Effect of grain size on patterns and drivers of plant species richness on a sub-Antarctic island

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Abstract

Environmental and biotic factors drive species richness patterns, but the nature of this relationship can vary with sampling grain. Understanding the scale-dependent effects of these factors is crucial for interpreting species richness patterns in ecosystems experiencing rapid environmental change. We investigated the effects of local environmental drivers on plant species richness at small (1 x 1 m) and large (3 x 3 m) sampling grains, and the factors correlated with differences in richness between the two grains, on a sub-Antarctic island. Broadly, richness was higher in warmer (i.e., lower altitude, north-facing) and wetter (i.e., higher topographic wetness index, lower distance from drainage line) sites, and in more topographically heterogenous (i.e., steeper slopes) sites. Additionally, there was some evidence of competition with a keystone plant limiting species richness, though this was only evident at low elevations. However, the effects of several drivers on richness depended on spatial grain. Differences in species richness between large and small grain sizes were more pronounced at low elevations, indicating that there is more compositional heterogeneity at low altitudes at both grains. Richness was positively related to northness at large grain size but not at small grain size, suggesting that higher northness increases local turnover at a grain size $> 1 \text{ m}^2$. On the other hand, TWI boosted richness at small but not large grains, implying that competition limited coexistence at low TWI, and that higher TWI only resulted in more species coexisting at a grain of 1 m2, while having no effect on richness at large grains. Our study therefore highlights that drivers of plant species richness can vary with sampling grain, suggesting that environmental effects on local species turnover affect richness patterns at different grains. Assessing how the influence of such drivers differ with grain size provides insight into local patterns of species assemblage.

Introduction

Species richness is a widely used biodiversity metric in ecological and conservation studies. It reflects the compositional and organisational structure of communities of living organisms (Hillebrand et al., 2018), and is widely used as an indicator of the conservation value of ecosystems (Shokri and Gladstone, 2013, Capmourteres and Anand, 2016). Species richness shifts relatively predictably in response to changing biotic and abiotic factors in a wide range of organisms (Gaston, 2000, Hillebrand et al., 2018). Understanding such shifts, and the ecological processes associated with them, is fundamental in appreciating spatial diversity patterns (Myers et al., 2000, Hanson et al., 2020) and consequently predicting the impacts of global environmental change (Kreft and Jetz, 2007, Lopez et al., 2022).

Several factors have been proposed to explain patterns of species richness. For example, good support exists for the water-energy hypothesis (Currie et al., 2004, Field et al., 2005, Kreft and Jetz, 2007, Hawkins et al., 2003) which states that at high latitudes, ambient energy restricts species richness, whereas at low latitudes, water limitation becomes more important (Hawkins et al., 2003, Hufnagel and Mics, 2022). Plant physiological limitations, such as tolerance to desiccation and frost, can further constrain species distributions and richness (Currie et al., 2004, Hawkins et al., 2003). Resource, environmental or topographic heterogeneity can result in higher microhabitat diversity, allowing for the coexistence of more species (Pausas and Austin, 2001, Stein et al., 2014). Nutrient availability generally shows a hump-shaped relationship with species

richness, as few species tolerate nutrient-deficient environments, more species tolerate intermediate nutrient levels, and a smaller number of competitive species become dominant and suppress other species at high nutrient levels (Graham and Duda, 2011, Mittelbach et al., 2001). Biotic interactions, such as competition, mutualism and facilitation, can also limit, or increase, species richness (Van Dam, 2009, le Roux et al., 2012, Marques Dracxler and Kissling, 2022, Stachowicz, 2001).

Given the scale-dependent nature of biodiversity (Chase et al., 2018, Spake et al., 2021), it is crucial for studies examining diversity patterns and drivers to account for scale. Indeed, patterns and drivers of species richness can be influenced by spatial grain, i.e. the measurement unit or area within which species occurrences are quantified (Whittaker et al., 2001). Species richness is the count of species per unit area, and therefore, the choice of grain size may affect the species richness measured (Bhatta et al., 2018). The underlying processes that shape species assembly of plant communities may differ between different grain sizes (Martínez-Villa et al., 2020), resulting in different biotic and abiotic factors regulating species richness at different grain sizes (Kallimanis et al., 2007). For instance, Powell et al. (2013) demonstrated that invasive plant species significantly reduce native biodiversity at small spatial grains, with the effect diminishing at larger grains. On the other hand, butterfly species richness in Borneo was minimally affected by forest disturbance from logging at smaller grains, but the effect was more pronounced at larger sampling grains (Dumbrell et al., 2008). Therefore, to enhance our understanding of these patterns, some studies argue in favour of adopting a multi-scale approach, recognising the multidimensional nature of biodiversity (Chase et al., 2018, Spake et al., 2021).

