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Rates of species introduction to a remote oceanic island

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The introduction of species to areas beyond the limits of their natural distributions has a major homogenizing influence, making previously distinct biotas more similar. The scale of introductions has frequently been commented on, but their rate and spatial pervasiveness have been less well quantified. Here, we report the findings of a detailed study of pterygote insect introductions to Gough Island, one of the most remote and supposedly pristine temperate oceanic islands, and estimate the rate at which introduced species have successfully established. Out of 99 species recorded from Gough Island, 71 are established introductions, the highest proportion documented for any Southern Ocean island. Estimating a total of approximately 233 landings on Gough Island since first human landfall, this equates to one successful establishment for every three to four landings. Generalizations drawn from other areas suggest that this may be only one-tenth of the number of pterygote species that have arrived at the island, implying that most landings may lead to the arrival of at least one alien. These rates of introduction of new species are estimated to be two to three orders of magnitude greater than background levels for Gough Island, an increase comparable to that estimated for global species extinctions (many of which occur on islands) as a consequence of human activities.

Keywords: alien species; Gough Island; homogenization; introductions; island biogeography; Southern Ocean

1. INTRODUCTION

The frequency of unintentional introductions of non-domesticated species to areas that lie beyond the limits of their natural distributions has been huge. Pimentel (2001) estimates that in the past 10 000 years more than 400 000 species have been moved from one region of the Earth to another by human agency. Movements of this magnitude follow logically from the scale and increasing rapidity of transport of people and goods about the planet. The often large numbers of alien species that occur in different countries and on different land masses, and the species traits, ecosystem properties and features of the introduction process that lead to the observed variation have been much debated (e.g. Drake *et al.* 1989; Williamson 1996; Lonsdale 1999; Blackburn & Duncan 2001*a*,*b*). Likewise, there has been considerable discussion about the often significant economic, management and conservation consequences of introduced organisms (see, for example, Vitousek *et al.* 1996; Williamson 1996; Perrings *et al.* 2000; Pimentel *et al.* 2000; Lee 2001; Simberloff 2001).

Two issues seem to have attracted much less explicit and particularly empirical attention. The first is the relation between the level of human activity in an area and the number of introductions that result (McKinney 2001, 2002). Although the latter may be known, the former is typically rather difficult to quantify, particularly over protracted periods, often because of the number of routes by which introductions can be achieved, the large magnitude of human activities and the lack of a suitable historical record of human movements.

The second issue is the sheer spatial extent rather than the overall level of the areas to which the unintentional introduction of one or more non-domesticated species has occurred. Introductions have been reported, often on an anecdotal or case-by-case basis, as having occurred at many remote locations (e.g. Wace 1961; Wace & Dickson 1965; Steffan 1970, 1972; Wace & Holdgate 1976; Bonner 1984; Chapuis *et al.* 1994; Dingwall 1995; Ernsting *et al.* 1995; Chown *et al.* 1998, 2001; Bergstrom & Chown 1999; Nickoll & Disney 2001). However, the number of species introduced to isolated areas with even rather low levels of human activity has been less well characterized, particularly for taxonomic groups other than plants.

In this paper, we report the results of an explicit investigation of the probable rates and scale of unintentional introduction and establishment of pterygote ('winged') insect species to Gough Island, one of the most remote and supposedly pristine temperate oceanic islands.

2. METHODS

Gough Island (40°17′–40°22′ S, 9°52′–10°01′ W) lies in the middle of the South Atlantic, *ca.* 350 km south–southeast of the Tristan da Cunha island group. It is part of the UK Dependent Territory of Tristan da Cunha, and is administered from there. The 6500 hectare (ha), mountainous island formed as a result

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of Neogene orogenic volcanism (Maund *et al.* 1988). With the exception of a low-lying plateau at its southernmost end, most of the land rises steeply to ridges and peaks between 700 m and 910 m above sea level. The island has a temperate oceanic climate with strong prevailing westerly winds; the mean annual precipitation, recorded on the southern plateau (*ca.* 70 m above sea level) between 1963 and 1990, was 3154 mm, and the mean monthly temperatures, recorded during the same period and at the same altitude, varied between 8.9 °C in August to 14.5 °C in February. These conditions support an altitudinal succession of vegetation types, from coastal 'tussock grassland' through to 'lowland fernbush', 'wet heath', 'peat bog' and 'feldmark and montane rock' communities (Wace 1961). The relative lack of human influence on Gough Island has resulted in the island being declared a wildlife reserve under the Tristan da Cunha conservation ordinance of 1976, gaining scientific/strict nature reserve status under IUCN category I in 1985, and being designated a world heritage site (under criteria iii, iv) in 1995. The conservation importance of the island has been underlined in the findings of recent priority area analyses (Chown *et al.* 2001).

