

# Anthropogenic origin of island entomofaunas: a case study of Diptera and Odonata

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## Abstract

Several examples of modern entomofaunas (particularly orders Diptera and Odonata) of remote islands, and to a lesser degree, recently colonized continents were considered. The author presents taxonomic, biogeographical, logical, and molecular-genetic arguments to support the idea that the modern composition of these entomofaunas can be effectively explained by the anthropogenic invasion that has occurred within the last 3000 years. The author estimates that rare undoubted cases of natural colonization do occur on islands once every one to three million years. It is assumed that pre-anthropogenic entomofaunas were poorer, but much more endemic. If so, entomologists should consider this when proposing taxonomic hypotheses. Molecular genetic methods can verify the author's conceptual idea.

## Keywords

Biogeography, anthropogenic invasions, biological globalization, island entomofaunas, Diptera, Odonata



I dedicate this publication to the memory of Dutch dipterist Dr. Paul Beuk who died suddenly at March 02, 2025, at the age of 59. In 2002, Paul Beuk created the [diptera.info](http://diptera.info) website. Gradually, many group specialists began to collaborate with [Diptera.info](http://Diptera.info), and the site became a unique resource that helps to identify any Diptera from any corner of our planet. Presently, the community [diptera.info](http://diptera.info) consists of three to four thousand people, both experts and amateurs.

## Introduction

During the Earth's history, continents have converged and diverged many times. Generally speaking, the divergence of landmasses leads to an increase in biodiversity (unless, like Antarctica, the continent drifts to the South Pole), and their convergence accordingly leads to a decrease in biodiversity. The latter event can be called biological globalization. The last major convergence of continents happened when the Isthmus of Panama connected North and South America. This happened about three million years ago, recently by geological standards, so the event's consequences have been well studied. Regarding mammals, it was mainly South American animals that became extinct: many marsupials and edentates, unique South American ungulates. North American mammals of high-ranking taxa experienced less decline in diversity during the invasion of the southern continent and were much more successful (Marshall 1988; McDougall 2001).

The formation of the Isthmus of Panama is an event in which humanity is not to blame. But we are guilty of the extermination of many animal species, the destruction of rich natural landscapes, which are replaced by wastelands, and the increase in the concentration of greenhouse gases in the atmosphere. We are also responsible for anthropogenic biological globalization, which is the subject of this publication.

Plants are the basis of the trophic pyramid and provide an easy example of man-made biological globalization. We see how the flora around us has changed: invasive Caucasian giant hogweed (*Heracleum mantegazzianum*), American bigleaf lupine (*Lupinus polyphyllus*), boxelder maple (*Acer negundo*), and goldenrod (*Solidago canadensis*) are everywhere. Once seen, it is impossible to forget the horrible African landscapes: water reservoirs overgrown with American water hyacinth (*Eichhornia crassipes*), and dryland with neat rows of Australian eucalyptus trees. Invasive plants destroy natural communities more efficiently than a team of woodcutters.

Botanists know which plants are natural and which are invasive. Ornithologists also distinguish autochthonous inhabitants from colonist species. Let us consider, for example, the island of Mauritius (Lepage 2021). A long time ago, pigeons flew to Mauritius and turned into flightless birds the size of a turkey known as the dodo. Much later, Madagascar turtle doves flew to the island, and their descendants, during the time of isolation, turned into a special species named the pink pigeon, which has until now avoided extinction. These are autochthonous species. On the other hand, common myna birds were recently brought onto the island. (There have never been land mammals on Mauritius, as on all remote islands, including New Zealand; rats, cats, mongooses, pigs, and others were brought there – unfortunately for the indigenous inhabitants.)

So, botanists and vertebrate zoologists are good at distinguishing autochthonous species from invasive ones, and the time and circumstances of the latter's appearance are often known. But when it comes to insects, detailed information is available only for a few species, such as the Colorado potato beetle (*Leptinotarsa decemlineata*), which was first described as a modest beetle that feeds on the leaves of Solanaceae family plants, then turned into an invasive potato pest. Firstly, few insects are of such great economic importance. Secondly, anthropogenic biological globalization began much earlier than serious entomology. If the Colorado potato beetle had been described 100 years later, it would have been difficult to figure out that the homeland of this Holarctic insect is the Rocky Mountains. Today, when it comes to many insects with a formally Holarctic distribution, nobody usually raises the matter of whether such range results from anthropogenic transatlantic invasion or has any other natural explanation. Similarly, when examining island entomofaunas, the question of the natural (like the Mauritian pigeons) or anthropogenic (like the Mauritian myna starlings) way of an insect getting to the island is rarely asked. Meanwhile, a recent invasion of a species to an island means, for example, that the appearance of diverse color forms is quite explainable by genetic drift during the invasion, yet it is clear that the isolation time is insufficient to describe such forms in the status of a new species.