Spatial grain has a significant influence on the patterns and drivers of species richness in areas with high beta diversity. For instance, in environments with high local beta diversity, even a small reduction in grain size can lead to a reduction in species richness per sampling unit (Tuomisto et al., 2017). In contrast, when local beta diversity is low, there is more stability and consistency in species composition across spatial scales. Thus, in environmentally heterogeneous landscapes, which often exhibit higher beta diversity, there is a notable advantage to adopt a multi-scale approach to understand biotic and abiotic factors shaping species richness. For instance, the productivity-species richness relationship is notably affected by sampling grain size (Whittaker et al., 2001). Coarse grains exhibit a monotonically positive relationship, whereas finer grains show a hump-shaped pattern, with maximum species richness at intermediate productivity (Virtanen et al., 2013). This phenomenon is attributed to be diversity likely being higher in productive environments, which explains why species richness increases with productivity at larger, but not smaller, grains. Based on these observations, the importance of spatial grain in explaining patterns of species richness can be expected to depend on the landscape's characteristics. In relatively homogeneous landscapes with gradual environmental changes, spatial grain will have less influence. Conversely, in heterogeneous environments that offer a greater number of microhabitats, spatial grain becomes more important. Therefore, assessing drivers of richness at different scales can help explain variation in the relative importance of other variables in determining species richness in a given area (Radinger et al., 2015).

Traditionally, small grain studies investigate patterns and drivers of local variations in species richness, while larger grains take into consideration accumulation of species at local scales and are mostly used in understanding broader patterns and drivers of diversity (Tuomisto et al., 2017). At large grain sizes (several kilometres) macroclimatic variables are usually the best predictors of richness variation; at medium grain sizes (typically, kilometres to meters) topographic factors most strongly influence patterns of species richness (Keil and Chase, 2019, Kalkhan and Stohlgren, 2000). Larger grains are generally favoured for studies assessing species richness patterns over large sampling area, where the large sampling unit effectively averages over within-grain heterogeneity (Sreekar et al., 2018). At smaller grains (meters to centimetres) other factors such as soil nutrition and vegetation characteristics (including type, growth form, and trait characteristics) can become important (Kalkhan and Stohlgren, 2000, Keil and Chase, 2019). The importance of biotic interactions is also scale-dependent, typically being considered particularly influential at smaller grain sizes (Huston, 1999, McGill, 2010, Willig et al., 2003). At smaller grain, the competitive effects of dominant species can be more pronounced, leading to exclusion or suppression of subordinate species. In contrast, at large grain, the effects of competition might be diluted, allowing a more diverse array of species to coexist and

exploit a broader range of resources (Wisz et al., 2013, Araújo and Rozenfeld, 2014).

Performing ecological studies at different grains increases understanding of the spatial component in the underlying drivers of species richness (He et al., 2002, Otypková and Chytry, 2006). While the choice of grain size affects the estimation of species richness (Bhatta et al., 2018, Tuomisto et al., 2017), it also potentially affects the type of factors influencing the observed species richness and the magnitude of the factors' effects in any ecosystem (Chase and Knight, 2013). Therefore, grain size must be carefully chosen and accounted for in ecological studies as it can impact the observed patterns. Understanding the scale-dependent nature of biodiversity and accounting for spatial grain in studies are crucial for a comprehensive interpretation of species richness patterns and drivers.

Cold ecosystems are important areas of conservation, largely due to their strong vulnerability to changing environmental conditions (Olson and Dinerstein, 2002, Bennett et al., 2015). These systems generally support fewer species than warmer systems (Hawkins et al., 2003) and possess weaker ecosystem resilience to changes (Boelter and Mueller, 2016), and poorer biotic resistance to invasions (Pertierra et al., 2022). Energy and water dynamics play a large role in species richness for cold climates; as energy inputs are low, there are fewer species, allowing only low-growing plants (Walker et al., 2001, Marini et al., 2008). Thus, plant species richness patterns usually follow a simple energy-water relationship gradient (Hawkins et al., 2003). Biotic interactions, such as herbivory, also play a role in shaping species richness in cold environments (Olofsson et al., 2009). For example, reindeer decrease plant species richness in low-productivity sites but increase richness in productive sites (Sundqvist et al., 2019). Moreover, biotic interactions between species of a community (or guild) can shift from competitive to facilitative along environmental gradients; this can significantly impact richness patterns in colder environments (Choler et al., 2001). Understanding drivers of species richness, particularly how grain size can affect such drivers, is of particular importance in colder regions because they are disproportionately affected by global climate changes, and often harbour specialised biodiversity adapted to cold environments.

