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Taxonomic homogenization and differentiation across Southern Ocean Islands differ among insects and vascular plants

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ABSTRACT

Aim To investigate taxonomic homogenization and/or differentiation of insect and vascular plant assemblages across the Southern Ocean Islands (SOI), and how they differ with changing spatial extent and taxonomic resolution.

Location Twenty-two islands located across the Southern Ocean, further subdivided into five island biogeographical provinces. These islands are used because comprehensive data on both indigenous and non-indigenous insect and plant species are available.

Methods An existing database was updated, using newly published species records, identifying the indigenous and non-indigenous insect and vascular plant species recorded for each island. Homogenization and differentiation were measured using Jaccard's index (JI) of similarity for assemblages across all islands on a pairwise basis, and for island pairs within each of the biogeographical provinces. The effects of taxonomic resolution (species, genus, family) and distance on levels of homogenization or differentiation were examined. To explore further the patterns of similarity among islands for each of the taxa and groupings (indigenous and non-indigenous), islands were clustered based on JI similarity matrices and using group averaging.

Results Across the SOI, insect assemblages have become homogenized (0.7% increase in similarity at species level) while plant assemblages have become differentiated at genus and species levels. Homogenization was recorded only when pairwise distances among islands exceeded 3000 km for insect assemblages, but distances had to exceed 10,000 km for plant assemblages. Widely distributed non-indigenous plant species tend to have wider distributions across the SOI than do their insect counterparts, and this is also true of the indigenous species.

Main conclusions Insect assemblages across the SOI have become homogenized as a consequence of the establishment of non-indigenous species, while plant assemblages have become more differentiated. The likely reason is that indigenous plant assemblages are more similar across the SOI than are insect assemblages, which show greater regionalization. Thus, although a suite of widespread, typically European, weedy, non-indigenous plant species has established on many islands, the outcome has largely been differentiation. Because further introductions of insects and vascular plants are probable as climates warm across the region, the patterns documented here are likely to change through time.

Keywords

Biological invasions, non-indigenous species, Southern Ocean Islands, spatial scale, sub-Antarctic, taxonomic homogenization, taxonomic resolution.

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INTRODUCTION

Non-indigenous species are a pervasive feature of the global landscape. Although only a relatively small, and taxonomically variable, proportion of these introduced species become invasive (Williamson & Fitter, 1996; Jeschke & Strayer, 2005, 2008), they have nonetheless substantially affected species and ecosystems (Mack *et al.*, 2000; Blackburn *et al.*, 2004; Bergstrom *et al.*, 2009). How many more introduced species particular areas can support is an important question. Not only can answers to it provide general ecological insight (Stohlgren *et al.*, 1999, 2008; Tilman, 1999; Fridley *et al.*, 2007; Sax *et al.*, 2007), but the likelihood and nature of saturation as well as the proportional increase in invasive species will also have profound consequences for the future of indigenous populations and ecosystems (Hulme, 2006; Sax & Gaines, 2008). Moreover, the ongoing extent of successful establishment of non-indigenous species will determine how much further biotas are likely to be homogenized.

Biological homogenization occurs when regionally distinct biotas are replaced with more cosmopolitan ones (McKinney & Lockwood, 1999; Olden & Poff, 2004; Olden, 2006). Its effects are different from those of single-species invasions, and are of concern because they may lead, *inter alia*, to food web simplification, declining resistance to environmental change and susceptibility to further invasions (Olden *et al.*, 2004). Species introductions, extinction of indigenous species, or some combination of the two processes can all lead to homogenization, although in some instances these processes can also lead to biotic differentiation (Olden & Poff, 2003). The likelihood of differentiation relative to homogenization is partly a consequence of spatial scale: distant biotas tend to be homogenized by species introductions, whereas those less widely separated tend to be differentiated, largely as a consequence of the autocorrelation structure that is typical of most indigenous biotas (Olden & Poff, 2003; McKinney, 2005; Qian & Ricklefs, 2006; Spear & Chown, 2008). However, the patterns may also be substantially more complicated (Olden *et al.*, 2006; Cassey *et al.*, 2007).

Despite a rapidly growing literature on the spatial and temporal patterns and consequences of homogenization (e.g. Clavero & García-Berthou, 2006; Marchetti *et al.*, 2006; McKinney, 2006; La Sorte *et al.*, 2007, 2008; McKinney & La Sorte, 2007), much of the work continues to focus on a relatively restricted set of taxa and a common set of areas. Indeed, in general, the literature on homogenization (mostly taxonomic homogenization) concerns vascular plants, fish and birds, investigated in continental areas, mostly in the Northern Hemisphere (Olden & Rooney, 2006; McKinney, 2008). A growing number of studies concern other continental regions (e.g. Castro & Jaksic, 2008; Olden *et al.*, 2008) and islands (Smart *et al.*, 2006; Cassey *et al.*, 2007; Castro *et al.*, 2007). However, with only a few exceptions (e.g. Duncan & Lockwood, 2001; Olden *et al.*, 2006; Smith, 2006; Spear & Chown, 2008), the literature largely remains focused on birds, plants and fish. In consequence, the situation for other taxa remains

unknown. For example, invertebrates, which not only are species-rich (Hawksworth & Kalin-Arroyo, 1995) but also have been introduced widely, often with substantial impacts (Beggs & Rees, 1999; O'Dowd *et al.*, 2003; Sanders *et al.*, 2003; Aldridge *et al.*, 2004), have not been widely investigated in this respect. Such a situation, while of concern given the calls for better understanding of homogenization and differentiation (Olden, 2006; McKinney, 2008), is hardly surprising. Comprehensive inventories of indigenous and introduced invertebrates for continental areas are rare (although see Roques *et al.*, 2009) and even for islands are not especially common. An absence of information on insects has long been considered one reason why an understanding of the patterns of alien introduction in this group is less well developed than for other taxa (for discussion see Simberloff, 1989; Vázquez & Simberloff, 2001; for notable exceptions see Lawton & Brown, 1986; Gaston *et al.*, 2003; Suarez *et al.*, 2005; Ward *et al.*, 2006; Roques *et al.*, 2009).