Because of its isolation, and because the terrain makes landfall difficult, it is extremely unlikely that prehistoric human colonists arrived at Gough Island, and there is no evidence that they did so. The first recorded human landfall was made in 1675 (Wace 1969). Subsequent visitors included members of sporadic scientific/cartographic expeditions, and commercial sealing and whaling expeditions of the nineteenth and early twentieth centuries (Wace & Holdgate 1976). The number of landings by sealing gangs, scientific expeditions and other parties before 1955 was determined from the published historical literature (e.g. Morrell 1832; Wace 1969; Bruijn *et al.* 1979; Busch 1985; Headland 1989) and from unpublished information provided to C. Hänel from several sources (see Acknowledgments). Although the earliest historical information (from the seventeenth century) is sparse (owing mostly to very few visits), information from the eighteenth century onwards is reliable and relatively complete owing to more careful recording of shipping, sealing and scientific visits to the region. Since the Gough Island Scientific Survey of 1955–1956 (Holdgate 1965), a South African meteorological station has been established on the island (the island's only standing human construction), with a small (typically 6 ± 2) annually rotated staff (see expedition membership reported in the *S. Afr. J. Antarctic Res.*) that seldom travels much beyond its immediate vicinity. The number of landings on the island in the period 1956–2000 was determined by using the published literature (e.g. Headland 1989), limited circulation newsletters of the South African Weather Bureau in which expedition members usually report events such as the exchange of goods with fishing vessels, and unpublished voyage schedules of the South African research and supply vessel, the S. A. *Agulhas*. For each visit, the likely origin of the vessel responsible for transport of the visitors (in some instances the last port of call differed from the country operating the vessel), whether the vessel was involved primarily in fishing, sealing or research, and whether the vessel had visited the nearby populated island of Tristan da Cunha was recorded. In the last case, it was assumed that fishing vessels (usually crewed by South Africans and Tristan Islanders) and the relief voyages (but not emergency supply or rescue voyages) of the S. A. *Agulhas* always called at Tristan da Cunha before proceeding on to Gough Island, because this is currently the normal procedure. In no cases have ships actually docked at the island, owing to the absence of a harbour. Transfers to the island have been either by boat or, since the 1970s, also by helicopter landings at the meteorological station.

The invertebrates of Gough Island have been subject to two intensive systematic studies (see Holdgate (1965) for a history of zoological exploration in the Tristan da Cunha island group). The first was part of the Gough Island Scientific Survey of 1955–1956 (Holdgate 1965). This study was detailed in terms of the pterygote insects, and achieved much under difficult conditions, although the smaller soil animals (which will not concern us here) were under-worked. A relatively depauperate invertebrate fauna was documented, a pattern in common with other Southern Ocean islands (Gressitt 1970). Less than half of the world's insect orders were found to be present, and those occurring were shown to be impoverished in species numbers and exhibited little, if any, radiation (for full species lists see Holdgate (1965)).

The second detailed study, the Gough Island Terrestrial Invertebrate Survey (GITIS), was conducted in 1999–2002 (Chown *et al.* 2000; Jones *et al.* 2002, 2003). Over a continuous 2-year period of fieldwork, a wide array of sampling techniques (including hand searching, Tullgren extractions and Malaise traps) were used at many sites across the island with the explicit intention of compiling a comprehensive record of the island's terrestrial and freshwater invertebrates. The resultant material was sorted and identified, with the assistance of several taxonomic specialists (see Acknowledgements).

Based on these surveys, we have categorized the free-living pterygote insect species (excluding vertebrate parasites) recorded from Gough Island as: (i) indigenous; (ii) introductions first recorded in native habitats in 1955–1956; (iii) introductions first recorded in native habitats in 1999–2002; or (iv) introductions only ever recorded as pests in the meteorological station and not found to occur in native habitats (1955–2002). The status of species as indigenous or introduced was established from information on their wider distributions and biology, and through consultation with appropriate experts. The indigenous flora and fauna of Gough Island (along with that of the other islands of the Tristan da Cunha group) show greater affinities with South American stocks than with those from the closer African landmass (e.g. Brinck 1948; Frey 1954; Rand 1955; Holdgate 1960, 1965; Kuschel 1962; Moore 1979; Jones *et al.* 2003), and prevailing westerly winds and ocean currents may favour natural colonization from South American sources (reflected in the predominant source of vagrant birds arriving in these islands (Williams & Imber 1982; Cooper & Ryan 1994)).