Research on species richness patterns and drivers in cold environments has been strongly concentrated in the northern hemisphere, with temperate forest biomes in North America and Europe being the primary focus of most publications (Lawler et al., 2006, Wells et al., 2022, Mott and Clarke, 2018, Bennett and Classen, 2020). Less research has investigated patterns of species richness in the cold ecosystems of the southern hemisphere, particularly the sub-Antarctic and Antarctic ecosystems (Lawler et al., 2006, Bennett and Classen, 2020), with only some exceptions (Chown et al., 1998, Griffiths and Waller, 2016, Rozzi et al., 2008). Therefore, the aim of this study was to assess the drivers of vascular plant species richness on the sub-Antarctic Marion Island, and to assess whether grain size is important in determining patterns and drivers of species richness.

Materials and Methods

Study area

The Prince Edward Islands (PEIs) consist of Marion Island (46deg 54' S, 37deg 45' E; area: c. 270 km²) and the smaller Prince Edward Island (46deg 38' S, 37deg 57' E area: c. 45 km²), which are located in the Southern Indian Ocean. The islands are of volcanic origin, and are believed to be approximately half a million years old (Chown and Froneman, 2008). Marion Island, the higher of the two islands, reaches an altitude of 1230 m (Chown and Froneman, 2008). The PEIs are home to a considerable population of globally threatened seabird species, and several plant and insect species (Crawford et al., 2003, Jones and Ryan, 2010, Chown and Convey, 2016, Chau et al., 2020). The islands have two major biomes: the sub-Antarctic tundra, located in lowland areas, and sub-Antarctic polar desert, which lacks vascular plants and is limited to higher elevations (Smith and Mucina, 2006). The tundra vegetation has been broadly divided into three mapping units: Coastal Zone, Inland Vegetation and Fellfield Vegetation (van der Merwe et al., 2023).

The PEIs have an oceanic climate with average annual temperatures of approximately 6.5degC, annual precipitation of around 2000 mm, high humidity and strong winds (Chown and Froneman, 2008). Climatic conditions on the islands are changing rapidly in step with global climate change, with temperatures having

increased by 1.2degC and precipitation decreased by 25% since the 1960s (le Roux and McGeoch, 2008, Smith, 2002). Additionally, invasion by some plant and animal species is transforming some of these islands' landscapes, especially on the more heavily impacted Marion Island (Gremmen et al., 1998, McGeoch et al., 2015, Houghton et al., 2019). Biologically, the PEIs constitute a fairly simple system, with few vascular plant species (around 22 native and 6 persistent invasive aliens) (Chau et al., 2020, Greve et al., 2017). Because of these factors, as well as the island's isolation, Marion Island is a good model system for studying various ecological processes.

Data

Vegetation surveys were carried out on Marion Island from 2018 to 2019. A total of 464 vegetation plots were placed throughout the island in a random stratified design to represent each of the geologies (i.e., red scoria, black lava and grey lava) (Rudolph et al., 2021). Sampling was carried out in 3 x 3 m plots and in the centrally nested 1 x 1 m plots (Appendix Figure A1). The identity of all vascular plant species in the main and nested plot was recorded. *Azorella selago* was excluded from the vascular plant species richness count in each plot, but its presence was recorded as its occurrence would be used as a predictor of species richness in subsequent analyses.