Here we address this situation by making use of a comprehensive inventory of indigenous and non-indigenous insect species available for the Southern Ocean Islands (SOI) (Chown *et al.*, 1998, 2005; Greve *et al.*, 2005). Specifically, we assess the extent of change in faunal similarity caused by non-indigenous species introductions across the entire region, and how this relates to distances between island pairs. Following the approach developed by Cassey *et al.* (2007), we also undertake analyses at the level of major groups of islands identified across the region (Indian, Pacific and Atlantic Provinces, *sensu* Lewis Smith, 1984; see also Chown, 1990) to assess the extent to which similarity changes when assessed at the 'global' and regional levels. Although some of the island groups in the region, such as the Tristan da Cunha group (Holdgate, 1960) and Crozet Islands (Frenot *et al.*, 2001), can be thought of as archipelagos, the most common practice for the region to date has been to consider the islands in the context of particular biogeographical regions (e.g. Lewis Smith, 1984; Greve *et al.*, 2005). We use these islands and this group for two reasons. First, the insects of the region have been comprehensively surveyed (e.g. Jones *et al.*, 2003; Greve *et al.*, 2005; Lee *et al.*, 2007), thus making the region suitable for assessment of homogenization. Few other areas of the globe have such comprehensive insect surveys available for them (see above). Second, we use insects as an exemplar for the invertebrates because data for other invertebrate groups across the region are less comprehensive.

Previous investigations have identified vascular plant species richness as a major correlate of both introduced and indigenous insect species richness (Chown *et al.*, 1998, 2005). In consequence, we also investigate change in vascular plant similarity associated with established introductions for the same set of islands. Changing patterns of plant similarity, especially at higher taxonomic levels [given that many insects are oligophages and that dietary preference tends to be at higher taxonomic levels (Strong *et al.*, 1984; see also Chown *et al.*, 1998)] might indicate potential for further change in insect faunas. For example, homogenization of floras at higher

taxonomic levels is likely to promote homogenization of phytophagous insects, whereas differentiation might lead to the opposite change through time. Moreover, by investigating both taxa, the indigenous components of which show rather different patterns of similarity across the region (Greve *et al.*, 2005), insight into the patterns of introduction across the region can also be achieved. To date, it has been suggested that the terrestrial vascular flora and fauna of the region are being homogenized because of the widespread introduction of European 'weedy' species (Frenot *et al.*, 2005; Greve *et al.*, 2005). However, the extent of homogenization is dependent not only on patterns of introduction, but also on the spatial backdrop of indigenous species distributions (Olden & Poff, 2003, 2004; Cassey *et al.*, 2007). Therefore, an explicit investigation of changes in similarity is required.

MATERIALS AND METHODS

Region and taxa

The islands of the Southern Ocean represent some of the only land in the Southern Ocean, and span *c.* 37°–60° S. They are relatively poor in terrestrial species by comparison with northern continental areas at similar latitudes, support large colonies of breeding seabirds and seals (Bergstrom & Chown, 1999), and have a high conservation value, recognized by World Heritage status in several cases (de Villiers *et al.*, 2005). The islands are characterized by predominantly oceanic climates (cool, wet and windy), and vary in size, age, geology and proximity to the nearest continent (Chown *et al.*, 1998; Bergstrom & Chown, 1999). Most currently have no permanently resident human population (with the exceptions of Tristan da Cunha and the Falklands). However, they are regularly visited by research expeditions and tourists. Historically, widespread human exploitation of land-breeding marine mammals has taken place on the islands, dating back to at least the 1800s. Early human inhabitants deliberately introduced several vertebrates species and some plant species (Frenot *et al.*, 2005), and since the discovery of the SOI many insect and plant species have been introduced to them accidentally. Moreover, because these islands are isolated, small in size, and have relatively low levels of human activity, it is reasonably straightforward to monitor alien invasion (Chown *et al.*, 2008).

An existing database of indigenous and non-indigenous plant and insect species distribution across the SOI (Greve *et al.*, 2005) was updated, using new records of indigenous and introduced species (e.g. Turner *et al.*, 2005; Lee *et al.*, 2007) and used for this study. Species status (either indigenous or non-indigenous) had been determined previously (Chown *et al.*, 1998). All non-indigenous species were included, with no distinction made between invasive and established species, although cultivated plants that occur on the Falklands and Tristan da Cunha Islands were excluded. In the few instances where the status of newly recorded plant species has not been determined (Turner *et al.*, 2005; Amey *et al.*, 2007), the species

was regarded as indigenous if it was present on neighbouring islands as an indigenous plant, and occurred in an undisturbed location away from human infrastructure. Six plant and five insect species have been recorded as non-indigenous on some islands and indigenous to others, and these previous categorizations were accepted.