In the following "Results and Discussion" section, I will give several independent examples related to the taxonomy and biogeography of two insect orders: Dip-tera and Odonata, both organisms fly actively and fairly well. In my view, the picture will be the same when analyzing the situation with other orders of insects. Based on the analysis of the given examples the following statements are proposed:

1. Anthropogenic biological globalization made a far greater contribution to the modern distribution of insects than is commonly believed.
2. Natural migrations, especially across marine space, are much rarer than believed.
3. The anthropogenic or natural way of invasion should be taken into consideration when proposing taxonomic hypotheses.

## Results and discussion

1. There is one species of dragonfly – *Pantala flavescens* Fabricius, 1798 (Fig. 1), that is capable and even programmed for migration, and in this respect is superior to many birds, not all of which are capable or prone to long-distance migration. Numerous in South Asia *P. flavescens* has spread throughout the thermal belt zone of the Earth, even reaching Easter Island. Young *P. flavescens* spread across the globe; their swarms flying across the ocean from India to Africa have been frequently observed. Every spring, tropical *P. flavescens* fly in Japan and southern Russia (primarily the Caucasus and Primorsky Krai), with some specimens reaching the latitude of the Moscow region. Usually, dragonflies only breed once and die when autumn/ winter comes, the following year the story repeats itself (Onishko and Kosterin 2021: 449–454). *P. flavescens* is a species with modernized natural selection. Instead of the traditional extermination of the less adapted in favor of the most successful, the species solves the problem of overpopulation according to Kipling:

"...Send forth the best ye breed –  
Go bind your sons to exile..."

Kipling J. R. The White Man's Burden.

However, *P. flavescens* is a unique case, other dragonflies do not have such a prominent colonisation tendency.

Among butterflies (Lepidoptera) there is also a species famous for its migrations – the monarch (*Danaus plexippus* Linnaeus, 1758). Monarchs undertake an incredible migration across North America for 3–4 thousand kilometers year after year. A side effect of this lifestyle is frequent transatlantic strays of monarchs (Naimark 2014).

Among the order of Diptera, I do not know of such obligatory migrants; however, they are much less studied than dragonflies or butterflies.

The following may be concluded: among insects, there are species for which long-distance migrations are the norm, but these species are unique.

2. The genus *Lispe* Latreille, 1796 (Diptera, Muscidae) is distributed worldwide and includes about 200 species, all predators. They can often be found running on silt at the water's edge. It is hard to catch most members of the genus with a net. However, *Lispe pygmaea* Fallen, 1825 (Fig. 2) prefers to sit on grass stalks in damp meadows – it is easily caught even by an inexperienced collector, all it takes is to run a net through the grass. It is a species of non-synanthropic small fly (5 mm), distributed throughout Eurasia from Portugal to the Far East. *L. pygmaea* could find suitable meadows in North America, but it didn't get a chance to use the Bering Bridge: the surroundings of Chukotka and Alaska were too cold for it. *L. pygmaea* is a common species in the Primorsky Krai of Russia and northeast China (Vikhrev 2016).

Insect fauna of Japan is very well studied compared to other countries, but *L. pygmaea* was not known there until the XXI century, even though, as mentioned before, it is easy to collect. However, entomologists are restless people and, in 2014, two new species similar to *L. pygmaea* were described from Japan. Coincidentally I was working on the world fauna of the genus and had to deal with these discoveries (Vikhrev 2016: 180–181). My Japanese colleague never mentioned the name *Lispe pygmaea* in the article: he compared his "species" with other species of *Lispe*. However, from the descriptions and photographs (Shinonaga 2014) it was clear that the described *L. japonica* is in fact *L. pygmaea*, as well as his *L. aureola*, but the latter with golden versus grey dusting (rather common among the specimens of *L. pygmaea*). I synonymized both Japanese species with *L. pygmaea*, and my dipterologist colleagues agreed with my conclusions (Pont 2024).



**Figures 1–2.** 1. *Pantala flavescens*; 2. *Lispe pygmaea* (photos: Basile Morin and maherjos-diptera.info respectively).

By default, entomologists explain similar introductions of species previously not noted with the drifting of a flying insect: "brought by the wind". Indeed, the distance to Japan from the continental Far East is 400 km, and from South Korea, it is only 250 km. Looking at the map, it becomes clear that with a tail west wind, you can't miss Japan. Yet why was *L. pygmaea* brought to Japan only in the XXI century? It is easy to guess under what circumstances *L. pygmaea* finally "flew" to this country, knowing that both specimens were not collected just anywhere but in the

garden of the Tokyo Imperial Palace. It did not fly in, but "sailed" along with some plants or lawns imported for the imperial garden from China.

There is more to the colonization of *L. pygmaea*. Earlier on, a work was published (Hardy 1981) on the Muscidae of the Hawaiian Islands: it was proposed to consider that, in addition to *L. pygmaea* itself, there were two more endemic species on the islands. To my American colleague's credit, he did not conceal that the new "species" were remarkably similar to the well-known *L. pygmaea*. In his opinion, the difference between the species was in the fine structure of the male genitalia. Here I will not give taxonomic arguments as to why I do not agree with Hardy, those who wish can read my article (Vikhrev 2016). Biogeographical arguments are more than enough. May we no longer consider the hypothesis that a swarm of *L. pygmaea* was once carried by a storm with the accuracy of a ballistic missile across the entire Pacific Ocean for 7 thousand kilometers to the island of Oahu? What are the other possibilities of it getting there? The specific date and circumstances of the Polynesians settling in Hawaii are debatable, the most common hypothesis is that they arrived about 1000 years ago from the islands of present-day French Polynesia (Irwin 1992). However, because *L. pygmaea* has not been reported anywhere else in Oceania, it couldn't have been brought to Hawaii by the Polynesians. Since the beginning of the XIX century, US industrialists began large-scale sugar cane cultivation in Hawaii. As mentioned above, *L. pygmaea* is not found in North America either. However, in the middle of the XIX century, workers from northern China were actively brought to the Hawaiian plantations. In China, as we remember, *L. pygmaea* is very common! Then the entire population of the island of Oahu (*L. pygmaea* is not present on other Hawaiian Islands thus far) consists of the descendants of several specimens that arrived around 1850. The past 150 years are by no means an insufficient period for speciation. Therefore, *L. pygmaea* in Japan and the Hawaiian Islands is the result of a recent anthropogenic invasion.

3. From the point of view of the inhabitants of the Old World, America is also an island, only a very large one. More accurately, "almost" an island, because 10–15 thousand years ago, when the level of the World Ocean dropped, the Bering Land Bridge existed in the place of Bering Strait today, connecting Alaska with Chukotka. Assuming the climate of Chukotka and Alaska was about the same as it is now, only cold-resistant species of insects could use the Bering Land Bridge. Admittedly, there are many species like this among Diptera. Looking at the Diptera fauna of North America, most of Canada is inhabited by Holarctic (i.e. found both in America and Asia) cold-loving species, whose populations have only recently been separated by the Bering Strait. South of Canada, the continent is inhabited by more thermophilic species, among which there are endemic and Holarctic ones. Endemic species and genera have different origins, for example, among the Muscidae of North America many natives from South America moved north across the Isthmus of Panama. Among the "Holarctic" species of the southern half of North America, most are pseudo-Holarctic, as these are the species that entered America as a result of the anthropogenic invasion. This will be the subject of the third story.

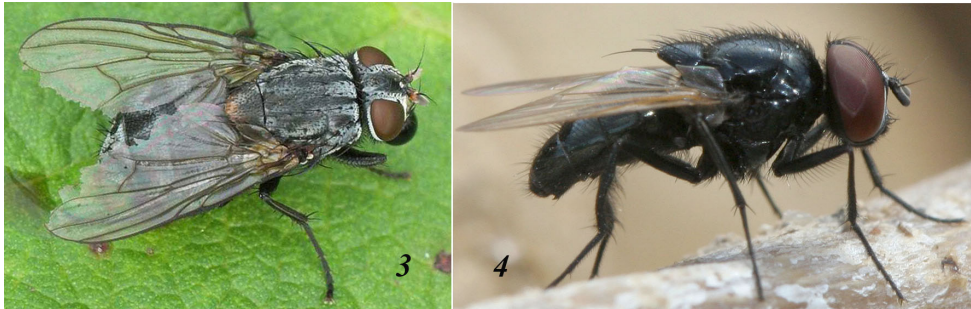
Recently, my colleague and I worked on a revision of the genus *Muscina* Robineau-Desvoidy, 1830 (Diptera, Muscidae). The species *Muscina prolapsa* Harris, 1780 (Fig. 3) was considered trans-Holarctic: it is common in both Europe and North America; according to the literature, it is found in China (Vikhrev, Esin 2023). In that case, *M. prolapsa* should be found in Central Asia and southern Siberia. However, not one specimen of *M. prolapsa* collected east of the Caspian Sea was found in the Zoological Museum of Moscow State University and the Zoological Institute of the Russian Academy of Sciences collections. It turned out that *M. prolapsa* has never been recorded from continental China or Japan, and there is only a single report of this species for Taiwan, which, most likely, is based on a misidentification. Thus, the "textbook" way of getting to America across the Bering Strait for *M. prolapsa* was impossible: it is too thermophilic for Chukotka and completely absent in Asia. Then how did *M. prolapsa* get there (dipterologists are convinced that the place of origin of the genus *Muscina* is Eurasia, not America)? An obvious assumption according to Occam's razor presumption offers itself: *M. prolapsa* was brought to America from Europe by people. Not intentionally, like rabbits to Australia, but completely unnoticed.

*M. prolapsa* is a synanthropic species; its larvae develop in rotting organic matter, and adults feed on it. Why shouldn't it come to America on the ships of European settlers? The ship's hygiene was far from good. Are there other arguments for the importation, rather than the hypothesis of a "tailwind"? There are. For example, the same species colonized all islands of Macaronesia on the way from Europe (Pont 2024): the Canaries, Madeira, and even the Azores (1500 km from Portugal). Did they also get there by the tailwind? By the way, here we see an example of the double standards that entomologists use, without even noticing. Insects cannot overcome the Bering Strait, which is 90 km wide, but they can fly to a much more distant small island for some unknown reason! The first is predominantly true, and with the second I completely disagree.

There is another argument. My American colleague and I recently published a paper on the fly family Sciomyzidae (Vikhrev, Murphy 2022). Sciomyzidae are not synanthropic, they prefer a cool climate, and their larvae are mollusc parasites. The Bering Land Bridge was a natural route to or from America for them, and they were not interested in the settlers' ships. We compared the sequences of the mitochondrial gene encoding cytochrome oxidase I (*COI*) of northern Sciomyzidae species – the ones that should have walked across the Bering Land Bridge 10–15 thousand years ago. We wanted to see how many differences had accumulated over 10 thousand years in the *COI* gene of individuals of the same species collected in Eurasia and America. The results obtained showed that *COI* sequences of Palaearctic and American specimens accumulated about 1% differences, i.e. there were 5 to 8 substitutions in different species in the analyzed area (658 bp) of the *COI* gene (Vikhrev, Murphy 2023: Table 3). Next, let us compare the same *COI* sequence of *M. prolapsa* specimens collected in Europe or America, and add as a control another thermophilic synanthropic species of Muscidae – *Hydrotaea ignava* Harris, 1780 (Fig. 4),

also thriving on the islands of Macaronesia, as well as in the American continent itself. The result showed zero substitutions in the *COI* sequence! The sequences are freely available and anyone can check for themselves: [https://bench.boldsystems.org/index.php/Taxbrowser\\_Taxonpage?taxid=523](https://bench.boldsystems.org/index.php/Taxbrowser_Taxonpage?taxid=523).

It proves the following: when the first entomologists studying the local Diptera fauna appeared in America 150 years ago, many European flies had long settled across the vastness of the American continent. So, entomologists silently assumed that these species had always lived here. In reality, in front of us is an invasive species, the same as maple, lupine, and goldenrod, only the flora mostly arrived from America to Europe, and the fauna vice versa!



**Figures 3–4.** 3. Female of *Muscina prolapsa* (photo: Tim Worfolk); 4. Male of *Hydrotaea ignava*.

4.1. I am working on a revision of the genus *Neomyia* Walker, 1859 (Diptera, Muscidae). Bottle-green flies (Figs 5, 6), whose larvae develop in cow dung, and imago feed on it (buffaloes suit as well, other ungulates are much less suitable). The Italian dipterologist Bezzi published detailed descriptions of two species of *Neomyia* from Fiji (Bezzi 1928). Additional taxonomic comments on these species were given in a recent work on the Muscidae fauna of Fiji (Pont & Couri 2021). *Neomyia* from Fiji mainly differs in color, so far, their taxonomic relationship with other species of the genus remains unclear.

I do not have specimens from Fiji, and there is no possibility to examine European collections either. Should we accept the inability to clarify the situation? I think that biogeographical and historical facts can help. Since *Neomyia* is a cow dung fly, it must have arrived on the islands with humans, as humans were the ones who brought mammals to Fiji. Even if this fly had once been brought onto the archipelago by the wind, it would have nothing to do without cows. It is believed that in their long voyage canoes, the Polynesians carried chickens, dogs, and pigs (only chickens could reach Easter Island). It is unlikely that this zoo could satisfy *Neomyia* and there is indirect evidence that the Polynesians didn't bring these flies. Between Fiji and Australasia lies the Vanuatu archipelago, which was settled five hundred years earlier than Fiji, and the travelling Polynesians could not have evaded it. The Muscidae fauna of Vanuatu has been studied and published (Couri et al. 2010):

*Neomyia* is absent there (it is difficult to overlook). Thus, the Fijian *Neomyia* does not live on Vanuatu pigs, but lives exclusively on Fijian cows, which were brought to Fiji by Europeans only 150–200 years ago, and *Neomyia* unlikely before. If the time-frame is established correctly, then the question is: dear colleagues, do you seriously suggest that 150 years from the invasion is enough for the appearance of two good species of the genus *Neomyia* in Fiji?

Cases of "instantaneous speciation" are known in plants, for example, the appearance of a tetraploid banana immediately reproductively isolates it from a diploid ancestor. However, such incidents are not yet known in insects.



**Figures 5–6.** *Neomyia lauta*: 5 – female, 6 – male.

In general, how much time/generations are needed for speciation? Unfortunately, we know very little about this. The only species whose evolutionary history has been well studied is *Homo sapiens*. The branches of *Homo* (human) and *Pan* (chimpanzee) separated 6 million years ago. Chimpanzees remained more or less the same chimpanzees; 2–4 million years ago they split into actual chimpanzees (east of the Congo River) and bonobos (to the west of it) – two good, but very similar species.

The genus *Homo* has changed radically both in appearance and internally. We are not like chimpanzees, although we are very close genetically – this is the result of rapid evolution under strong directional selection. Sapiens and Neanderthals have been apart for 600 thousand years (30–40 thousand generations); when they met again, there was partial reproductive isolation: interbreeding was possible and took place, but the viability of hybrids was reduced.

About other animals, we know little for a fact. Recall that over 10–15 thousand years of the existence of the Bering Strait fly populations of one species in Chukotka and Alaska have accumulated 1% differences in the mitochondrial cytochrome oxidase gene. It is believed that for reproductive isolation and, therefore, for the species status of two populations, more than 3% substitutions in this gene are required, although this boundary is justified very arbitrarily. There is a reason to believe that in large taxa which are small in number (elephants), speciation is faster than in small, numerous and often breeding ones (mice). Thus, genetic drift (random fluctuations in gene frequency) is a more effective catalyst for speciation than selection

(purposefully changing gene frequencies). In this sense, insects correspond more to mice than to elephants, more precisely like mice to the second power. However, island populations have a significantly expressed genetic drift: the first bottleneck – during settlement, the following – with each cyclone, drought and other tribulations.

Recently, revising a group of species *Phaonia latipalpis* Schnabl, 1911 (Muscidae), we encountered a situation that we explained precisely by genetic drift (Vikhrev, Erofeeva 2023: 15–17). In the Russian Far East, species of this group are easily distinguishable from each other by morphological features, yet, on the island of Kunashir it is impossible to draw a border between species. However, in this case, we cannot say anything about the presence or absence of reproductive isolation between continental and island populations.

My reasonings are based on the present understanding of the history of Oceania and the mechanisms of speciation. These ideas (especially on speciation) may be false, but there are no alternatives for today. Is it possible to discuss the fauna and flora of Fiji, without even considering the possibility that the entire Muscidae fauna (Diptera) is the result of introduction if not in the last 300, then in the last 3000 years?!

4.2. You can look at the problem from another angle. In the book "Biogeography of Islands" (Whittaker & Fernandez-Palacios 2007: 83–93) the authors discuss in detail the correlation between remote islands species diversity and the range of distance from the mainland. Based on the dominant concept of immigration due to natural causes, the further the island is, the less biodiversity there should be, other things being equal. Indeed, the immigration rate should depend on the distance similar to the correlation between illumination and the distance to the light source (i.e. if the distance increases  $N$  times illumination drops by  $N^2$  times). For example, the above-mentioned Vanuatu archipelago is about twice as close to Australasia than the Fiji archipelago, therefore, natural immigration to Fiji should occur 4 times less often. However, this dependence is not observed for most taxonomic groups, the Muscidae faunas of Fiji and Vanuatu are represented by approximately the same number of species. The authors suggest additional parameters and assumptions should be considered to explain most of the observed facts. This reminds me of the ancient efforts to save the geocentric system of the world with the help of epicycles and other ingenious ideas. Meanwhile, it is enough to assume that (almost) all Muscidae end up in Fiji and Vanuatu due to recent anthropogenic introduction, and no other explanation is required.

5.1. Getting back to the dragonflies. All of them are agile and actively flying insects, many species are prone to local migrations. Unlike Diptera, there are no synanthropes among them; some species tolerate proximity to people and pollution of water bodies, and others successfully use rice fields or human-dug ponds, but no more than that. Dragonflies also differ from Diptera in the absence of pupae i.e. resting stage. Let us explore the biogeography of this order quite unlike flies.

I am not a dragonfly specialist, only an amateur, but the biogeography of island faunas seems to be an area where logical conclusions are easier for people who look at the problem somewhat from the outside. Here is a list of dragonflies from Fiji: [http://hbs.bishopmuseum.org/fiji/pdf/tr38\(15\).pdf](http://hbs.bishopmuseum.org/fiji/pdf/tr38(15).pdf). By species, the world's Odonata fauna is 30 times smaller than the Diptera fauna, so the taxonomy of dragonflies is explored far better, and there are solid grounds for trusting species identification. The dragonflies of Fiji list have the following structure: 1) the ubiquitous *P. flavescens*, as discussed above; 2) 20 species of endemic damselflies (Zygoptera) belonging to two endemic genera *Nesobasis* Selys, 1891 and *Melanesobasis* Donnelly, 1984; 3) 20 species of dragonflies from different families, indistinguishable from their maternal populations in southern Asia, including both agile fliers and small ones, clearly incapable of long flights. How can this list be explained?

Let's assume that dragonflies sometimes travel to Fiji with a tailwind or fly there actively. Then the following picture will be observed:

- a) *P. flavescens* has flown and continues to fly in, island specimens are indistinguishable from the main population;
- b) 20 million years ago (let's take the average value), the ancestors of the genera *Melanesobasis* and *Nesobasis* flew to Fiji, altered very much and gave an adaptive radiation of 20 species;
- c) between 20 million years ago and today, the remaining 20 species arrived in Fiji.

Why are these last 20 species indistinguishable from the same species in the Sunda Islands and southern Asia? If the hypothetical model were correct, there would be species that had accumulated some differences between 20 million years and now. We don't see these differences! Then we have to bring another hypothesis: all 20 species indistinguishable from Asian relatives appeared in Fiji equally recently. When exactly recently? The Fiji Islands are in the middle of the "thermostat" – Pacific Ocean. That's where the difference between winter and summer, and between day and night is marginal, and the ice ages creeping over Europe were not noticeable. Is there a difference in Fiji between three million and three thousand years ago? None, except for one thing: 3000-300 years ago, the island's colonisation began and ships sailed there. Ships sailed together with dragonflies that sat on the railings to catch their prey, not noticing how they floated off the shore, and then it was too late...

5.2. New Zealand odonatologist Marinov published an article on the biogeography of Oceania (Fig. 7) dragonflies (Marinov 2015). The review is long, 58 pages: the author meticulously collected all the information on the topic; a lot of outdated information alongside interesting data. For example, about Norfolk Island which belongs to Australia but is geographically closer to New Zealand (distance – 750 km). Skilled observations of Norfolk's Odonata have been going on for 100 years. During this time, many species were added to the dragonfly fauna including some that would have been difficult to miss had they been there before. We should agree

that these observations confirm my assumption about the massive anthropogenic biological globalization in the last hundreds of years.

A significant part of Marinov's work is devoted to the level of island endemism, which, according to the author, is particularly high for species taxa. In section 4.1. I discussed that the genetic bottleneck during settlement often immediately gives some morphological differences between the island population and the maternal one. Notice that reproductive isolation is difficult to prove; no one has done genetic analysis even in such a primitive form as I did in section 3. Let's look at the endemic taxa of the genus level. There is no doubt that they are the result of long-term reproductive isolation on any given remote archipelago. In his work, Marinov collected and presented the necessary information. I excluded from consideration the Solomon Islands, which are close to New Guinea and rich in biodiversity, and New Zealand, which was part of the eastern piece of the split Gondwana and not easy to interpret. I reviewed only clearly young and highly isolated islands. The picture turned out like this:

a) Vanuatu (700 km from the Solomon Islands) – *Vanuatubasis* Ober & Staniczek, 2009, an endemic genus from the Coenagrionidae family;

b) New Caledonia (1300 km from Australia) – 4 genera: *Caledargiolestes* Kennedy, 1925; *Caledopteryx* Kennedy, 1925; *Eoargiolestes* Kalkman & Theischinger, 2013, and *Trineuragrion* Ris, 1915. All from the Argiolestidae family;

c) Pohnpei Island (1400 km from New Guinea) – the genus *Pacificothemis* Asahina, 1940, Libellulidae;

d) Fiji (1750 km from the Solomon Islands) – 2 genera: *Melanesobasis* and *Nesobasis*, both Coenagrionidae;

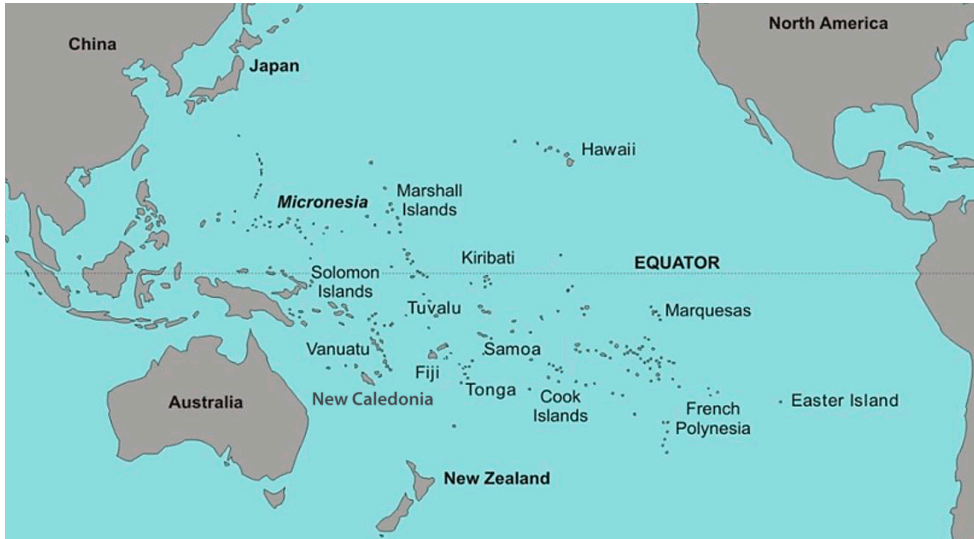
e) Samoa (2700 km from the Solomon Islands) – 2 genera: *Amorphostigma* Fraser, 1925 and *Pacificagrion* Fraser, 1926, both Coenagrionidae;

f) Marquesas Islands (6300 km from the Solomon Islands): *Hivaagrion* Hamalainen & Marinov, 2014, Coenagrionidae.

It is hard to assume that there is a law of nature according to which only dragonflies from the exotic Australo-New Guinean family Argiolestidae always fly to New Caledonia, and only members of the Coenagrionidae family fly to Fiji and Samoa. I propose a much more economical explanation: once there was a single flight of dragonflies from the Argiolestidae family to New Caledonia; afterwards, odonatologists divided the descendants of this natural colonization into 4 genera (fairly or not), but, in essence, this is a single taxonomic clade. Then in Fiji and Samoa, there was only one flight each, this time from the Coenagrionidae family; the descendants were divided into two genera, but they are again the descendants of a single settlement, one clade. How to divide them into genera is a secondary question.

If my reasoning is correct, the 20 million years should be divided into 6–7 ancient immigrations, with an approximate probability of one natural colonization of dragonflies to remote islands in 2–3 million years. Then the remaining dozens of dragonfly species of the Oceania islands result from an anthropogenic invasion, that occurred in the last 3000 years. If we exploit the above-applied logic from dragon-

flies to Diptera, it turns out that on all Oceania islands (excluding New Zealand) there is not a single endemic genus of the Muscidae family. Entomologists (both odonatologists, dipterologists, and all others) often describe island forms as new species but had better limit themselves to the status of a subspecies until proven otherwise.



**Figure 7.** Map of Oceania.

## Conclusions

I. When it comes to insects in general, and Diptera in particular, the hypotheses of "carried by the winds" or "active flight" of species even to not very distant (especially to distant) overseas territories should be considered as extremely unlikely. Such events sometimes happen, but very rarely – once in millions of years. Instead, anthropogenic invasion of species in recent hundreds of years should be considered as the primary hypothesis. For synanthropic Diptera, the introduction explains almost 100% of the facts, and for non-synanthropic ones at least most of the faunas of remote islands. Recent anthropogenic invasion is the primary hypothesis for explaining the appearance of synanthropic species in North and South America, and synanthropic species should be understood as not only ones associated with human habitation and the organic matter accompanying housing, but also ones associated with crop production, and especially with livestock.

II. When making assumptions about the timing of the introduction, historical events should be considered. For example, the ships of the first settlers, which resembled Noah's Ark (no matter who sailed: Polynesians, European colonists of