A digital elevation model (DEM, produced at 1 m resolution but resampled to 20 m here) was obtained from the surveyor general (South Africa). DEMs describe terrain and elevation for a given area, enabling studies on habitat suitability, landscape connectivity, hydrological processes, and climate-related ecological patterns. They prove especially valuable in challenging, inaccessible locations on Marion Island, where physical measurements are difficult to obtain. Using this DEM, the following parameters were extracted for each plot: elevation, topographical wetness index (TWI) which was used as a proxy for soil moisture, hillshade, slope, northness, distance to the nearest drainage line, distance to the coast, and elevation. TWI was calculated using the SAGA GIS tool (Bohner and McCloy, 2006): TWI = ln (AS/tan β) where AS is the drainage area (in m²) and β is the local slope gradient (in %) (Beven and Kirkby, 1979). Slope and hillshade were calculated with the tools Slope and Hillshade respectively in ArcMap 10.8.1. The hillshade function is a proxy for potential incident solar radiation (Najafifar et al., 2019). Northness was calculated using the formula northness = cos(aspect) in radians, where aspect was calculated with function Aspect in ArcMap from the DEM. The distance from the nearest drainage line was calculated using the topographic database from the DEM and the distance to the coast was calculated using the Euclidian Distance tool in ArcMap.

A layer of mean land surface temperature was created by averaging monthly temperatures from Leihy et al. (2018). Because temperature was not available for some coastal cells, these were interpolated using the Kriging downscaling method. This temperature layer was then resampled using the bilinear technique to 20 x 20 m resolution, and the mean temperature for each plot extracted. Geology was extracted from Rudolph et al. (2021). Distance of plots to the nearest research base or field hut was calculated as a proximity for the intensity of human activities.

Although elevation can be used as a proxy for temperature, we included both temperature and elevation in our models since elevation also accounts for a broad range of factors beyond temperature alone. For example, elevation on Marion Island may also influence factors such as habitat structure, incident solar radiation, and soil characteristics, which can impact species richness independently of temperature. Moreover, as elevation increases, the influx of biotic inputs from mammal and bird species on the island diminishes, resulting in soils at higher elevations exhibiting reduced nutrient content (Haussmann et al., 2013).

Predictor variables were selected as proxies for groups of species richness drivers: mean temperature, elevation, distance to coast, northness and hillshade as proxies for temperature and energy inputs; TWI and distance to nearest drainage line as proxies for water availability; slope, geology, and distance to nearest base/hut as proxies for topographical and environmental heterogeneity; and presence/absence of A. *selago* as a biotic interaction, as *Azorella selago*, a keystone species on the island, serves as a favourable establishment site for other plant species, particularly in higher elevations and on dry, nutrient-poor soils – areas other plant species would not colonise independently (le Roux and McGeoch, 2004, le Roux and McGeoch,

2010).

Statistical analysis

Predictor variables were tested for collinearity. Distance to coast, which was highly correlated to elevation (r = 0.75), was excluded from further analyses (Appendix Table A1).

The native species richness and alien species richness per plot at grain sizes of 9 m² and of 1 m² were response variables in statistical models. We included ecologically relevant interaction terms in our analyses. Underlying geology can influence soil moisture (Huang et al., 2016, Kopec, 1995), and the effect of elevation on species (Gerdol et al., 2017). Furthermore, we expected that northness and elevation interact, since north-facing slopes receive more sunlight in the southern hemisphere (Saremi et al., 2014), which might particularly be beneficial to high elevation sites which are generally cooler. Hillshade could affect soil moisture, with wetter soils occurring in areas receiving less solar radiation (Najafifar et al., 2019). In addition, elevation also affects the biotic interaction effect of *A. selago* on co-existing species, as the cushion plant facilitates plants at high elevations but competes with them at low elevations (le Roux and McGeoch, 2010). Therefore, the interaction terms geology*TWI, geology*elevation, northness*elevation, hillshade*TWI, and presence/absence of *A. selago* *elevation were included.

We also investigated the factors correlated with the *difference* in species richness between the large (9 m^2) and small (1 m^2) spatial grains (henceforth ' Δ_{9-1} ') to assess what may be shaping differences in patterns and drivers of richness at different grain sizes. To calculate the difference in species richness between grain sizes, the species richness of the nested central 1 m^2 subplot was subtracted from that of the larger 9 m^2 plot. We then tested which of the above predictor variables and the interaction terms were related to Δ_{9-1} . By identifying the drivers of the difference in richness between large and small grain, we could determine whether local turnover occurs and what factors could be contributing to turnover.