While the SOI have been well surveyed (Chown *et al.*, 1998; Chown & Convey, 2007), survey effort varies among islands, and for this reason we excluded Beauchêne (Falkland group), Pingouins, Apôtres and Est (Crozet group). Well surveyed islands with absences of either insects or plants were included. Analyses were undertaken for the entire region, and among island pairs for each major biogeographical region identified by Lewis Smith (1984) – South Atlantic Province, South Pacific Province and South Indian Province, but with distinctions drawn between Amsterdam and St Paul and the other South Indian Province Islands, and the Tristan da Cunha group and the South Atlantic Province islands. This resulted in five regions: Amsterdam Group (Amsterdam, St Paul); South Indian Province (Cochons, Heard, Kerguelen, Marion, McDonald, Possession, Prince Edward); Tristan Group (Gough, Inaccessible, Nightingale, Tristan da Cunha); South Atlantic Province (East Falkland, West Falkland, South Georgia); and South Pacific Province (Antipodes, Auckland, Bounty, Campbell, Macquarie, Snares).

Homogenization

Homogenization was measured for both insects and vascular plants (hereafter 'plants') as a change in Jaccard's index (JI) of similarity between islands as a result of introductions. ESTIMATES WIN 7.51 (Colwell, 2005) was used to calculate the total number of species, number of shared species and JI for each island comparison. Each island was compared with every other island resulting in 231 pairwise comparisons, following the methods adopted by Spear & Chown (2008). To examine homogenization at a regional scale, pairwise comparisons were made between islands within provinces: 15 pairs for the South Pacific Province, 21 for the South Indian Province, one pair for the Amsterdam Group, six for the Tristan Group, and three for the South Atlantic Province.

Although homogenization may also be a consequence of extinction, the level of human-induced extinction in these systems is not well known. To date, no extinctions among the insects and plants have been reported, despite substantial impacts of some invasive vertebrate species, which have included local extirpations of bird species (see discussion in Chapuis *et al.*, 1994; Chown *et al.*, 2001; Frenot *et al.*, 2005). Moreover, none of the species considered has been accorded IUCN Red List status, thus no suggestion exists that extinction is plausible within the next 50 years [see Spear & Chown (2008) for the use of the Red Lists to forecast homogenization by extinction].

To elucidate further the extent of homogenization across the taxonomic hierarchy, analyses were also conducted at the genus and family levels. While such analyses provide insight

into the broader processes underlying introduction and establishment (see Greve *et al.*, 2005), they can also start to provide some insight into functional homogenization, because many traits in insects have substantial amounts of variance partitioned at higher taxonomic levels (Chown *et al.*, 2002; Chown & Gaston, in press).

The spatial patterning of homogenization was investigated by examining change in percentage similarity with distance between island pairs. The distance between islands was calculated using Shirokov's spherical law of cosines (Dale, 2005) based on island locations defined by Chown *et al.* (1998). Change in similarity between island pairs was plotted against corresponding pairwise island distance. This was done at species, genus and family levels for the insect and plant assemblages.

Island similarity, distribution and occupancy

Because substantial differences in levels of homogenization and differentiation were found among the two taxa and the island regions, the data were explored further using two approaches. First, the extent to which the relationships among islands differ when only non-indigenous or only indigenous species are investigated was examined for each of the taxa. Cluster analyses, based on the JI similarity matrices and using group averaging, as implemented in PRIMER v. 5.1.2 (Plymouth Marine Laboratory, Plymouth, UK), were used (see also e.g. McInnes & Pugh, 1998; Greve *et al.*, 2005). Much less of a signal of regional distinction among the biogeographical provinces in the non-indigenous than in the indigenous species datasets would be expected if a similar group of 'European weedy species' (see Frenot *et al.*, 2005) had been introduced across all islands. In addition, to identify how similar islands are within each biogeographical province, the frequency distributions of pairwise similarity values were plotted for indigenous insects and plants, and then the frequency distributions of change in similarity following introductions for each biogeographical province were plotted (see Cassey *et al.*, 2007). To understand further the mechanisms underlying changes in similarity, the extent to which species were widely or narrowly distributed across the region was examined by plotting occupancy frequency distributions for the species in each taxon. Furthermore, the most widespread families were determined by calculating the number of islands on which each family occurs for both indigenous and non-indigenous insects and plants. Families that occur on eight or more islands (more than the first quartile) were identified and, if present, the contrasting indigenous or non-indigenous occurrence of the same family was then assessed.

RESULTS

At all taxonomic levels, the SOI insect fauna has become homogenized as a consequence of the introduction of non-indigenous species (Fig. 1). By contrast, the SOI vascular flora

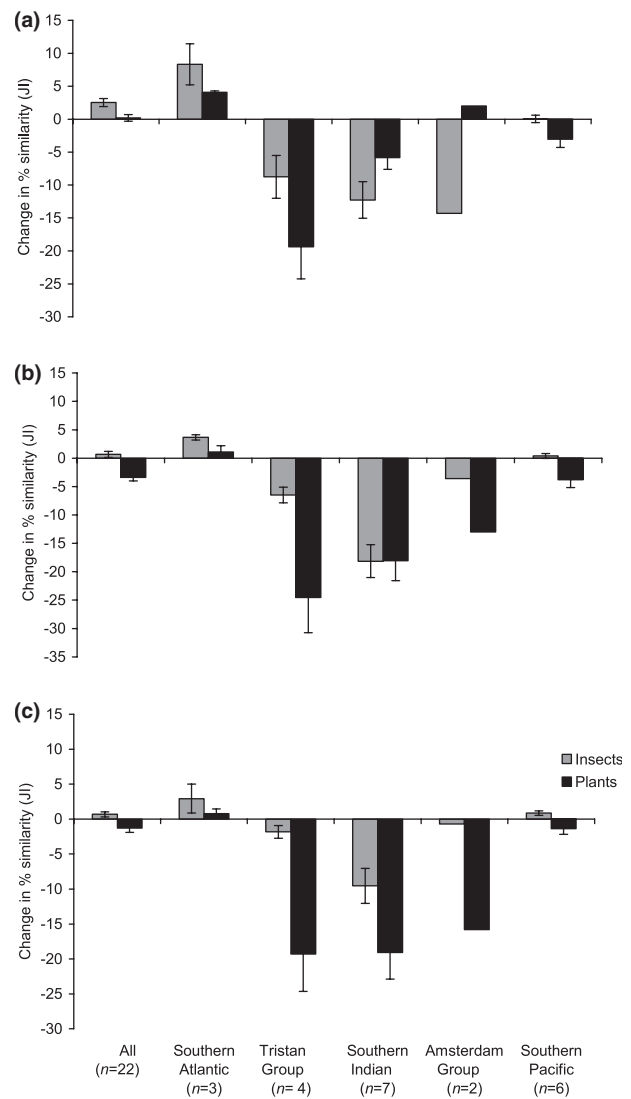


Figure 1 Homogenization and differentiation (\pm SE) of Southern Ocean Islands and islands within biogeographical regions, due to the introduction of non-indigenous species. Homogenization is measured as a positive change in Jaccard similarity, while differentiation is a negative change in Jaccard similarity. The analysis was conducted at three taxonomic hierarchical scales: (a) family, (b) genus and (c) species. No error bars are presented for the Amsterdam group because it includes only two islands.

has become differentiated (Fig. 1) at the genus and species level but homogenized at the family level. On a smaller, provincial scale, the introduction of non-indigenous species has had differing impacts on the insect and plant assemblages. Non-indigenous species have led to differentiation of the insect and plant assemblages across the South Indian Province and in the Tristan group, while the opposite is the case for the South Atlantic Province (Fig. 1). The South Pacific Province shows the same trend as is found for the overall analysis. The Amsterdam group shows differentiation of the insect fauna across all taxonomic levels, to varying levels, while the plants are differentiated at genus and species levels (Fig. 1b,c), but

plant families are homogenized (Fig. 1a). The greatest change has taken place in the Tristan Group vascular flora, which has been differentiated substantially [at both species (19%) and generic (25%) levels] as a consequence of the introduction and establishment of non-indigenous species. By contrast, and at least at species level, changes in insect assemblage similarity are typically < 10%.

Homogenization increases with distance at all taxonomic levels (Fig. 2). At the level of genera and species, the relationship between distance and homogenization differs between insects and plants (Fig. 2). Following introduction of non-indigenous species, insect assemblages are homoge-

nized once the distance between island pairs exceeds 3000 km, while for plant assemblages, the distance among island pairs must exceed 8000 km before homogenization is typically found. Nonetheless, some island pairs continued to show differentiation of the plant assemblages following introductions at as much as 10,000 km. At the family level, the relationship between pairwise distances and the extent of homogenization is more similar for the two taxa, although differentiation remains the more common outcome for the plants.

Among other factors, the initial similarity of assemblages among islands determines the extent to which homogenization