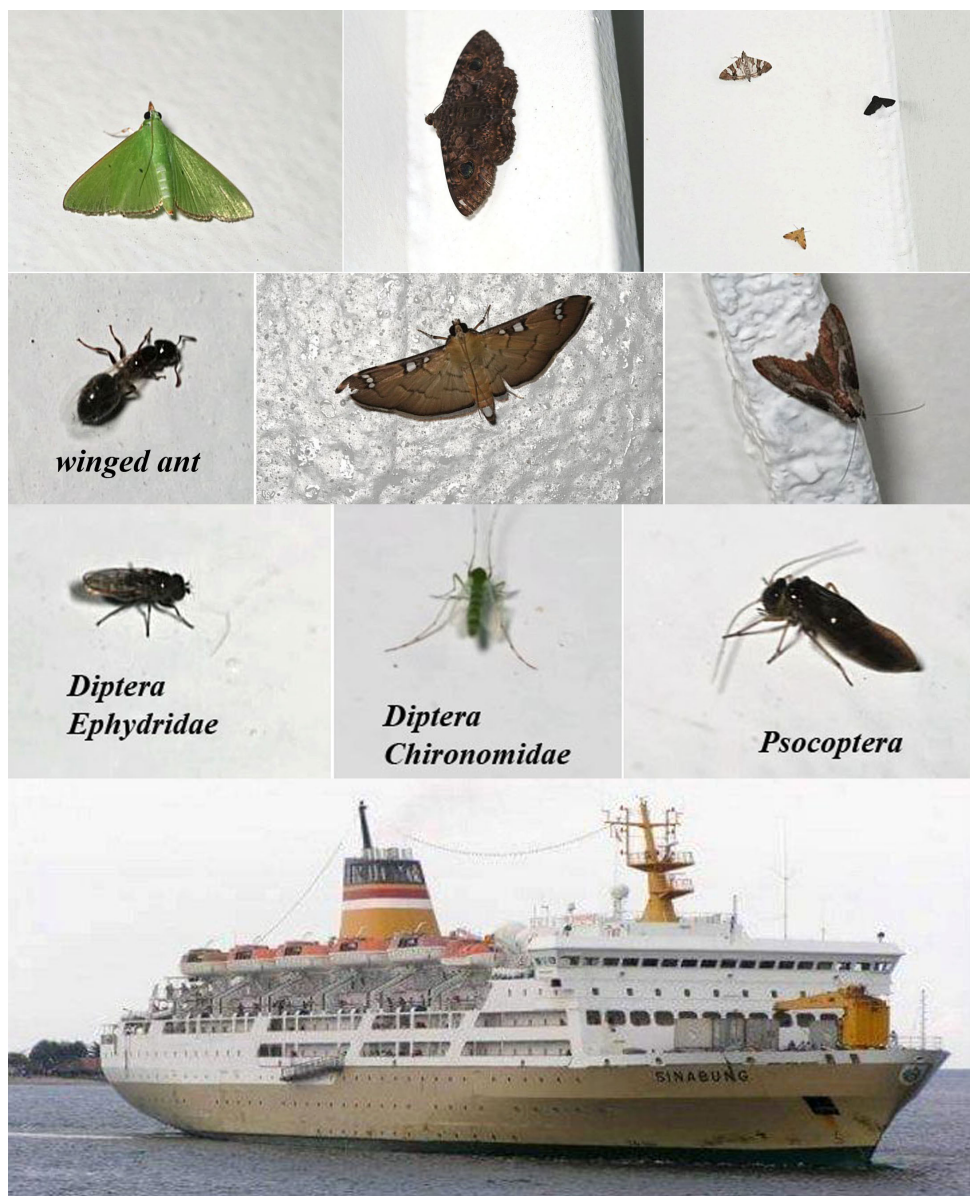
America or Asian workers), seem like optimal candidates as opposed to modern ships that meet high sanitary standards.

These plausible dates should be taken into account when proposing taxonomic hypotheses. Thus, the presence of a population in an overseas territory for two hundred years, in the vast majority of cases, is completely insufficient for the occurrence of reproductive isolation of the introduced population from the maternal one. Moreover, such a period is not enough for the island population to split into several species within itself.

III. If there was at least one island left on the planet never visited by people, then it would be possible to directly verify the conclusions of this publication. There are no more islands like this left. However, it is quite possible and necessary to confirm or contradict my beliefs indirectly.

III.1. Molecular phylogenetics should be involved: compare the genomes of individuals from islands and the mainland, simply by comparing the sequences of the mitochondrial cytochrome oxidase gene (*COI*), for a start, as described above in section 3 for species of synanthropic Diptera from Europe and America. For example, the BOLD website has an enormous open-access sequence database for the *COI* gene. However, there is a problem. At present, in the entire BOLD database, there is not a single *COI* sequence of a representative of the Muscidae family from any island of Melanesia or Macaronesia. If someone visits any of these islands, collects insects there, identifies them and makes *COI* sequences, then much will immediately become clear. The *COI* gene is not always an effective tool, but the task certainly has a solution: super-conservative genes have allowed us to establish the first branching of life – the division into clades of bacteria and archaea; super-variable genes allow us to establish paternity; therefore, any branching and its timing from 4 billion years ago to the present can be reliably established and approximately dated, the question is only in the cost of effort and resources.

III.2. Observations are also needed. I asked Roman Farkhutdinov (Russia, Ufa) for them while sailing on the passenger ship SINABUNG (Fig. 8) from Surabaya to Jayapura in December 2024. The urban ports of Indonesia are unattractive for insects as is a modern passenger ship that underwent sanitation in Surabaya. At first, Roman thought that no one would fly in. However, migrants appeared in smaller ports and at night stops. Dozens of recorded species and hundreds of collected specimens of Lepidoptera, gatherings of winged ants, Diptera, and even dust lice (Psocoptera) (Fig. 8). It is not easy to track the fate of small insects, but some butterflies successfully reached Jayapura, overcoming 1000–2000 km (Farkhutdinov pers.com).



**Figure 8.** Modern passenger ship SINABUNG and the insects that migrated on it (photo: Roman Farkhutdinov).

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