We tested for spatial autocorrelation in the response variables using Moran's I. Moran's I values were small, but significant, suggesting some spatial autocorrelation (Table A2). Therefore, to account for spatial autocorrelation, we opted for simultaneous auto-regressive models (SAR) (Kissling and Carl, 2008), particularly the SAR_{err} model. We tested the effects of the explanatory variables on species richness at each grain size, and on Δ_{9-1} , using SAR models. These statistical analyses were run assuming a Poisson distribution. Best subset models with the best set of predictors were created using the dredge function from the MuMIn package, with model selection based on the lowest Akaike information criteria (AIC) values (Barton and Barton, 2015).

Alien species, especially where they are abundant and/or have high cover, may mask the effects of environmental drivers on native species richness. This prompted us to (a) initially repeat the above analyses only using a subset of the plots where alien species were absent. However, on Marion Island, alien species tend to be more prevalent in coastal areas with biotic inputs, than in inland areas or areas far from any bird or seal colonies (Haussmann et al., 2013, Figure 1). Most coastal plots had some alien species present (Figure 1); therefore, this analysis led to us excluding many of the coastal plots with the highest native species richness. We thus present these results in the supplementary materials but do not further discuss them. Instead, we repeated these analyses using a subset of the data where (b) alien cover was less than 10% in the plots, assuming that such low alien cover is unlikely to significantly affect patterns of richness of native plants.

For alien species, analyses were conducted on the full dataset, and also for a subset of plots where (c) at least one alien species was present because we assumed that some alien species may not have reached niche equilibrium with the environment (i.e., range occupancy of all suitable sites) on Marion Island (le Roux et al., 2013b) and that if there is at least one alien species in a plot, it is likely that more alien species may have had time to colonise the plot.

All statistical analyses were run in R, version 4.2.0, using functions from the spdep (Bivand et al., 2006), car (Fox et al., 2012), mass (Ripley et al., 2013), nlme (Pinheiro et al., 2017), ape (Paradis and Schliep, 2019), MuMIn (Barton and Barton, 2015) and ggplot2 (Wickham et al., 2021) packages.



Figure 1: Elevation map of Marion Island showing the position of sampling plots. Plots in which only native species (blue), and plots in which native and alien species (red) were recorded are shown.

Results

Out of the 464 plots sampled, 95 plots contained alien species (Figure 1). At the large grain, maximum species richness was six per plot (mean = 2.81 ± 1.33), whilst at the smaller grain it was five native species per plot (mean = 1.99 ± 1.03). The maximum native Δ_{9-1} was four species per plot (mean = 0.82 ± 0.87). On the other hand, maximum alien species richness per plot was three at the large grain (mean = 0.23 ± 0.49), and two at the small grain (mean = 0.13 ± 0.35). The maximum alien Δ_{9-1} was two (mean = 0.10 ± 0.34) (Figure 2).



Figure 2: Species richness frequency per plot: \mathbf{a} and \mathbf{b} , native and alien species respectively at 3×3 m grain; \mathbf{c} and \mathbf{d} , native and alien species respectively at 1×1 m grain; \mathbf{e} and \mathbf{f} , native and alien species difference

in richness between grains (Δ_{9-1}) respectively. The dotted lines show the mean richness values for native (blue) and alien (red) plants.

Drivers of native species richness

At large grain $(3 \times 3 \text{ m})$, northness and slope were significantly positively related to native species richness, and distance to nearest drainage negatively influenced species richness. Native species richness decreased with elevation, but at low elevation, richness was higher in the presence than absence of *A. selago*, and at high elevation lower in the presence than in the absence of *A. selago* (Figure 3, Table 1a).

At small grain $(1 \ge 1 \le n)$, species richness decreased with elevation, while slope and TWI were positively related to species richness (Figure 3, Table 1a).

No further action was taken for the subset of the plots where alien species were absent (results shown in Table A3). Results were similar at both large and small grains for native richness when only plots with alien cover less than 10% were considered, with some exceptions (highlighted in Table A4, Figure A2, e.g., richness decreased with hillshade at both large and small grains and the effect of northness on richness was dependent on elevation).

Both elevation and TWI negatively influenced native Δ_{9-1} , whilst northness and presence of *A. se-lago* positively influenced native Δ_{9-1} (Figure 3, Table 1b).

Similar results were obtained for the dataset of plots with alien cover < 10%. However, higher native Δ_{9-1} occurred in distances closer to drainage lines compared to further away only when alien cover was below 10% (Table A4).

Drivers of alien species richness

At large grains, alien species richness declined with increasing elevation, but absence of A. selago led to higher alien species richness compared to its presence at low elevation (with this effect reversed at higher elevations) (Figure 4, