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The Biogeography of Coccinellidae in the Pacific Area

Chazeau, J., Dr., ORSTOM, BP A5. Noumea, New Caledonia

Abstract: This paper is an attempt to sum up our knowledge of the coccinellid fauna in the Pacific area.

About 560 species have been recorded from the area, in which Australia has been included because it is essential for a proper understanding of the Melanesian insular faunas.

Major points emerging from this study are: a significant reduction in the number of species from west to east; the prevalence of Oriental and Australian influences over American influences; the difficulty of determining faunal characteristics for most sub-regional units; the great difference between the New Guinean and Australian faunas, the former, though not well investigated as yet, displaying a much stronger Oriental influence and a wide variety of endemic forms; recent artificial dispersal by man for purposes of biological control, which may sometimes completely mask the original fauna.

It must be admitted that a great deal of taxonomic work remains to be done before we can claim to have a comprehensive biogeographic synthesis of this family in the Pacific.

The family Coccinellidae is important among the Coleoptera both because of its size and because of the role of the species in agricultural and sylvicultural ecosystems: most species prey upon potential pests, but some are mycetophagous or phytophagous.

This provisional synthesis on the Pacific fauna is based essentially on a study of species distribution and the faunal relationships between the various areas of the Pacific. The study covers the Central and South Pacific, from Australia to Hawaii and French Polynesia, and from Micronesia to New Zealand. It is not exhaustive because species inventories are incomplete, and there is a need for revision of faunas presumed well-known, using modern taxonomic methods.

General Review of the Fauna

Relative Sizes of Faunas

About 560 species and 85 genera have been recorded, and all the subfamilies (*sensu* Sasaji 1968) are present. Faunal size varies greatly from one area to another: at one extreme Australia contains approximately 48 % of the known fauna of the Pacific, whilst at the other an island like Marcus (Minami Tori Sima) has less than 0.2 %. Only New Guinea, with 27 % of the fauna, can be compared to Australia. The other areas are much less rich: New Zealand (9 %), New Caledonia (8 %), Hawaii (8 %), Fiji (6.5 %), French Polynesia (5 %), archipelagos like Vanuatu, the Solomons, the Carolines, or the Mariana Islands (4 %), and finally, small islands and archipelagos such as Marcus, the Volcano Islands (Kazan Retto), Wake, Wallis and Futuna, the Marshall Islands, Kiribati (Gilberts) and even Samoa which, in the present state of knowledge, contain less than 2 % of the Pacific fauna.

Species-Area Relationship

The regression line of the number of species over area has a positive slope; the gradient of the regression line differs significantly from zero (d.o.f.: 17; $t = 8.46$).

Relationship with Geographical Isolation

The measurement of geographical isolation is difficult; here we will consider it as being essentially the distance between

the area under study and the continental masses, and this usually increases from west to east.

Thus the Marianas and Carolines have considerably more species than the Marshalls or Kiribati. No doubt the species-area effect also operates, making the effect of isolation difficult to distinguish. Nevertheless, it can be seen that New Caledonia has more species than Fiji for an equivalent area, and Samoa has fewer species than the Marianas or Carolines although the two latter have only half the area of Samoa. Moreover, French Polynesia, with a land area 25 % greater than Micronesia, contains only 28 species compared to 49 for Micronesia.

Hawaii, whose fauna is particularly rich considering its isolation, is an apparent exception. In fact, it will be shown that this richness is to a large degree artificial, since only 9 species are regarded as indigenous compared to 44 species for New Caledonia, 28 for Fiji or 22 for Vanuatu, for an equivalent surface area.

Distribution of Tribes

Three tribes are excluded from this analysis because their presence is undeniably artificial: the Hyperaspini in Hawaii, the Oeneini in Fiji and perhaps in Micronesia and French Polynesia, and the Aziini in Fiji. Three other tribes have not been reported: the Platynaspini, the Lithophilini, and the Exoplectrini.

Four of the 15 tribes occurring naturally in the Pacific are not represented in Australia: the Ortaliini and the Aspidimerini are found only in New Guinea and in the Marianas; the Cranophorini is represented only in New Zealand and, elsewhere, principally in South Africa and South America; and the Sukunahikonini is pan-tropical and appears not to be present in Australia, but it is much less widely distributed towards the east.

Endemic Faunas

Percentages of Endemicity

Examination of the proportions of endemic species shows that, again, Australia, New Guinea and New Zealand have the highest (88 to 70 % of the faunas).

Most archipelagos, for example the Cook Islands, Samoa and French Polynesia, the Marshalls, Kiribati and Hawaii, contain few endemics. These low percentages of endemicity may be related to their small number of species. However, it is noticeable that the islands and archipelagos of the Melanesian Arcs have greater proportions of endemics (41 to 48 % for New Caledonia, 17 to 21 % for Vanuatu, 14 % for the Solomons), as do certain Micronesian archipelagos (Carolines 58 %, Marianas 23 %), and these islands and archipelagos are closer to the continental masses and must have been colonized before those mentioned above. If we exclude New Zealand which has very few Polynesian affinities, Polynesia is the poorest region in proportion of endemic species, presumably because of the late and limited colonization of this area, the most isolated in the Pacific.

The situation is the same at the generic level: 26 % of Pacific genera are endemic to their area (22 genera); the proportion is about 30 % for Australia, 17 % for New Zealand, 10 % for New Guinea, 6 % for the Carolines and for New Caledonia (only one genus). Other areas have no endemic genera.

To summarize, endemic species at the archipelagos level are practically absent east of the 180° meridian, with 3 exceptions: *Menochilus samoensis* (Arrow) in Samoa; *Paraphellus sp.* in the Cook Islands; and *Scymnus (P.) insularis* Bohemann in French Polynesia. In contrast, Australia, New Guinea and New Zealand have 87 % of the known endemics: Australia 54 %, New Guinea 25 %, and New Zealand 8 %.

Genera Involved in Endemism

In the continental areas and certain large islands endemism involves a large number of genera: the number decreases noticeably with greater isolation. Thus, endemic species are found in 37 genera in Australia, 34 in New Guinea, 12 in New Zealand and in New Caledonia, but in only 9 for the whole of Micronesia, 5 for Vanuatu and 3 for the Solomons. East of Fiji only 3 isolated endemic species occur.

This phenomenon may be directly related to the number of ecological niches available, and also to the earlier arrival of more diversified taxa. The first point may explain the explosive speciation of certain groups in the largest areas: in Australia, *Rhyzobius* (55 endemic species), *Scymnus* (37), and to a lesser degree *Nephus* (19), *Orcus* (16), and *Scymnodes* (14); in New Guinea, *Henosepilachna* (19) and *Diomus* (13); and in New Zealand, *Veronicobius* (13). Moreover, the genera involved in endemism in Australia differ from those involved in New Guinea.

Non-Endemic Faunas and their Geographical Origins

Pacific Wides

A group of 6 species is present throughout the Pacific. This group is characteristic of, and common to, the Pacific area: 3 species are Oriental aphidophagous coccinellids with polyphagous tendencies, *Coccinella repanda* Thunberg, *Coelophora inaequalis* (F.), and *Harmonia arcuata* (F.); and 3 are Austro-melanesian, *Cryptolaemus montrouzieri* Mulsant (coccidophagous), and *Henosepilachna sparsa vigintisexpunctata* (Boisduval) and *Henosepilachna vigintioctopunctata* (F.) (phytophagous).

Australia and New Guinea

Australia (40 species) and New Guinea (45 species) have 22 species in common; this figure includes the Pacific wides and 11 species not existing elsewhere. Whereas New Guinea contains 18 species (40 % of its non-endemics) of Oriental origin absent from Australia, Australia has only 4 species of Oriental origin (10 % of its non-endemics) absent from New Guinea. Twelve Australian species appear to be autochthonous and to have dispersed into the Pacific without colonizing New Guinea. At the generic level, 8 genera present in Australia are absent from New Guinea, and 14 genera recorded from New Guinea are not represented in Australia.

Clearly, New Guinea and Australia are much more different in their coccinellid faunas than their geographical proximity would suggest, and the Oriental influence is considerably more marked in New Guinea than in Australia.

New Zealand

Of 15 species, 8 are common with Australia and 3 of these are Pacific wides. The others, of varying origin, appear to have been dispersed by man.

Solomon Islands and Vanuatu

These archipelagos show many similarities: in each, of a total of 19 or 20 species, half are present in Australia, including the 6 Pacific wides; the remainder comprises Melanesian and Oriental species, with one indigenous species of Micronesian origin and 2 intentional introductions into Vanuatu.

New Caledonia

About 80 % of New Caledonian non-endemics occur also in Australia (18 species out of 23): the 6 Pacific wides, 7 Melanesian or Austro-melanesian species, and 5 Australian species. The other non-endemic species are fairly widely distributed throughout the Pacific, and one is Oriental.

It is interesting to note that 10 species (43 %) occur also in New Guinea, approximately half as many as occur in Australia.

Fiji

The Australian influence is noticeable less strong in Fiji than in New Caledonia: 38 % of the 26 non-endemic species occur in Australia. This percentage includes the 6 Pacific wides, and the Papuan influence is almost as great (38 %) as it is in New Caledonia. The remainder of the fauna is of mixed origin: Pacific (12 %), Melanesia (12 %), Indonesia, Philippines.

Central and Southeast Polynesia

Non-endemic species constitute almost the totality of the known fauna. In Samoa, as in Wallis and Futuna, Pacific wides and species of central Pacific distribution represent more than 70 % of the total; species common with Australia are Pacific wides. In the Cook Islands and French Polynesia, the Australian influence is paradoxically stronger, and the number of intentional introductions is high: more than 39 % of the non-endemic fauna.

Hawaii

Not one of the 42 known species is endemic, and it is recognized that 80 % of them have been introduced intentionally. The 9 indigenous species include approximately equal numbers of American, Austro-melanesian, Polynesian species and Pacific wides.

Micronesian Archipelagos

In the Marianas the Oriental and east-palearctic influences are particularly strong: 60 % of the fauna; the remainder is Micronesian, Austro-melanesian, American or intentionally introduced. In the Carolines, the influences are similar.

The Marshall Islands and Kiribati have in common all the species present on Kiribati, including 3 of the Pacific wides; most of the species in common have a broad Pacific distribution and the Oriental influence is moderate.

The Bonin Islands (Ogasawara Gunto), in contrast, display strong east-palearctic and Oriental influences (respectively 50 % and 25 % of the fauna), which is not surprising given their geographical position.

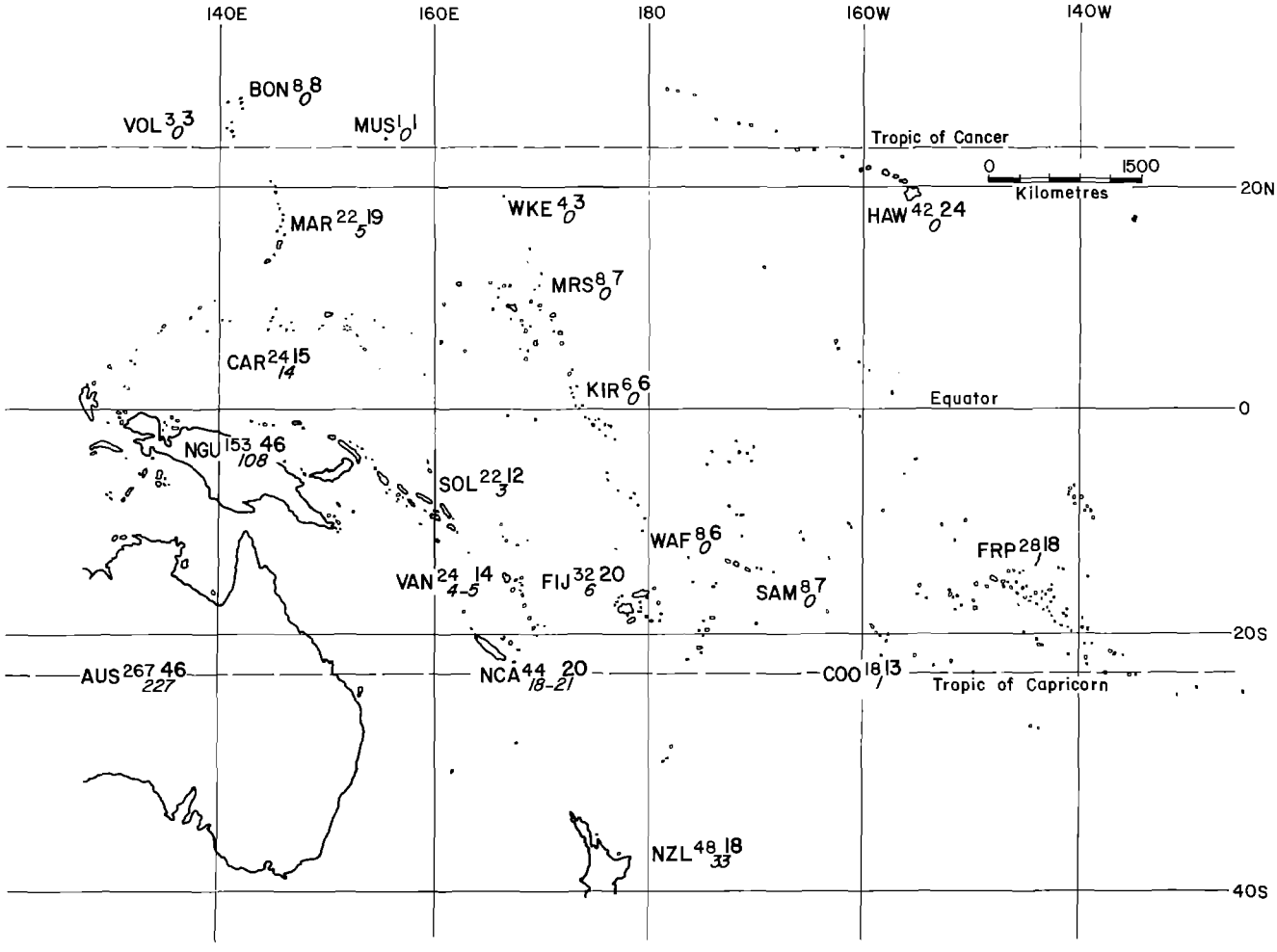
Lastly, the non-endemic fauna of the Volcano Islands, Marcus and Wake, is small and heterogeneous, suggesting accidental introductions by man.

Attempt at Characterization and Comparison of Faunas

We have attempted to characterize the faunas of the main geographical areas, basing our study essentially on the analysis of indigenous species; intentional introductions will be treated later.

The Pacific as a Faunal Unit

As would be expected from the large surface area and geographical diversity of Pacific, the family has no faunal characteristics truly specific to the region. The species which might be considered as characteristic of the Pacific generally due to their frequent presence, are not numerous (6 species, or approximately 1 %), and half of these are Oriental, the others being clearly of Austro-melanesian origin.



Figures indicate: the number of species; the number of genera (large type); the number of endemic species (italics).

AUS = Australia	BON = Bonin Islands	CAR = Caroline Islands	COO = Cook Islands
FIJ = Fiji	FRP = French Polynesia	HAW = Hawaii	KIR = Kiribati
MAR = Mariana Islands	MRS = Marshall Islands	MUS = Marcus	NCA = New Caledonia
NGU = New Guniea	NZL = New Zealands	SAM = Samoa	SOL = Solomon Islands
VAN = Vanuata	VOL = Volcano Islands	WAF = Wallis and Futuna	WKE = Wake

Fig 1 Distribution of Coccinellidae in the Pacific area.

Australia and the Melanesian Arcs

The differences between the faunas of New Guinea and Australia are much greater than their geographical proximity would lead us to suppose, particularly if we consider the relatively high mobility of species of the family.

Nevertheless, this observation must not lead us to underestimate the influence of the Australian continent in the Western Pacific. Although a large number of Melanesian genera and species are absent from Australia, endemicity of the fauna of the Melanesian Arcs is much more marked at a local than a regional level; to be more precise, no species present in all the territories of the Melanesian Arcs is absent from Australia. The various archipelagos of the Arcs have in common only the 6 Pacific wides, and the exclusion of Fiji adds only a single species to this list, *Henosepilachna urvillei* (Montrouzier).

Micronesia

Determining the characteristic elements of a Micronesian unit is also difficult, even if we limit ourselves to the 4 large archipelagos: apart from the Pacific wides, only 3 species are common to all, and one of these was introduced intentionally. However, the Marianas and Carolines have 8

species in common, of which only one is exclusively Micronesian and one other Melano-micronesian, and all the known species of Kiribati are present on the Marshalls.

The characteristic of the Micronesian fauna, like that of Melanesia, is the juxtaposition of the endemic species of each archipelago, and the strong Oriental and east-palearctic influences over the westernmost islands, influences quite different in quality from that affecting New Guinea.

Central and Southeast Polynesia

In the central Pacific where endemic species are rare, the Polynesian characteristic, on analysis, appears to be rather an attenuation of the western influence (Oriental in particular), than a truly distinctive fauna. Thus, Samoa and French Polynesia have only 5 species in common, of which 3 are Pacific wides. Three species, however, seem peculiar to this area: *Stethorus siphonulus* Kapur, *Megalocaria tricolor fijiensis* Crotch, *Scymnus ocellatus* Sharp.

Human movements have no doubt been an important dispersal factor: thus, Hawaii and French Polynesia have 10 species in common, of which at least 7 are indigenous in the latter territory and 6 do not belong to the group of Pacific wides.

Present Dispersal by Man

Recent Accidental Introductions

Insularity is an isolation factor. But, because of the faunal unbalance which results from it, insular ecosystems are vulnerable to accidental introductions brought about by an increase in human mobility. Despite the existence of strict phytosanitary regulations, such introductions are frequent. No doubt they would be more frequent if these measures did not exist, but we must not overestimate the practical effectiveness of legal barriers in the Pacific islands.