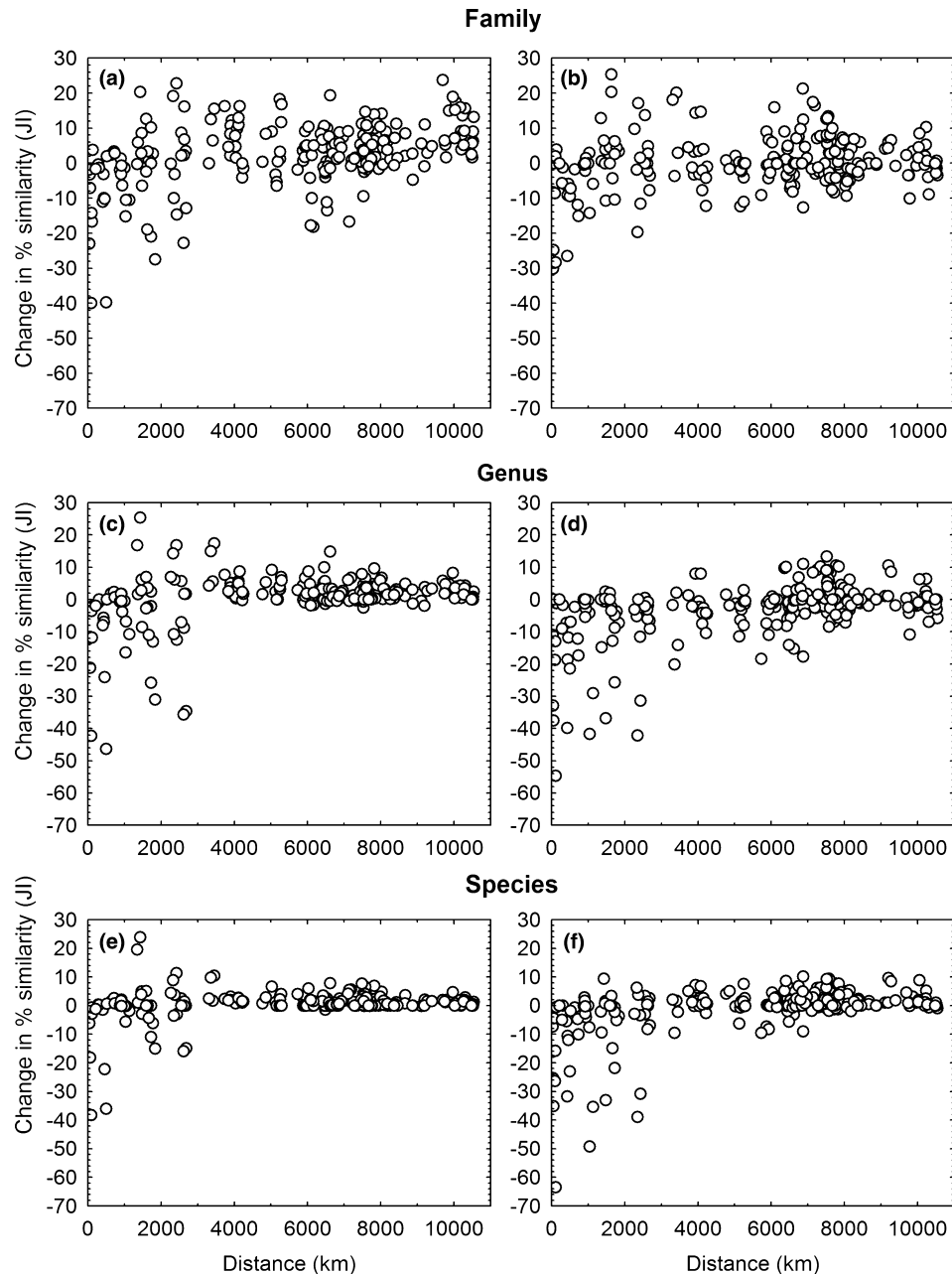


Figure 2 Pairwise comparisons of insect (a,c,e) and plant (b,d,f) taxonomic homogenization over distance for all Southern Ocean Islands at the three taxonomic levels: family, genera and species.

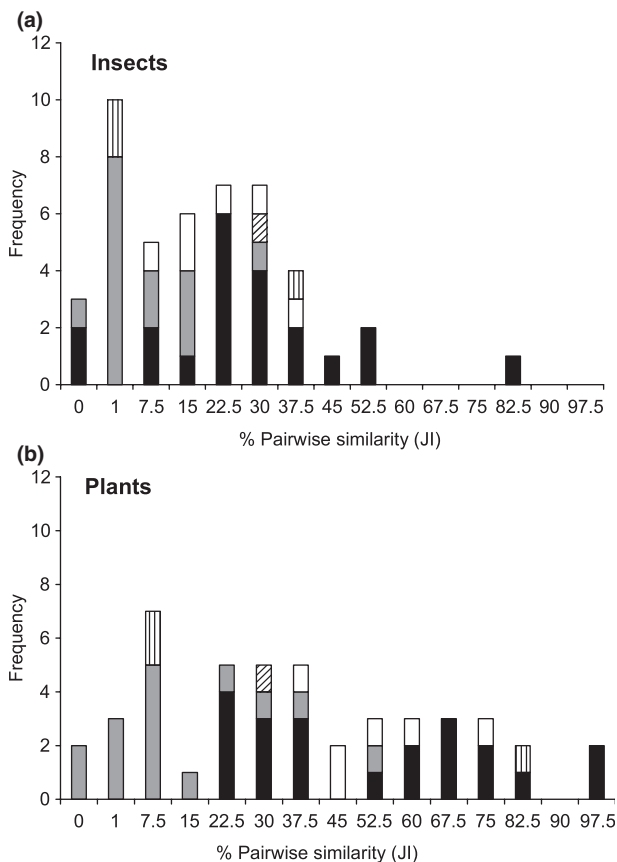


Figure 3 Frequency distributions of pairwise similarities between islands, within each biogeographical province, for indigenous (a) insects and (b) plants. South Indian Ocean Province, black; South Pacific Ocean Province, grey; Tristan Group, white; South Atlantic Province, vertical lines; Amsterdam Group, diagonal lines.

or differentiation might take place. Across all of the SOI, based on Jaccard's similarity index, plant assemblages are more similar among islands than are insect assemblages (Fig. 3). Moreover, the total numbers of introductions of plants have also been considerably higher than those of insects (284 relative to 183), with high numbers of these introductions being confined to one or two islands (see Appendix S1 in Supporting Information). Together, these two factors at least partially account for the homogenization of insect assemblages and the differentiation of plant assemblages across the SOI.

Indigenous species cluster together within the biogeographical provinces (as defined here and by Lewis Smith, 1984) (Fig. 4). For non-indigenous insect species, islands within provinces typically remain grouped together in the cluster analysis (except for Bounty and McDonald, which lack non-indigenous species). However, the relationships among provinces differ from those obtained using the indigenous species (Fig. 4). By contrast, the province groupings are not retained in the cluster analysis of the non-indigenous plants. This result suggests that similar non-indigenous species of plants have indeed been introduced across the region, whereas for insects, introductions tend to differ among provinces. This result is confirmed by the fact that within the insects, 61% of the non-

indigenous species occur on one island, whereas for the plants 46% occur on one island and 20% occur on four or more islands, with one species, *Poa annua*, occurring on 20 of the 22 islands examined (Appendix S1). Expressed in a different manner, the 10 most widely distributed non-indigenous plant species occur on a median of 13 islands, whereas for insects the median is 8, a significantly lower number (Mann–Whitney U -test $Z = 3.42$, $P = 0.00013$). However, this difference was still not sufficient to result in homogenization of the plant assemblages by comparison with the insects (Fig. 5). Indeed, among island pairs, plants have undergone more (and larger) differentiation events than insects. This is presumably a consequence of the substantial similarity of the plant assemblages among islands to begin with. Using the same metrics, within the insects 63% of the indigenous species occur on one island and only 4% occur on four or more islands, whereas for the plants 28% occur on one island and 18% occur on four or more islands, with one species, *Blechnum penna marina*, occurring on 18 of the 22 islands examined. Thus, the 10 most widely distributed indigenous plant species occur on a median of 13 islands, whereas for insects the median is 6 (the difference is also significant, Mann–Whitney U -test $Z = 3.79$, $P = 0.00001$). This effect persisted across the taxonomic levels examined (Fig. 2).

