Species richness and turnover among indigenous and introduced plants and insects of the Southern Ocean Islands

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Abstract. Simultaneously investigating variation in species richness and turnover for indigenous and introduced communities holds great promise as a means to understand the relative contributions of ecological processes to community structure. Such insight will advance understanding of the ways in which environmental change may affect future community dynamics. Using a recently developed multi-site turnover metric, zeta diversity ($\zeta$), we explored species turnover patterns across indigenous and introduced insect and vascular plant communities of the Southern Ocean Islands. In addition, we used updated species occurrence and high-resolution environmental data to reexamine previously described patterns and drivers of species richness across the region. Species richness variation in indigenous insect and vascular plant communities was largely explained by island isolation and temperature, whereas human visitation frequency was strongly associated with introduced species diversity of both groups. Indigenous communities of both plants and insects had faster rates of species turnover across sites and less inter-island connectivity than their introduced counterparts. Zeta diversity analyses suggested that stochastic processes were more influential than niche-related processes on the observed patterns of turnover of indigenous insects. Meanwhile, turnover patterns of introduced insects and indigenous and introduced vascular plants were indicative of the dominance of niche-related processes. These outcomes highlight very different diversity patterns across indigenous and alien communities and indicate that different ecological processes may underlie diversity variation across these islands and taxonomic groups.

Key words: connectivity; dispersal limitation; distance decay; niche differentiation; similarity; stochastic processes.

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INTRODUCTION

Antarctica, its surrounding islands, and the Southern Ocean represent more than 30% of the Earth’s surface. Despite low eukaryote diversity on the continent itself, the Southern Ocean and its isolated islands have a rich biota. Although the patterns and processes underlying species richness variation in the region are well known (Chown et al. 2015, Crame 2018), key areas remain in need of further exploration. Among these, understanding species turnover is especially important. Investigations of turnover provide a useful observational approach to discern the likely importance of various processes thought to underlie broad-scale diversity variation (Chase and Myers 2011, Socolar et al. 2016). Indeed, their outcomes have led to new insights concerning the structure of diversity, its temporal change, and underlying mechanisms (Dornelas et al. 2006, 2014, Myers et al. 2013, Magurran et al. 2018). Despite their utility, formal investigations of turnover have been relatively limited across the region (Greve et al. 2005, Ellingsen et al. 2007, Gremmen et al. 2007, Shaw et al. 2010).

Simultaneous investigations of richness variation and turnover for indigenous and introduced
species may also be of considerable value for understanding the likely mechanisms underlying spatial variation in diversity. Species introductions provide unintentional, yet insightful, experiments in ecology (Brown 2014). For example, speciation is likely to play a significant role in determining variation among indigenous communities at regional scales (Ricklefs 1987, Vellend 2016), whereas among communities of introduced species, speciation is much less relevant (Chown and Convey 2007). Thus, should similar patterns in richness and turnover be found among indigenous and introduced species, there would be strong support for further focusing on the role of ecological mechanisms underlying richness variation and turnover generally (Evans et al. 2005, Socolar et al. 2016). Similarly, differences in the form of species–area relationships can provide insight into potential differences in factors structuring indigenous and introduced assemblages (Li et al. 2018). Several works have now highlighted the utility of simultaneously investigating richness variation and turnover patterns in indigenous and invasive species for understanding the relative contributions of ecological processes and the likelihood of the way in which environmental change might differentially affect these different communities (Sax and Gaines 2006, Marini et al. 2009, Socolar et al. 2016, Guo et al. 2018, Li et al. 2018).

The ecological insights from simultaneous investigations of richness and turnover among indigenous and invasive species are likely to be especially useful for identifying the mechanisms underlying diversity variation across the Southern Ocean Islands, and for forecasting how this might be likely to change into the future given rapid climate change in this region (Jones et al. 2016). These islands have a rich indigenous terrestrial biota (Lord 2015, Chown and Convey 2016), and despite their relative isolation and limited human occupation (several of these islands are unoccupied, and many only by scientific stations; de Villiers et al. 2006), most also have a substantial introduced terrestrial biota (Frenot et al. 2005). Although previous studies have investigated either richness patterns and their correlates (Abbott 1974, Chown et al. 1998, Selmi and Boulinier 2001) or elements of turnover (Greve et al. 2005, Shaw et al. 2010), simultaneous consideration thereof has been limited.

Joint consideration of these patterns is especially useful for forming a baseline to understand the dynamics of anticipated change (Dornelas et al. 2014, Gotelli et al. 2017, Magurran et al. 2018). Moreover, since the foundational studies across the Southern Ocean Islands, information on the biotas has been updated (Lord 2015, Chown and Convey 2016), and more accurate data on potential explanatory variables have become available, largely due to recent advances in remote-sensing technologies (e.g., high-resolution elevation models; Farr et al. 2007). For example, Chown et al.’s (1998) investigation of potential drivers of richness estimated land surface temperatures (LSTs) from sea surface temperature data, whereas now, high-resolution remote-sensed LST data are available (e.g., the MODIS LST dataset; NASA LP DAAC 2015).

New techniques for analyzing turnover have also been developed. One of the most promising of these is zeta diversity ($\zeta$) (Hui and McGeoch 2014). Zeta diversity ($\zeta_i$) measures the average number of species shared by multiple ($i$) communities, so comprehensively representing the spatial structure of multi-species distributions (Hui and McGeoch 2014). All incidence-based beta-diversity metrics can be expressed in terms of $\zeta_1$ and $\zeta_2$. By contrast, with three or more sites, the set of species shared by a particular combination of these sites is uniquely represented by the higher order components of zeta, that is, $\zeta_3$, $\zeta_4$ $\ldots$, $\zeta_i$ (Hui and McGeoch 2014). Thus, zeta diversity reconciles several biodiversity patterns, offers potential insights into the relative contributions of stochastic and niche assembly processes, and can provide a means to understand biodiversity responses to environmental change (Hui et al. 2018). Yet its potential has not yet been examined in the context of understanding differences in both the form and likely processes underlying community spatial variation among indigenous and introduced species.

Here, we therefore investigate richness variation and its likely drivers and turnover across the Southern Ocean Islands. We focus specifically on vascular plants and terrestrial insects because these two groups are well surveyed across the islands owing to decades of systematic investigations (see overviews in Gressitt 1970, Vernon et al. 1998, Lord 2015, Chown and Convey 2016), and because the local processes structuring these
communities are well understood (le Roux et al. 2005, 2013a, Convey 2007, Hermant et al. 2013, Lord et al. 2013, Convey et al. 2014, Chown and Convey 2016, Lehnebach et al. 2017). Based on the outcomes of these studies, and the differences in processes that likely underlie indigenous versus invasive species (Sax and Gaines 2006, Marinini et al. 2009, Brown 2014, Socolar et al. 2016, Guo et al. 2018), we make the following predictions. First, we expect that temperature should have an influence on indigenous and introduced vascular plant and insect richness, as a proxy for environmental energy availability and stress (Evans et al. 2005a), but with an accompanying role for plant richness variation in indigenous insects because of the groups’ typically strong association with vascular plants (Strong et al. 1984). Some previous investigations (Abbott 1974, Chown et al. 2005) have suggested that island area is less important an influence on richness variation than is expected from theory (Rosenzweig 1995) and found elsewhere at similar scales (Kreft et al. 2008), while others have suggested the converse (Williams 1982). We reexamine these ideas using updated information. Second, we expect that some measure of human activity, essentially a proxy for propagule pressure (Lockwood et al. 2009), should contribute significantly to richness variation in introduced vascular plants and insects and that island isolation, which is typically important in accounting for variation in richness across islands (Rosenzweig 1995), should not play a role for these groups as a consequence. Third, given that the species of vascular plants and insects introduced to these islands tend to be similar across the region (Frenot et al. 2005, Newman et al. 2018), and given the mounting evidence for different continental origins for indigenous groups on different archipelagos in the region (Morrone 1998, Moon et al. 2017), we expect turnover to be lower and the distance decay of similarity slower in the introduced compared with the indigenous species. We also expect that turnover will be lower for indigenous vascular plants compared with indigenous insects, given strong winds and zoochory facilitate the long-distance dispersal of plant propagules in the region (Muñoz et al. 2004), whereas Southern Ocean Island insects show a globally unusual tendency toward a reduction in dispersal abilities (Roff 1990).

**METHODS**

**Region and taxa**

Here, we define the Southern Ocean Islands (SOIs) as oceanic islands ranging from the Tristan da Cunha Island group at ~37° S to the South Shetland Islands at ~62° S (Appendix S1: Fig. S1). These islands are characterized by low temperatures, typically oceanic climates, and relatively low human disturbance (de Villiers et al. 2006) and vary in age, area, geology, ice cover, and degree of isolation (Shaw et al. 2010). We also include an Antarctic Peninsula site to capture the sole insect species of the Antarctic continent, but undertake analyses with and without the site to determine whether the inclusion of a continental site has an effect on the overall species richness trends (see Appendix S2).

We based the analyses on recently updated presence-absence biodiversity databases for the region (Shaw et al. 2010, Lord 2015, Chown and Convey 2016). These databases incorporate the outcomes of long-standing and often ongoing systematic diversity surveys, taxonomic work, and ecological research undertaken over many decades (Dreux 1966, Gressitt 1970, Meurk 1975, Dreux and Voisin 1988, 1992, Frenot et al. 2001, Jones et al. 2003, Posadas 2008, Lord 2015, Chown and Convey 2016). While some new indigenous species have been discovered in recent years (Clements et al. 2007), and some cryptic species revealed through new genomic techniques (Grobler et al. 2011), inventories for indigenous species have largely remained unchanged, indicating complete surveys. By contrast, new introduced species have continued to be recorded. Introduced species have changed the terrestrial SOI communities substantially, either by increasing species richness (Gaston et al. 2003), by competing with or predating upon native species, or as vectors of plant diseases (Lebouvier et al. 2011). Thus, the indigenous species inventories for each separate island or island group are likely to be close to complete, while those for the introduced species represent the currently known status of each island.

**Species richness**

To investigate patterns in, and the potential underlying drivers of, variation in species richness across the region, negative binomial
generalized linear models (GLMs) were used. Species richness was modeled as a dependent variable of both abiotic and human factors. Species richness of each of the four focal groups (indigenous and introduced vascular plants and insects) was calculated as the number of unique species of each group on each SOI. Abiotic factors (area, isolation, mean temperature, and thermal heterogeneity) were calculated using geographic information systems and high-resolution remotely sensed temperature data, where available (insects, 23 SOIs; plants, 18 SOIs; Appendix S2). High-resolution data were not available for six SOIs, so coarse-resolution environmental data were also used for all SOIs to produce alternative GLM analyses using the full complement of SOI species richness data available (insects, 29 SOIs; plants, 22 SOIs). Analyses with high-resolution data were preferable for our purposes as the fine spatial resolution of these data allowed for thermal habitat heterogeneity, a measure of niche diversity, across each SOI to be quantified (Appendix S2). Analyses using coarse-scale data were, therefore, used primarily to test the robustness of the high-resolution results and ensure that the removal of SOIs for which high-resolution data were unavailable did not significantly affect GLM outcomes. Human factors, quantified as visitation rank (see Appendix S2 for the procedure used for ranking), were included in introduced species richness models as a proxy for propagule pressure.

Additional GLMs with high-resolution environmental data, corrected for multiple comparisons using the false discovery rate method (Benjamini and Hochberg 1995), were fitted for both indigenous and introduced insects to incorporate potential interactions with vascular plant richness given theoretical expectations of such an association (Strong et al. 1984, Lewinsohn and Roslin 2008) and previous empirical outcomes both for elsewhere (Zhang et al. 2016, Kemp and Ellis 2017) and for the region (Chown et al. 1998) demonstrating such a relationship (sites with vascular plant and high-resolution temperature data, 18 SOIs). The GLMs with high-resolution environmental data were also repeated with the Antarctic Peninsula site excluded to determine whether the inclusion of this continental site affected the overall trends (results presented in Appendix S3: Table S3). Global Moran’s I tests were used to test for significant spatial autocorrelation in GLM residuals, using the spdep package (version 0.5-88; Bivand and Piras 2015). If spatial autocorrelation was significant in the GLM residuals, Moran’s eigenvectors, which explicitly model the spatial signal, were added as predictors in the GLM (results presented in Appendix S4). Pseudo-$r^2$ values were calculated to evaluate the amount of species richness variation explained by the fitted GLMs.

**Species turnover**

Zeta diversity ($\zeta$) metrics (Hui and McGeoch 2014) were used to explore species turnover in the SOI indigenous and introduced insect and vascular plant communities. Zeta diversity is the average number of species shared by $i$ sites. Zeta diversity values for orders greater than 2 provide information on the turnover of widespread species in the community (i.e., those shared by more than two sites), whereas $\zeta_2$ and other pairwise turnover metrics are biased toward turnover in rare and endemic species with limited distributions (Hui et al. 2018). Zeta diversity values for each focal group were calculated for $\zeta$ orders 1 to 5 ($\zeta_1$–$\zeta_5$) using the zeta.decline.mc function in the zetadiv package in R (version 1.1.1, Latombe et al. 2018). Zeta diversity values were not calculated for $\zeta$ orders > 5 because few SOI species are shared across six or more islands; therefore, $\zeta$ values for all focal groups approach zero at higher orders. Eleven insect species were recorded as indigenous on some islands and introduced on others in the database (see species list in Appendix S5). To prevent the over-estimation of species turnover, these species were excluded from the introduced species dataset for the turnover analysis. To enable the comparison of groups with differing species richness, all $\zeta$ values were normalized by dividing each sample $\zeta_i$ value by the corresponding value of $\zeta_1$ (i.e., sample species richness). For sites with no shared species, normalized zeta values were set to zero (i.e., sites with no shared species are perfectly dissimilar) to maintain the same number of sites across analyses of indigenous and introduced species. The maximum number of samples from which $\zeta$ diversity was calculated was set as 10,000 in each analysis.

To understand turnover variation among the communities, the distance decay function from
the zetadiv package was used to calculate the spatial distance decay of $\zeta$ diversity for $\zeta_2$ and $\zeta_3$. Here, we expected that the spatial distance decay of $\zeta$ diversity might be faster for indigenous relative to introduced species. Our expectation is based on the fact that rates of dispersal to these islands, where investigated, are much higher for introduced than for indigenous species for insects (Gaston et al. 2003), and are expected to be so for plants (compare Lee and Chown 2009 with Bartish et al. 2012, Lehnebach et al. 2017), despite much variation in dispersal strategies among the members of these taxa (Carlquist 1965). For each taxonomic group and pairwise combination of SOIs, sample $\zeta$ turnover values (i.e., the number of species shared between two sites) were grouped into ten discrete 1000 km distance intervals by the distance between sites, for sites separated by up to 10,000 km. For each distance interval, mean $\zeta_2$ diversity values were calculated. This categorization was applied because the sample distance decay data were highly zero-inflated and over-dispersed because many SOI pairs ($\zeta_2$) and triplets ($\zeta_3$) share no insect or vascular plant species. This analysis was repeated for $\zeta_3$, where sample turnover values were grouped into distance intervals by the mean distance between three sample sites. Linear regression models were then fitted to explore relationships between the mean number of shared species between sites ($\zeta$) and distance between sites. Chord plots were drawn using the circlize package (Gu et al. 2014) to illustrate spatial patterns of pairwise turnover.

Next, given the proposal that differences in the form of $\zeta_i$ decline might provide a useful first indication of whether turnover is largely stochastic or underpinned principally by niche differentiation processes (Hui and McGeoch 2014), exponential (abbreviated as exp) and power-law (abbreviated as pwl) models were fitted to observed $\zeta_i$ decline curves for each of the four focal communities. Akaike Information Criterion weights ($w_0$:AIC; qpcR package, ver. 1.4-0; Spiess 2014) were calculated to estimate the relative likelihood that either the exponential or power-law model best described the relationship between $\zeta$ diversity and sample number, $i$.

Where $\zeta_i$ decline takes an exponential form, stochastic assembly processes could potentially be expected to dominate turnover among communities, whereas its power-law form might reflect predominance of niche differentiation processes in driving turnover (see Hui and McGeoch 2014, Hui et al. 2018). In an exponential model, the chance of observing a species at an additional site does not depend on the species’ current occupancy (scale independency), whereas a power-law model best fits data where species have different probabilities of occupying an additional site (e.g., commonly occurring species are more likely to occur in a new site than rare species; see Hui and McGeoch 2014). The rate of $\zeta_i$ decline with sample number ($i$) also provides information on the prevalence of widespread versus rare species in a given community (Hui and McGeoch 2014). A relatively steep rate of $\zeta_i$ decline infers that proportionally few species in the community are shared across multiple sites, whereas a shallow rate of decline describes communities with many species common to multiple sites.

All analyses were conducted in R statistical software (version 3.3.3; R Core Team 2017).

RESULTS

Species richness

Distance to the nearest continent (a measure of isolation) and mean LST (a proxy for energy availability and environmental stress) were significant predictors of indigenous insect and indigenous vascular plant richness (Table 1). Indigenous species richness declined with increasing island isolation and was positively correlated with mean LST. When indigenous vascular plant richness was added to the insect model, plant richness was significantly correlated with indigenous insect richness (Table 1). Human visitation frequency was a significant predictor of introduced insect and introduced vascular plant species richness (Table 1). Frequently visited SOIs (i.e., those with the lowest visitation rank) had higher alien richness than those visited less frequently. Introduced insect richness was also positively related to mean LST (Table 1). Island area and LST range, both proxies for niche diversity, were not significant in the high-resolution models for any of the four focal communities (Table 1). Models using high-resolution data explained much of the variation in
species richness (pseudo-$r^2$: 0.65–0.86; Table 1). Spatial autocorrelation was significant only in the residuals of the indigenous insect richness model excluding plant richness (Appendix S4: Table S2). When the spatial signal was included in the model, mean LST and corrected island area were significant predictors of indigenous insect richness, with isolation excluded given the incorporation of a spatial vector (Appendix S4: Table S1). In the coarse-resolution models that included the full complement of Southern Ocean Island (SOI) sites with low-resolution climate data, island area was positively correlated with indigenous insect and indigenous vascular plant richness (Appendix S3: Table S1). Removing the continental Antarctic Peninsula site from the high-resolution insect models did not affect the overall species richness trends (Appendix S3: Table S3).

### Species turnover

Indigenous insects had higher rates of species turnover (i.e., lower overall normalized mean $\zeta$ diversity values) across the SOIs, when compared to introduced insects (mean norm. $\zeta$ ± SD: indig. insect: $\zeta_2 = 0.040 \pm 0.11$, $\zeta_3 = 0.004 \pm 0.03$, $\zeta_4 < 0.001 \pm <0.01$, $\zeta_5 < 0.001 \pm <0.01$; alien insect: $\zeta_2 = 0.052 \pm 0.09$, $\zeta_3 = 0.007 \pm 0.02$, $\zeta_4 = 0.001 \pm <0.01$, $\zeta_5 < 0.001 \pm <0.01$). Likewise, indigenous vascular plants had higher rates of species turnover (lower normalized mean $\zeta$ diversity values) than introduced vascular plants, with the exception of $\zeta_2$, where indigenous and introduced plants had, on average, the same number

#### Table 1. Negative binomial generalized linear model outcomes for the relationships between environmental factors and Southern Ocean Island insect and vascular plant richness.

<table>
<thead>
<tr>
<th>Model</th>
<th>df (pseudo-$r^2$)</th>
<th>Predictor</th>
<th>Model coeff.</th>
<th>SE</th>
<th>$z$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Indigenous insects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without indigenous plants</td>
<td>22 (0.65)</td>
<td>Area</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>1.49</td>
<td>0.270</td>
</tr>
<tr>
<td></td>
<td>8.24</td>
<td>Isolation</td>
<td>−0.60</td>
<td>0.14</td>
<td>−4.45</td>
<td>&lt;0.001***</td>
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<td></td>
<td>2.34</td>
<td>Temperature (mean)</td>
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<td>0.03</td>
<td>3.28</td>
<td>0.002**</td>
</tr>
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<td></td>
<td></td>
<td>Thermal heterogeneity</td>
<td>−0.05</td>
<td>0.03</td>
<td>−1.57</td>
<td>0.235</td>
</tr>
<tr>
<td>With indigenous plants</td>
<td>17 (0.86)</td>
<td>Area</td>
<td>&lt;0.01</td>
<td>&lt;0.01</td>
<td>−0.48</td>
<td>&gt;0.999</td>
</tr>
<tr>
<td></td>
<td>8.88</td>
<td>Isolation</td>
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<td>0.13</td>
<td>−2.22</td>
<td>0.053</td>
</tr>
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<td></td>
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<td>Temperature (mean)</td>
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<td>0.03</td>
<td>0.61</td>
<td>&gt;0.999</td>
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<td>0.04</td>
<td>0.86</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Without introduced plants</td>
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<td>Area</td>
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<td>&lt;0.01</td>
<td>−0.54</td>
<td>&gt;0.999</td>
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<tr>
<td></td>
<td>8.88</td>
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<td>0.17</td>
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<td>0.343</td>
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<td>0.04</td>
<td>3.39</td>
<td>0.001**</td>
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<td>With introduced plants</td>
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<td>&lt;0.01</td>
<td>−0.89</td>
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<td>−3.46</td>
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<td>−6.50</td>
<td>&lt;0.001***</td>
</tr>
<tr>
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<td>5.61</td>
<td>Temperature (mean)</td>
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<td>0.03</td>
<td>3.97</td>
<td>&lt;0.001***</td>
</tr>
<tr>
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<td>0.05</td>
<td>1.15</td>
<td>0.250</td>
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<tr>
<td><strong>Introduced plants</strong></td>
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<td></td>
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</tr>
<tr>
<td>17 (0.68)</td>
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<td>&lt;0.01</td>
<td>0.05</td>
<td>0.958</td>
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<td>0.21</td>
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<td>0.262</td>
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<td></td>
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<td><strong>Human visitation</strong></td>
<td>−0.17</td>
<td>0.04</td>
<td>−4.24</td>
<td>&lt;0.001***</td>
</tr>
</tbody>
</table>

Notes: FDR-adjusted $P$ for insect models. $P < 0.05^*$, $P < 0.01^**$, $P < 0.001^***$. Significant terms in bold.
of species shared across two sites (mean norm. \( \zeta \pm SD \): indig. plant: \( \zeta_2 = 0.112 \pm 0.18 \), \( \zeta_3 = 0.031 \pm 0.06 \), \( \zeta_4 = 0.011 \pm 0.02 \), \( \zeta_5 = 0.005 \) \( \pm <0.01 \); alien plant: \( \zeta_2 = 0.112 \pm 0.12 \), \( \zeta_3 = 0.038 \pm 0.04 \), \( \zeta_4 = 0.017 \pm 0.02 \), \( \zeta_5 = 0.010 \pm 0.01 \)). Although indigenous insect and indigenous vascular plant communities are more species rich than their introduced counterparts, when richness was standardized, the indigenous SOI communities had on average higher rates of species turnover than introduced communities. Of the 795 indigenous insect species and 475 indigenous vascular plant species included in this study, only 26 insect (3.27%) and 45 plant (9.47%) species were shared across five or more islands (\( \zeta_3 \)). In contrast, of the 170 introduced insect species and 287 introduced vascular plant species, 24 insects (14.12%) and 44 alien plants (15.33%) were shared across five or more islands.

Overall, indigenous insects and vascular plants had faster rates of distance decay of species similarity than introduced species (Table 2). Across relatively short distances (<2000 km), island pairs shared a greater number of indigenous insect species than introduced insect species (Fig. 1; also see Appendix S6: Figs. S1 and S2). Likewise, proximal islands (<2000 km) shared a greater number of indigenous vascular plant species than introduced plant species. Conversely, introduced insects and vascular plants had slower rates of distance decay (i.e., numbers of introduced insect and vascular plant species shared by two sites (\( \zeta_2 \)) and three sites (\( \zeta_3 \)) were sustained across increasing distances; Table 2; Appendix S6: Figs. S1 and S2). In contrast to the other communities, introduced vascular plant species demonstrated a weak positive relationship between \( \zeta_3 \) similarity and mean distance between sites (Table 2). Islands that are further apart shared on average a greater number of introduced vascular plant species than more proximal island groups (Fig. 1; also see Appendix S6: Figs. S1 and S2).

More indigenous vascular plant species are shared across sites compared with indigenous insect species (Fig. 1). Indigenous and introduced vascular plants had consistently lower species turnover (i.e., higher normalized mean \( \zeta \) similarity values) than indigenous and introduced insect communities, across \( \zeta \) orders 2–5 (Appendix S6: Table S1). Additionally, while there are very few indigenous insects shared across island pairs separated by more than 2000 km, indigenous vascular plants are dispersed across greater distances (Fig. 1). A similar trend was also observed across groupings of three islands (\( \zeta_3 \); Appendix S6: Fig. S2).

The form of \( \zeta_i \) diversity decline with sample number (\( i \)) for indigenous insect communities followed an exponential relationship (Fig. 2; \( w_i \text{AIC: exp.} = 0.87 \), pwl. = 0.13). Conversely, the indigenous and introduced vascular plant communities and introduced insect communities were characterized by a power-law form of \( \zeta_i \) decline (Fig. 2; indig. plant \( w_i \text{AIC:} \exp. = <0.01 \), pwl. = >0.99; alien insect \( w_i \text{AIC:} \exp. = 0.19 \), pwl. = 0.81; alien plant \( w_i \text{AIC:} \exp. = <0.01 \), pwl. = >0.99). Indigenous insect species demonstrated a faster rate of \( \zeta \) decline with sample number (\( i \)) than introduced insect species (Fig. 2). Likewise, indigenous vascular plant species demonstrated a faster rate of \( \zeta \) decline than introduced vascular plants (Fig. 2). Relative to introduced species, few indigenous SOI species are widespread across the region.

**DISCUSSION**

Our findings, based on the most recent survey data and improved empirical information on potential richness correlates, reveal that area is not an important correlate of richness variation across the Southern Ocean Islands (SOIs), but that both temperature and isolation are important. They also substantiate the role of human
Fig. 1. Pairwise similarity of species communities across the Southern Ocean Islands. Chords indicate where species are shared between two sites with the thickness of each chord indicating the number of species. Indigenous insects exhibit localized clustering, while indigenous plants show higher levels of inter-regional similarity. Introduced communities of both taxa exhibit little localized clustering, indicating community connectivity across the study region. Note that a species shared among multiple sites will be counted more than once, so number of species shared is not indicative of site species richness. Sites are organized longitudinally and colored following Appendix S1: Figure S1.
activity for overcoming the significant isolation of the islands and thus influencing introduced species richness. The influence of temperature, the most important potential driver underlying variation in insect richness, once human visitor frequency is taken into account for the introduced species, is similar in form across both the indigenous and introduced insect communities, whereas this is not the case for the vascular plants. Substantial differences in the form and rate of species turnover are also clear among the four communities, reinforcing the idea that they are structured by quite different processes. Indeed, the form of turnover and distance decay was in keeping with our initial predictions that introduced insects and vascular plants should have lower turnover and a slower rate of distance decay than indigenous species.

Across the SOIs, variation in species richness of indigenous vascular plants and indigenous insects is explained by isolation and temperature, with a collinearity between indigenous plant and insect richness variation. These findings are broadly similar to the outcomes of previous investigations of the region (Chown et al. 1998, Selmi and Boulinier 2001). Isolation, however, has come to the fore in these new models, with area being much less important. These findings regarding area are in keeping with earlier discussions of the potential drivers of variation in the region (Gressitt 1970, Abbott 1974, Vernon et al. 1998), but contrast with global findings that identify area as an important variable explaining richness variation (Kreft et al. 2008, Roura-Pascual et al. 2016, Li et al. 2018), and with more restricted studies in the region (Williams 1982). Nonetheless, they are in keeping with expectations of the influence of energy on richness

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**Fig. 2.** Form (a) and rate (b and c) of ζ decline with number of localities (i) for normalized indigenous insect (solid black line; $\zeta = 2.37e^{-1.05i}$), introduced insect (broken red line; $\zeta = 1.13i^{-5.08}$), indigenous plant (broken black line; $\zeta = 1.03i^{-3.27}$), and introduced plant (dotted red line; $\zeta = 0.98i^{-2.89}$) Southern Ocean Island communities (all: $r^2 > 0.99$). Indigenous insects demonstrate an exponential form of ζ decline, whereas indigenous plants and introduced communities demonstrate a power-law form of ζ decline (a).
variation in non-water-limited systems (Wright 1983, Evans et al. 2005a). In the case of indigenous insects, however, it is not yet possible to distinguish the relative roles of indigenous plant richness, temperature, and isolation. Clearly, the latter both influence indigenous plant richness and may therefore be determining insect richness variation indirectly. Theory would certainly support a role for indigenous plant richness in determining insect richness variation (Strong et al. 1984, Lewinsohn and Roslin 2008). The extent to which this is the case on the islands is not entirely clear, however. While herbivorous insects dominate the faunas (Chown and Convey 2016), the majority of species are polyphagous or detritivores (Kuschel 1971, Crafford et al. 1986, Chown 1989, Morrone 2011). Given what is known also of local-scale distributions, it seems likely that a combination of these factors has been important in influencing diversity variation, together with some opportunity for local specialization as a consequence of glacial history (Chown and Convey 2016, Moon et al. 2017).

Human visitation has been identified previously as a factor influencing alien richness variation (Chown et al. 1998) and has been retained here too. These outcomes confirm the importance of human-mediated dispersal as a process influencing the richness of introduced taxa in the region (Gaston et al. 2003, Frenot et al. 2005, Lee and Chown 2009), in keeping with investigations elsewhere showing that for alien community richness, human activity is an especially important driver (Evans et al. 2005b, Hulme 2009, Guo et al. 2018, Li et al. 2018). Importantly, the inclusion of introduced plant richness in the models for variation in introduced insect species richness had little influence on them and was never found to be a significant variable. These findings are in keeping with the generally complex relationships found between introduced plants and insects (Spafford et al. 2013) and suggest that local conditions determining establishment (see also Lee et al. 2009) and propagule pressure are the most significant influences on introduced insect richness variation in the region.

Among the islands investigated here, communities of introduced vascular plant and insect species have lower species turnover (higher mean $\zeta_i$ values), higher inter-island connectivity, and slower rates of distance decay in similarity than their indigenous counterparts (Fig. 1). Thus, while introductions may differentiate SOI communities at a regional ($<2000$ km) scale, they have a homogenizing effect at a macroecological scale (>$2000$ km). This is particularly apparent for introduced vascular plant communities which show an atypical pattern of $\zeta_3$ diversity distance decay (Table 2; Appendix S6: Fig. S2d). Islands separated by great distances share more introduced plant species than more proximal islands. Such a turnover pattern is likely the result of the unequal human visitation and occupancy of the SOIs. Within regional groups, islands are visited at different rates (de Villiers et al. 2006). For example, Tristan da Cunha Island has a permanent human settlement and is far more disturbed by human activity than the nearby islands, Inaccessible and Nightingale. A similar pattern applies to the two islands of the Prince Edward group (Chown and Froneman 2008) and those of the Crozet archipelago (de Villiers et al. 2006). Moreover, the same alien plant species tend to be introduced, either purposefully or accidentally, across the SOIs, whereas alien insects often have more regional introduction origins (Greve et al. 2005) and, therefore, demonstrate a more typical distance decay of similarity (Appendix S6: Fig. S2b).

The exponential form of $\zeta_i$ decline suggests that stochastic processes, such as wind dispersal, might be more significant in determining turnover in indigenous insects than niche-related processes (Hui and McGeoch 2014). Conversely, the power-law forms of $\zeta_i$ decline for indigenous plants, introduced plants, and introduced insects suggest that niche-related processes dominate turnover among these groups, acknowledging that a continuum exists among these processes (Gravel et al. 2006, Latombe et al. 2015). These findings are in keeping with broad-scale and local studies of the groups. For example, niche-related processes have been found to influence diversity patterns for indigenous vascular plants across the region (le Roux et al. 2005, 2013a, Hermant et al. 2013, Lehnebach et al. 2017). Thermal niche-filtering processes also strongly influence introduced insects and other invertebrates (Chevrier et al. 1997, Lee et al. 2009, Lebouvier et al. 2011), and disturbance-resistance and human disturbance patterns strongly affect alien vascular plant communities (Frenot et al. 1998, 2001, le Roux et al.
processes for plants and insects on the islands.

might unveil the importance of different local

interactions that contribute to species sorting are

persal processes likely determine colonization of

human visitors to the region carry high propag-

load (Lee and Chown 2011, Chown et al.

What the underlying drivers are for indigenous insects is not yet fully clear. Stochastic dis-

participants of niche-related processes on the Southern Ocean Islands has not, however,

been presented (Chown and Convey 2016), although the low diversity of insect predators

and parasitoids suggests that some interspecific interactions that contribute to species sorting are

less common in the region than elsewhere (Convey 1996). Our findings suggest much scope for

further testing these tentative hypotheses.

In conclusion, we set out to consider patterns of richness variation and its likely drivers and

patterns of turnover across the Southern Ocean Islands. Our results show that temperature (as a

proxy for energy availability and environmental stress), isolation, and human activity are impor-
tant likely drivers of biodiversity patterns across the region. They also point to interactions

between indigenous vascular plant and insect diversity. The contributions of temperature and

isolation are significant given changing climates and increases in activity across the broader

Antarctic region more generally (Jones et al. 2016, Stewart et al. 2017, IAATO 2018). Moreover,

our outcomes also point to very different processes that might underlie turnover across the

region—highlighting the need for further work, including experimental manipulations, that

might unveil the importance of different local processes for plants and insects on the islands.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2358/full