As an example, since 1975 the increasing occurrence in New Caledonia of a species not previously recorded has been monitored *(Scymnodes lividigaster* Mulsant; origin: Australia ?; introduction: between 1972 and 1975 ?); and the appearance of *Chilocorus nigritus* (F.), probably introduced from Vanuatu where the first specimen was collected in 1977, was recorded in 1980. Chapin (1965) discusses similar recent accidental introductions into Micronesia of *Henosepilachna doryca* (Boisduval) (origin: the Philippines) and *Harmonia axyridis* (Pallas) (origin: Japan). No doubt similar cases exist in French Polynesia, as the mobility and small size of the species favours dispersal.

Intentional Introductions

The interest in the family for purposes of biological control has led to an increasingly large number of intentional introductions. Half of the areas under study (11 out of 20) has received at least one species. Hawaii holds the record with 32 species; other areas with a considerable number of introductions are French Polynesia (11 species), the Cook Islands (6 species) and Fiji (4 or 5 species): the Pacific appears to be a remarkable experimental field for these control measures.

These operations date from the beginnings of biological control; the introduction of *Coccinella undecimpunctata* L. into New Zealand to control aphids was in 1874 (Dumbleton 1936, quoted by Hodek 1973). *Rodolia cardinalis* Mulsant was sent to Hawaii by Koebele in 1890 (Perkins 1943) and this method of control has been favoured in the archipelago ever since.

There is a certain lack of clarity, on a taxonomic level, about many of Koebele's introductions (he is considered responsible for the establishment of 17 species of this family alone in Hawaii), but there is no doubt that the Hawaiian coccinellid fauna is largely artificial. However, it is possible that a few species, which have proved their dynamism elsewhere, were already present in Hawaii before their official introduction. In the same way, we lack precise data on the conditions under which several introductions were carried out in French Polynesia: it is therefore difficult to use them as a basis for significant conclusions.

In contrast, the introductions of American species (*Cryptognatha nodiceps* Marshall, *Cryptognatha simillima* Sicard, *Azya trinitatis* Marshall) to control *Aspidiotus destructor* Signoret in Fiji (Taylor 1935), still constitute an excellent model. More recently, in Vanuatu, attempts to control this important pest of the coconut palm led to the successful introduction in 1964 of a Micronesian species, *Pseudoscymnus anomalus* Chapin (Chazeau 1981), later introduced also into Hawaii (1970; Leeper 1976). The Cook Islands have also benefitted from several introductions which have modified the physiognomy and balance of the fauna, of which they make up almost a third (Walker et al. 1979).

It is foreseeable that the continuation of this practice where local predators appear to be deficient, will tend to enrich and homogenize the subregional faunas. Serious taxonomic studies should be carried out more often in such operations, in order to avoid expensive re-introductions of species already present.

Conclusion

In the Pacific there is an obvious attenuation of coccinellid fauna towards the east with increase in geographical isolation. The apparent exception (Hawaii) is artificial and the American influence is generally very limited.

The species which are very widely distributed make up a group which is small in number, but rather well diversified from a biological standpoint. Their dispersal appears to be the result of human activity rather than of natural pheno-

mena such as winds or currents. The rapid decrease in the number of endemics and in many cases in the number of species per genus as isolation increases seem to suggest relatively recent introductions, otherwise the geographical barriers would have considerably favoured endemic speciation; the number of ecological niches available, limited in the small islands, has also restricted speciation.

Unlike the theory put forward for other groups of coleoptera (Cerambycidae, Chrysomelidae; Gressitt 1956), it does not appear to be possible to affirm that the Pacific coccinellid fauna represents an attenuation of the Papuan fauna with a limited Australian influence. It is true that the Oriental influence is considerable, but the influence of Australia is marked in the Inner Melanesian Arc, and as far as New Zealand; however, the Australian influence decreases greatly in the Outer Arc (New Guinea and Fiji) and in the rest of the Pacific, where the Oriental influence is preponderant. Affinities with South African, South American or Indian Ocean faunas are at times surprising, but remain isolated cases, and maritime routes may sometimes suggest explanations.

The coccinellid fauna of New Guinea is very different from that of Australia; the Oriental influence is more pronounced and the richness of the fauna, which is not yet fully known, is remarkable. The oceanic nature of New Caledonia is not particularly pronounced for coccinellids; it is much more so in Fiji.

Recent interest in the family from the point of view of biological control has led to a profound modification of the fauna of certain areas as a result of repeated introductions. This effect is likely to increase, particularly east of the 180° meridian.

As is unfortunately so often the conclusion in studies of this type, there are many taxonomic gaps to be filled before we can claim to have a comprehensive biogeographical synthesis of this family in the Pacific.

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