanius* (Günther, 1939)* – OxytLath; *Paratettix cinereus* Bolívar, 1887* – ParaCine; *Pseudosystolederus sikorai* Günther, 1939* – PseuSiko; *Acrida madecassa* (Brancsik, 1892)* – AcridMada; *Acrida subtilis* Burr, 1902* – AcridSubt; *Calephorus ornatus* (Walker, 1870) – CaleOrna; *Chlorophlaeobella tananarive* (Dirsh, 1963)* – ChloTana; *Chromacrida radamae* (Saussure, 1899)* – ChroRada; *Chromacrida brunneriana* (Bolívar, 1893)* – ChroBrun; *Duronina chloronota* (Stål, 1876)** – DuroChlo; *Gymnobothrus variabilis* Bruner, 1910* – GymnVari; *Gymnobothrus madecassus* Bruner, 1910* – GymnMada; *Leptacris monteiroi hova* (Karsch, 1896)* – LeptMont; *Acorypha decisa* (Walker, 1870)*** – AcorDeci; *Catantops stenocrobyloides* Karny, 1907* – CataSten; *Catantopsis malagassus* (Karny, 1907)* – CataMala; *Catantopsis sacalava* (Brancsik, 1892)*** – CataSaca; *Parahysiella betsileana* Wintrebert, 1972* – ParaBets; *Pamphagella stenoptera* Descamps & Wintrebert, 1966* – PampSten; *Cyrtacanthacris tatarica* (Linnaeus, 1758)**** – CyrtTata; *Finotina radama* (Brancsik, 1892)* – FinoRada; *Nomadacris septemfasciata* (Serville, 1838)** – NomaSept; *Rhadinacris schistocercoides* (Brancsik, 1892)* – RhadSchi; *Eyrepocnemis smaragdipes* Bruner, 1910* – EyprSmar; *Eyrepocnemis brachyptera* Bruner, 1910* – EyprBrac; *Heteracris antennata* (Bolívar, 1914)* – HeteAnte; *Heteracris finoti* (Bolívar, 1914)* – HeteFino; *Heteracris nigricornis* (Saussure, 1899)* – HeteNigr; *Heteracris zolotarevskyi* (Dirsh, 1962)* – HeteZolo; *Gelastorrhinus edax* Saussure,

1899* – GelaEdax; *Acrotylus patruelis* (Herrich-Schäffer, 1838)**** – AcroPatr; *Acrotylus aberrans* Bruner, 1910* – AcroAber; *Aiolopus thalassinus rodericensis* (Butler, 1876)* – AioloRode; *Conipoda calcarata* Saussure, 1884* – ConiCalc; *Gastrimargus africanus* (Saussure, 1888)**** – GastAfri; *Locusta migratoria capito* (Saussure, 1884)**** – LocuCapi; *Oedaleus virgula* (Snellen van Vollenhoven, 1869)* – OedaVirg; *Paracinema tricolor* (Thunberg, 1815)**** – ParaTric; *Pycnocrania grandidieri* (Saussure, 1888)* – PycnGran; *Trilophidia cinnabarina* Brancsik, 1892* – TrilCinn; *Oxya hyla* Serville, 1831**** – OxyaHyla; *Spathosternum malagassum* Dirsh, 1962* – SpatMala; *Geloius nasutus* Saussure, 1899* – GeloNasu; *Geloius* sp.* – GeloSp; *Gymnohippus marmoratus* Bruner, 1910* – GymnMarm; *Gymnohippus* sp.* – GymnSp; *Phymateus saxosus* Coquerel, 1861* – PhymSaxo; *Phymateus* sp. – PhymSp; *Pyrgomorphella madecassa* Bolívar, 1904* – PyrgMada; *Rubellia nigrosignata* Stål, 1875* – RubeNigr; *Schultheisia biplagiata* Bolívar, 1905* – SchuBipl; *Ambositracris ornata* Dirsh, 1963* – AmboOrna; *Ambositracris cf. morati* Kevan, Akbar & Chang, 1971* – AmboMora; *Caprorhinus ranohirae* Kevan, 1963* – CaprRano; *Caprorhinus zolotarevskyi* Uvarov, 1929* – CaprZolo; *Caprorhinus kevani* Descamps & Wintrebert, 1966* – CaprKeva; *Dyscolorhinus squalinus* Saussure, 1899* – DyscSqua; *Dyscolorhinus vittatus* Kevan, Akbar & Singh, 1964* – DyscVitt; *Acanthomastax bifida* Descamps, 1964* – AcanBifi; *Apteropeodes nigroplagiatus* Bolívar, 1903* – ApteNigr; *Apteropeodes* sp1.* – ApteSpA; *Apteropeodes* sp2.* – ApteSpB; *Apteropeodes* sp3.* – ApteSpC; *Lavanonia* sp.* – LavaSp; *Wintrebertia* sp. – WintSp; *Tarachomantis cf. caldweli* Bates, 1863* – TaraCald; *Tarachomantis* sp1.* – TaraSpA; *Tarachomantis* sp2.* – TaraSpB; *Liturgusella malagassa* Saussure & Zehntner, 1895* – LituMala; *Polyspilota* sp.* – PolySp; *Chopardempusa neglecta* (Paulian, 1958)* – ChopNegl; *Popa spurca crassa* Giglio-Tos, 1917**** – PopaSpur; *Sipylodea sipylus* (Westwood, 1859)**** – SipySipy; *Antongilia laciniata* Redtenbacher, 1906* – AntoLaci; *Paracirsia cf. distincta* (Brunner von Wattenwyl, 1907)* – ParaDist; *Achrioptera impennis* Redtenbacher, 1908* – AchriImpe; *Aeluropoda insignis* Butler, 1882* – AeluInsi; *Gromphadorhina portentosa* (Schaum, 1853)* – GromPort; *Oxyhaloinae* g.sp1. – OxyhSpA; *Oxyhaloinae* g.sp2. – OxyhSpB; *Oxyhaloinae* g.sp3. – OxyhSpC; *Rhabdoblatta* sp. – RhabEpil; *Epilamprinae* g.sp. – EpilSp; *Pycnoscelinae* g.sp. – PycnSp; *Blaberidae* g.sp1. – BlabSpA; *Blaberidae* g.sp2. – BlabSpB; *Periplaneta* sp. – PeriSp; *Blattella lobiventris* (Saussure, 1895)** – BlattLobi.

Supplementary material 1

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Data type: Microsoft Excel file

Explanation note: Orthopteroid insects at 41 sites (5 habitats) of central and southern Madagascar in altitudes between 0 and 2250 m a.s.l. (March 6–30, 2015). (Abundance: 1: less than 3 adult specimens, 2: 3–10 specimens, 3: 11–100 specimens, 4: more than 100 specimens. Landscape type: N = natural, C = cultivated. Habitat: C = cultivated, MGS = mountain grassland & shrub, RF = rainforest, SAS = savanna and shrubland, SF = semiarid spiny forest). For full species names see App. 1

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