DISCUSSION

Patterns and mechanisms of homogenization and differentiation

The introduction and establishment of non-indigenous species across the SOI has led to homogenization of the insect biota. The extent of homogenization (*c.* 0.7%) across this large area is lower than or similar to that found at global and continental scales for other taxa. For example, for fish, similarity increases by up to 20% (Marchetti *et al.*, 2001; although see also Taylor, 2004). For ungulates at a global scale, the value is 2% (Spear & Chown, 2008). However, for birds globally, among oceanic archipelagos, within-ocean basin similarity changes vary between –5% and 7% (Cassey *et al.*, 2007). Whether the level of homogenization found for the insect assemblages here could be generalized to other areas is difficult to determine, but it seems likely that it would be higher than what might be found in continental areas because the insect fauna of the SOI is depauperate by comparison with other continental regions globally, and by comparison with the sub-Arctic (Gressitt, 1970; Vernon *et al.*, 1998; Chown & Convey, 2007). For SOI vascular plant species, differentiation was mostly found, by contrast with previous results of both continental studies, where homogenization levels of 0.01–0.8% have been found (McKinney, 2004; Qian & Ricklefs, 2006), and islands, for which homogenization of 2% has been reported for south-eastern Pacific oceanic islands (Castro *et al.*, 2007).

Differences in the initial similarity of the island plant and insect assemblages and differences in the number of non-indigenous plants and insects clearly account for the different

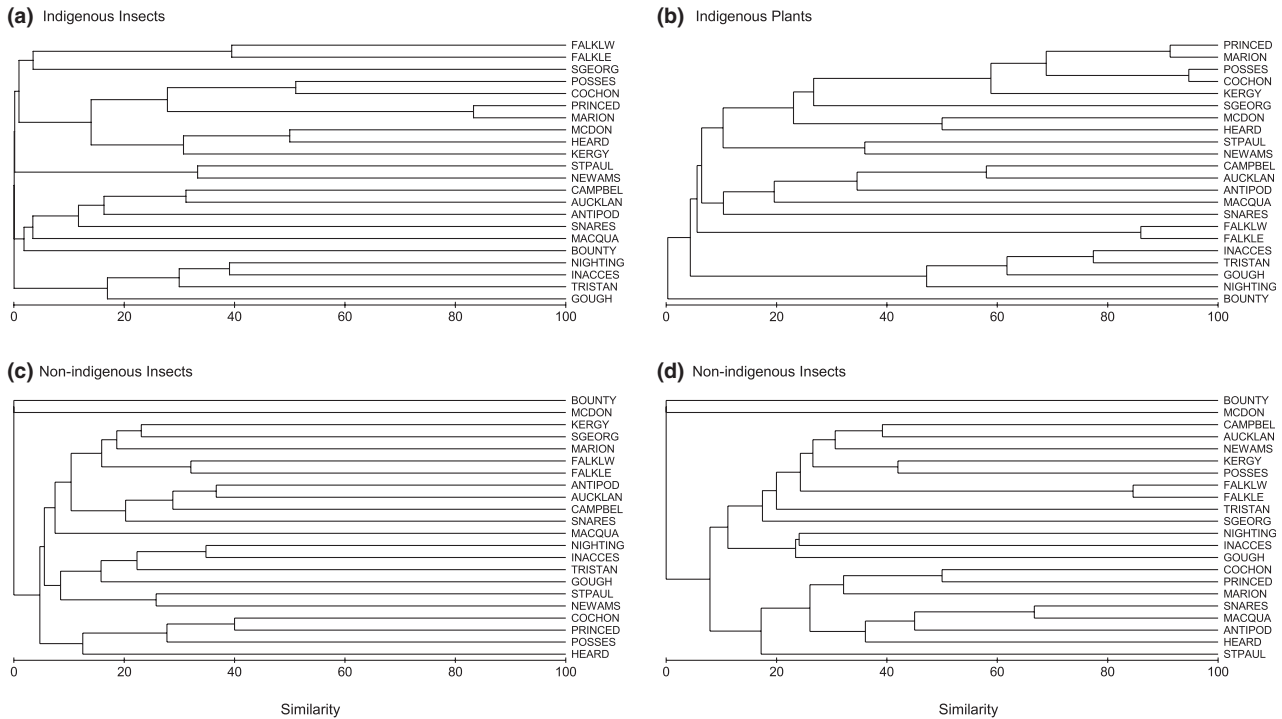


Figure 4 Dendrograms, based on cluster analyses using a Jaccard similarity matrices and group averaging, showing relationships among the Southern Ocean island biotas: (a) indigenous insects, (b) indigenous plants, (c) non-indigenous insects and (d) non-indigenous plants.