3. RESULTS AND DISCUSSION

Out of the 99 species of pterygote insects recorded from Gough Island, 28 are indigenous (six endemic to Gough Island, 10 potentially endemic to Gough Island and eight endemic to the Tristan da Cunha island group) and 71 are introduced (table 1; Appendix A). Of those introduced, 15 species have been recorded only from the confines of the meteorological station, and seem unlikely to spread further. The rest of the introduced species have been recorded in native habitats, and are all likely to have successfully established in as much as they have self-sustaining populations (typically being abundant and widespread). Overall, the proportion of pterygote insect species occurring on Gough Island that has been introduced is high compared with figures for other Southern Ocean islands (figure 1).

Table 1. The numbers of indigenous and introduced species of pterygote insects recorded from Gough Island.

		introduced		
	indigenous	recorded in native habitats in 1955–1956	first recorded in native habitats in 1999–2002	only recorded as meteorological station pests
Blattodea	0	0	0	2
Psocoptera	0	2	1	5
Hemiptera	1	4	4	0
Thysanoptera	2	0	6	0
Coleoptera	6	3	3	8
Diptera	16	11	13	0
Lepidoptera	3	3	0	0
Hymenoptera	0	2	4	0
total	28	25	31	15

All of the indigenous pterygote insect species recorded from Gough Island by the 1955–1956 survey were also recorded by the 1999–2000 survey. At least 12 indigenous pterygote insect species recorded by the 1999–2000 survey were not recorded by the 1955–1956 survey, probably half of these a result of improved taxonomy, the others being rare and not sampled in the first survey. The 1999–2002 survey also recorded an additional 43 introduced species, with two introduced species recorded in 1955–1956 (both meteorological station pests) being absent in 1999–2000. It seems likely that most of these additional species have been introduced since 1955–1956. If the same proportion of introduced species was present at the time of the first survey but went unrecorded, as was the case for indigenous species, then 24 species (36 including meteorological station pests) have been introduced since 1955–1956.

Approximately 51 landings were made in the period 1675–1956, although this is likely to be a somewhat conservative estimate. Of these landings, more than half were by commercial sealers originating primarily from North America, and only 10 were concerned with research (table 2). The construction and permanent, though annually rotated, occupation of the meteorological station has meant a considerable increase in the number of landings, which have also been augmented by exchanges of goods and personnel with the vessels (mostly just two) that have been licensed to fish around Gough Island since 1963. Thus, in the period 1957–2000, approximately 182 landings were made. Most of these were from vessels that departed from South Africa, of which approximately half were fishing vessels delivering goods and personnel to the island (table 2). In total, 71 visits (mostly by the South African research and supply vessel) were directly associated with meteorological monitoring, and limited biological and geological research activities at Gough Island (Cooper & Ryan 1994; Chown *et al.* 2000). In total, there have therefore been approximately 233 landings at Gough Island since its discovery. Most (*ca.* 78%) of these have occurred since the establishment of the meteorological station, which has one regular visit each year, with all goods and personnel now usually being transferred by helicopter. Overall, the frequency of landings since the first human landfall has been in the region of 0.7 per annum, although before 1956 this was probably in the region of 0.2 visits per year, and has increased to just over 4.1 visits per year since then.

Assuming a total of 233 landings on Gough Island, the recorded number of introduced species equates to one successful establishment with every three to four landings. Concentrating on those introductions that have occurred since 1955–1956, these have arrived at a rate of one species every five to eight landings (depending on whether meteorological station pests are included or not). If the entire flora and fauna were considered, these rates would be substantially higher, as species from several other taxonomic groups have also been introduced to Gough Island. Cooper & Ryan (1994) list 24 introduced species of plants, but this includes some that were introduced intentionally, and excludes subsequent unintentional introductions (see below). Introduced species also occur in several other invertebrate groups; for example, all of Gough Island's myriapod fauna (three species) have been introduced, as has the terrestrial isopod *Porcellio scaber*, and most of the island's molluscs (Preece 2001). A single species of introduced mammal, the house mouse (*Mus musculus*), currently occurs on the island.

The principal possible explanations for the high rate of successful establishment of introduced species on Gough Island are a high level of introduction 'effort', low biotic resistance or good environmental matching. There seems little reason to believe that particularly high numbers of individuals of given species arrive at the island, thereby enhancing the likelihood of establishing viable populations. Indeed, its geographical isolation and the low frequency of landings suggests quite the opposite, as does the proportion (28%) of established introduced species that are known to be parthenogenetic (Jones *et al.* 2003), a figure higher than that for most continental faunas (CSIRO 1991). Whereas, for insect and other species, greater levels of introduction effort of given species have frequently been found to be associated with an increased likelihood of establishment, even very small numbers of founder individuals can be sufficient to give rise to populations that persist (Green 1997; Memmott *et al.* 1998; Grevstad 1999; Forsyth & Duncan 2001).

It has long been held that high rates of establishment of introduced species may arise on islands from the depauperate nature of indigenous floras or faunas and the

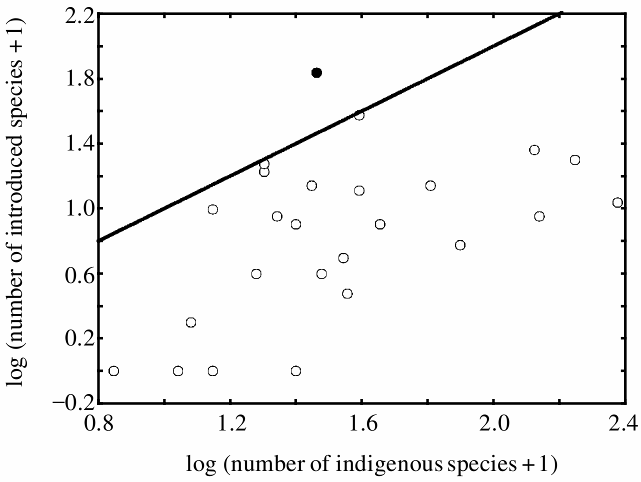

Figure 1. The relationship between the number of indigenous and introduced species of pterygote insects recorded from islands in the Southern Ocean. Gough Island is the filled circle, and the slope is the line of equality. Data from compilation in Chown *et al.* (1998), updated for Gough Island by records from GITIS (see text).

opportunities that these provide (for discussion see Wace & Holdgate 1976; Williamson 1996; Lonsdale 1999). Indeed, several of the introduced pterygote insect species on Gough Island, such as predatory beetles, fill ecological roles that previously seem to have been empty. None the less, recent studies have found little general support for the role of biotic resistance in determining geographical patterns of establishment of introduced species, but have found evidence for a dominant effect of climate matching (Lodge 1993; Chown *et al.* 1998; Pyšek 1998; Blackburn & Duncan 2001*a*; Gabriel *et al.* 2001), although some experimental work has provided evidence that more speciose assemblages may be more resistant to invasion (e.g. McGrady-Steed *et al.* 1997; Levine 2000; Kennedy *et al.* 2002). Certainly, the cosmopolitan but more temperate origins of many of the introduced species (most of which are also established, synanthropic species in the Western Cape Province of South Africa (Jones *et al.* 2003)) have meant that they are well adapted to the environmental conditions encountered on the island. Indeed, the relatively restricted seasonality in climate (resulting from the strong maritime influence) may well mean that populations have escaped the marked reductions in numbers that they would experience as a result of seasonally severe conditions, which might be characteristic of their ranges elsewhere.

Rates of establishment underestimate the frequency with which propagules (in the case of pterygote insects, presumably usually adult individuals) of alien species arrive at Gough Island. Williamson (1996) and Williamson & Fitter (1996) argue that a useful rule of thumb, the 'tens rule', is that *ca.* 10% of alien species found in the wild become established, and that *ca.* 10% of those established become pests (where, accepting the variance about such generalizations, *ca.* 10% means between 5% and 20%). On the basis that all of the introduced pterygote insect species that have been recorded in the field appear to have established, this would mean that 710 (355–1420) species of pterygote insects have actually at some time been introduced to Gough Island, or more than three species for every landing on the island. However, for their area, islands tend to support more introduced species than do continents (e.g. Brown 1989; Lonsdale 1999; Blackburn & Duncan 2001*b*). This suggests that the tens rule probably overestimates the number of introductions that have taken place on Gough Island. None the less, the rule perhaps provides a useful upper bound for an estimate of the number of introductions that might have taken place.

Geological, geomorphological and palynological evidence suggests that Gough Island emerged from the sea *ca.* 2–3 Myr ago, did not experience glaciation and has maintained a relatively stable flora for the past 43 000 years (Maund *et al.* 1988; Bennett *et al.* 1989; Hall 1990). Assuming both a uniform colonization rate, beginning 2 Myr ago, and that indigenous congeneric species are a consequence of *in situ* cladogenesis, only 21 colonization events, one occurring every 95 000 years, are required to explain the extant indigenous free-living pterygote insect fauna of Gough Island. Even assuming that 95% of all species on Gough Island have gone extinct, the colonization rate would still amount to only one species per millennium. By contrast, the rate of species introductions over the period of human activity at Gough Island (325 years), amounts either to 218 per thousand years (71 species in 325 years) or, assuming that the tens rule applies to islands, 2184 per thousand years. That is, a human-mediated colonization rate of two to three orders of magnitude greater than the background rate.

If applied to Gough Island, the tens rule would also mean that approximately seven species of pterygote insects should have attained pest status there. As defined by Williamson (1996), a pest species is one with a negative economic impact. Interpreted in the usual terms, the relevance of this on Gough Island would be somewhat limited. However, if any of those species that have established in the field seemed likely to, or did, pose a significant threat to the integrity of the indigenous flora and fauna, then considerable sums might have to be expended to combat the problem (under the Convention on Biological Diversity, the UK has an obligation to 'prevent the introduction of, control or eradicate those alien species which threaten ecosystems, habitats or species'). At least on other Southern Ocean islands, introduced animals and plants constitute one of the most significant threats to indigenous biotas (Bonner 1984; Chapuis *et al.* 1994; Dingwall 1995; Chown *et al.* 1998; Bergstrom & Chown 1999; Chown & Gaston 2000; Chown *et al.* 2001), as a result of direct effects such as predation (Ernsting *et al.* 1995), herbivory (Leader-Williams *et al.* 1987) and competition (Gremmen 1997; Gremmen *et al.* 1998; Frenot *et al.* 2001), and indirect effects such as the modification of local nutrient cycles (Smith & Steenkamp 1990). Although no examples have yet arisen among the introduced invertebrates where eradication has been seriously contemplated (although some of these species are among the most abundant invertebrates on the island), the accidental introduction of a small herb, procumbent pearlwort (*Sagina procumbens*), did cause such a problem (Gremmen *et al.* 2001). Indigenous to the Northern Hemisphere, this species is well known for its invasive tendencies in the Southern Hemisphere, where it can form large mats that greatly influence local biodiversity (Gremmen & Smith 1999; N. J. M. Gremmen and S. L. Chown, unpublished data).

Table 2. The number of landings made at Gough Island during the periods 1675–1956 and 1957–2000. Landings are indicated by provenance and by the major activity in which the vessels involved were participating.

1675–1956		1957–2000	
provenance	landings	provenance	landings
North America	23	South Africa	160
United Kingdom	13	United Kingdom	13
South Africa	12	Europe	3
Europe	2	unknown	3
unknown	1	South America	2
		Asian	1
total	51	total	182
activity		activity	
sealing	27	fishing	89
research	10	research	71
fishing	2	sealing	0

Discovery of the species on Gough Island in 1998 in the vicinity of the meteorological station was followed by the rapid implementation of an eradication programme that included weeding, herbicide application, the use of a specially imported boiler to heat the soil and thereby reduce the viable seed bank, and replanting of indigenous species in cleared areas (Gremmen *et al.* 2001). Although successful in eliminating visible plants, long-term and regular inspections of the area, in addition to further eradication treatments where required, will be needed to prevent the build-up and spread of a population. Whether complete eradication is a possibility remains open to debate, and there is a significant risk of propagules being transported (by human or other agency) to other areas of the island where control measures would be much more difficult to implement. This means that although eradication programmes are possible, given that they have been successful elsewhere (Veitch & Bell 1990; Newman 1994; Bester *et al.* 2000; Moro 2001) and have achieved a measure of success on Gough Island, they are unlikely to be practical.

In summary, our data from Gough Island indicate that even in remote locations, where human activities are very low by global standards, high rates of biological invasion are a pervasive feature of the landscape. Indeed, these rates are two to three orders of magnitude greater than background levels. Globally, recent species-level extinctions (most of which are on islands) are also taking place at a rate of two to three orders of magnitude greater than previous background levels (May *et al.* 1995). These elevated rates of introduction and extinction suggest that biotic homogenization (McKinney & Lockwood 1999) is taking place in two ways. Extinctions reduce the matching components of beta diversity (e.g. Krebs 1999) that contribute to place distinctiveness, whereas introductions enhance those that contribute to similarity. Because invasive species are often responsible for island extinctions, these two routes to homogenization are closely coupled. Therefore, simply by reducing the numbers of human visitors and increasing the stringency of quarantine procedures, the threat of homogenization can be much reduced on isolated islands.

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APPENDIX A: THE FREE-LIVING PTERYGOTE INSECTS RECORDED FROM GOUGH ISLAND

Insects alien to the island are indicated in bold; insects only recorded on the island post-1956 are indicated by ticks.

Blattodea	
Blattella germanica	√
***Deropeltis* sp.**	√
Psocoptera	
Cerobasis annulata	
Diptera	
Bradysia nocturna	
***Bryophaenocladius* sp.**	√
Calliphora croceipalpis	
Clunio cf. *africanus*	
Coelopa* cf. *africana	√

Psocoptera (*Continued.*)	
Cerobasis guestfalica	√
Ectopsocus briggsi	
Liposcelis bostrychophila	√
Liposcelis decolor	√
Liposcelis pubescens	√
Lepinotus inquilinus	
Psyllipsocus ramburii	√
Hemiptera	
Aulacorthum circumflexum	
Aulacorthum solani	
Cavariella aegopodii	√
Nothodelphax atlanticus	
Jacksonia papillata	
Myzus ornatus	√
Myzus persicae	√
Rhopalosiphum padi	
Rhopalosiphum rufiabdominalis	√
Thysanoptera	
Anaphothrips obscurus	√
Aptinothrips rufus	√
Frankliniella antarctica	√
Lissothrips sp.	√
Merothrips brunneus	√
Nesothrips inaccessiblensis	√
Thrips hawaiiensis	√
Thrips tabaci	√
Coleoptera	
Aridius sp.	
Cercyon depressus	
Cryptolestes pusilloides	√
Cryptophagus pseudodentatus	
Henoticus californicus	
Hylotrupes bajulus	√
Hylurgus ligniperda	
Lancetes dacunhae	
Liodessus involucer	
Notolinus hottentottus	
Oryzaephilus surinamensis	√
Pentarthrum carmichaeli	
Ptinella natvigi	√
Ptinus tectus	√
Quedius mesomelinus	
Sepedophilus filicornis	√
Sitophilus oryzae	√
Sphaeriestes sculptilis	√
Stegobium paniceum	√
Tristanodes scirpophilus	
Diptera (*Continued.*)	
Dicranomyia distans	
Dimecoenia spp. (5 + species)	√
Dimecoenia tristanensis	
Drosophila punctatonervosa	√
Fannia canicularis	
Fucellia tergina	
Leptocera caenosa	√
Limnophyes minimus	√
Lucilia sericata	
***Lycoriella* sp. A.**	√
***Lycoriella* sp. B.**	√
Megaselia rufipes	
Meoneura obscurella	
Mycophila fungicola	√
Ornithomyia parva	
Phthitia plumosula	
Prosopantrum flavifrons	
Psychoda albipennis	
Pullimosina heteroneura	√
Scaptomyza altissima	
Scaptomyza frustulifera	
Scatella sp.	√
Sciophila parviareolata	√
Spelobia parapusio	√
Symplecta holdgatei	
Symplecta sp.	√
Telmatogeton sp. near *sanctipauli*	
Thalassosmittia sp. near *thalassophila*	√
Thoracochaeta sp.	√
Thoracochaeta brachystoma	√
Thoracochaeta zosterae	
Lepidoptera	
Agonopterix goughi	
Dimorphinoctua goughensis	
Endrosis sarcitrella	
Monopis crocicapitella	
Peridroma goughi	
Peridroma saucia	
Hymenoptera	
Aphidius colemani	
***Diadegma* sp.**	√
***Kleidotoma* sp.**	
Phaenoglyphis villosa	√
***Stilpnus* sp.**	√
***Trichopria* sp.**	√

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