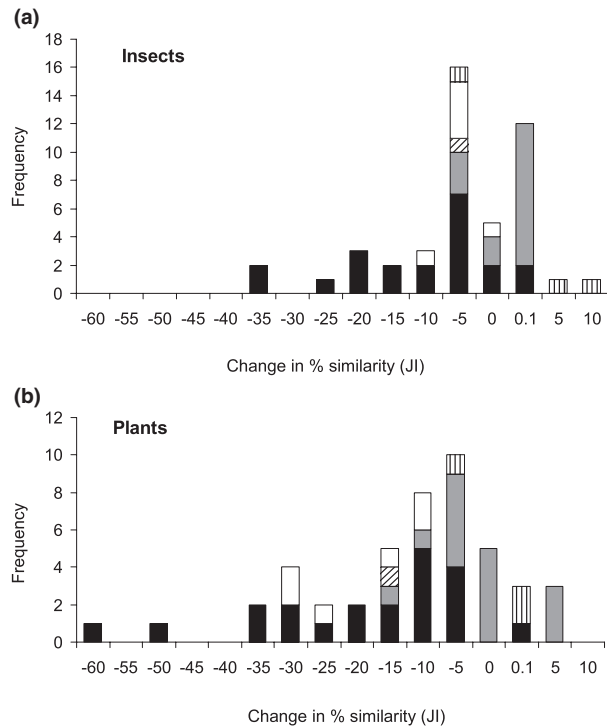


Figure 5 Frequency distributions of changes in pairwise similarities between islands, within each biogeographical province, following the inclusion of non-indigenous (a) insects or (b) plants. South Indian Ocean Province, black; South Pacific Ocean Province, grey; Tristan Group, white; South Atlantic Province, vertical lines; Amsterdam Group, diagonal lines.

response across the region between the two groups. The cluster analyses and numbers of widespread indigenous species reveal considerably greater similarity of indigenous plant assemblages than of indigenous insect assemblages across the region, and this is borne out by the analyses of nestedness undertaken by Greve *et al.* (2005). They demonstrated substantially and significantly greater nestedness in the vascular plants than in the insects, thus illustrating the typically greater similarity of plant assemblages among islands. These differences in the patterns of distribution between indigenous insects and plants were sufficient to overcome the opposite differences found in the non-indigenous species.

Distance, provincialism and assemblage change

Differences between the two taxa were also borne out by the change in assemblage similarity due to introductions with increasing distance between island pairs. For the insects, assemblages tended to become homogenized once distances of 3000 km had been exceeded at both species and genus levels. By contrast, for plants, non-indigenous species only led to consistent homogenization at the species level beyond 8000 km, and at the genus level differentiation at the maximum distance was still recorded. The 3000 km approximately corresponds to the minimum distance among provinces [for example, Tristan da Cunha (Tristan Group) lies *c.* 4000 km from Marion Island (South Indian Province); Heard Island (South Indian Province) is *c.* 4000 km from Macquarie Island (South Pacific Province)], and supports the much stronger provincial grouping of insects than that of the

plants (Greve *et al.*, 2005). Overall, these results correspond to Olden & Poff's (2003) predictions, and previous empirical work (e.g. Qian & Ricklefs, 2006; Cassey *et al.*, 2007; Spear & Chown, 2008), showing that introductions tend to result in differentiation at small distances and homogenization over larger distances (but see also McKinney, 2004, 2005).

Within provinces, this situation was different, with the patterns of change in similarity tending to be comparable among the groups, largely owing to the taxa showing stronger patterns of similarity among islands in their indigenous assemblages. The exception was the South Pacific Province, but this is likely to be a consequence of the low richness of plant and insect species on Bounty Island (as indicated by the high frequency of no change in Fig. 5) and the substantial difference between Macquarie Island and the other islands in the group (see also Greve *et al.*, 2005). The observed differentiation within the South Indian Province is attributed to the high similarity among indigenous assemblages, the highest indigenous similarity of all the island groups. The varying outcome at the larger spatial scale relative to the provincial scale bears out several of the findings of Cassey *et al.* (2007). First, patterns vary among provinces. For example, here the insect assemblages of the South Atlantic and South Pacific Province islands are homogenized both within the provinces and across all islands in the dataset. By contrast, insect differentiation has occurred within the Tristan da Cunha and Amsterdam groups and the South Indian Province. Furthermore, the most common pattern for plants is differentiation at both spatial scales, which is strongly influenced by indigenous plants being more similar between islands and across all islands (see also Greve *et al.*, 2005). This outcome bears out Cassey *et al.*'s (2007) suggestions that differences in evolutionary history among areas, and in spatial scale, both have significant influences on the assessment of changes in similarity that result from introductions (and presumably extinctions, but these have not been recorded for the SOI).

Functional homogenization

Although the current investigation concerned taxonomic homogenization (or differentiation) only, similar patterns at the higher taxonomic levels suggest that some degree of functional homogenization is also taking place. In the insects, functional traits such as cold-hardiness, thermal tolerance, desiccation resistance, metabolic rate variation, and variation in development rate are partitioned at higher taxonomic levels (Chown *et al.*, 2002). For example, more than 50% of the variance in metabolic rate and rate of water loss for insects in the data available is partitioned at genus and family levels. For body size, which is a close correlate of many functional attributes (Peters, 1983), somewhere between 35% and 60% of the variation in size is partitioned at taxonomic levels above genus (Chown & Gaston, in press). This means that increases in assemblage similarity at higher taxonomic levels mean increasing functional similarity among sites. Preliminary evidence exists of functional homogenization of plants in the SOI, in the form of the establishment of several fabaceous species (nitrogen-fixers), previously largely absent from the region, to nine islands and all provinces, which indicates an increase in functional diversity, but also functional homogenization (see Appendix S2).

Are SOI invaders European weedy species?

Previous investigations have suggested that a suite of common, European weedy species comprise a substantial proportion of the established non-indigenous species on the SOI. Despite the variation in extent of homogenization found among provinces and across the entire region, it is clear that the most widespread introduced taxa are typically of Northern Hemisphere origin, often from Europe. This is true both of the insects and the plants (Appendix S3). Indeed, examination of the taxa in both groups reveals that they comprise species well

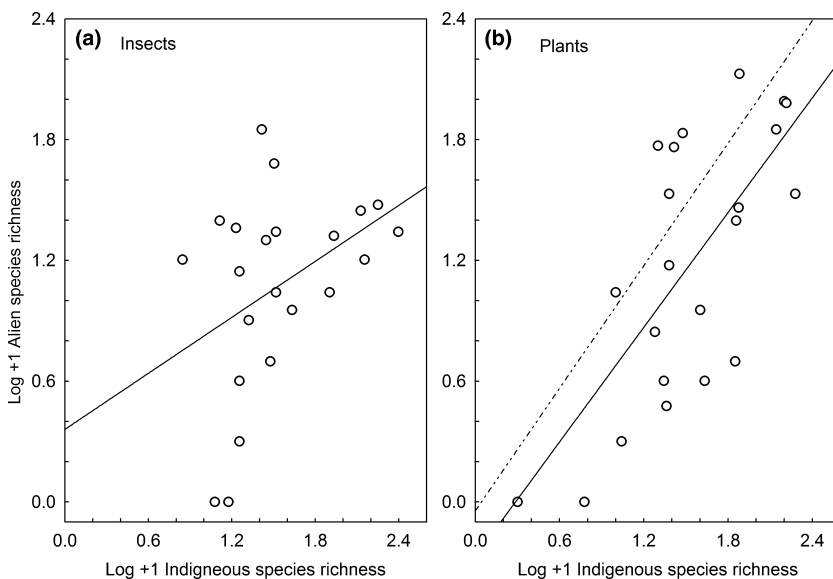


Figure 6 Indigenous and non-indigenous species richness of Southern Ocean Islands are not correlated for insects (a) [$F_{(1,20)} = 3.704, P > 0.069$], but are correlated for plants (b) [slope = 0.95 ± 0.21 , intercept = $-0.27 \pm 0.34, F_{(1,20)} = 20.16, P < 0.0002, r^2 = 0.48$, SE of estimate: 0.481]. The dashed line shows Sax & Gaines' (2008) 1:1 relationship for indigenous and non-indigenous plant species for 13 islands across the globe (ranging from tropical to cool temperate climate).

known for their introduction to other areas of the world (Holm *et al.*, 1977; Pyšek *et al.*, 2009; Roques *et al.*, 2009). Globally, the plant families containing the highest numbers of non-indigenous species are the Poaceae, Asteraceae and Leguminosae (containing Fabaceae), in descending order (Pyšek, 1998). On the SOI these families typically are also well represented, with the Poaceae (63) Asteraceae (42) and Fabaceae (17) containing the highest numbers of introduced species. Most of the families that contain the largest numbers of introduced species are well represented by indigenous species in the region. However, the Fabaceae is a notable exception because so few indigenous members of the Fabaceae are found on the islands (only one species occurs on one island). Among the insects, comparison of the patterns with other areas of the world is more problematic given the paucity of data on the group (see discussion in Simberloff, 1989; Vázquez & Simberloff, 2001). However, families that commonly contain many species of economic importance as pests, such as the Thripidae, Aphididae, Noctuidae and Calliphoridae (Annecke & Moran, 1982; Roques *et al.*, 2009), also contain the largest numbers of introduced species on the SOI.

Future scenarios

The data presented here represent a snapshot of the insect and plant assemblages of the SOI. How rates of invasion and the extent of similarity among islands and provinces in the region might change with time is not clear. At least for plants, the relationship between indigenous and non-indigenous species richness (Fig. 6b) is the same as that found in a global analysis by Sax & Gaines (2008), who found a 1:1 relationship (for the current data: slope $c. 1$, $t = 0.236$, $P > 0.05$, and intercept $c. 0$, $t = 0.802$, $P > 0.05$, on log–log scales). However, the relationship between indigenous and non-indigenous insect species was marginally non-significant ($F = 3.704$, $P = 0.069$) and certainly did not represent a 1:1 relationship (slope = 0.46, which is significantly < 1 , $t = 2.26$, $P < 0.05$). The reasons for these differences among the taxa and the factors underlying variation in richness across islands in the region have been explored in detail elsewhere (Chown *et al.*, 1998, 2005).

In terms of continuing non-indigenous introductions, few species are in cultivation on these islands, unlike other regions in the world, and considerable effort is undertaken by the managers of many of these islands to reduce introductions (e.g. de Villiers *et al.*, 2005). Thus, although much scope remains for further colonization and establishment of non-indigenous species, the rate at which this is likely to take place is probably far lower than the global average (Sax & Gaines, 2008). Climate change might alter this situation by increasing the match between climates of the islands and the ports from which most visitors depart (Kennedy, 1995; Chown *et al.*, 2005; Frenot *et al.*, 2005). Nonetheless, increasing attention is being given to ways to reduce propagule pressure to these islands (de Villiers *et al.*, 2005; Lee & Chown, 2009). Perhaps the most significant challenge will be to determine how to achieve this goal while not compromising the rate of change associated with natural

background colonization, which may well increase as climates warm across the region.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Occupancy of indigenous and non-indigenous species across the Southern Ocean Islands.

Appendix S2 Widespread indigenous and non-indigenous insects and plant families across the Southern Ocean Islands.

Appendix S3 The most commonly occurring non-indigenous insect and plant species across the Southern Ocean Islands.

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BIOSKETCH

Justine D. Shaw is interested in community ecology, island biogeography and invasion biology. She has a particular interest in invasive species, conservation ecology and conservation planning of Southern Ocean Islands ecosystems.

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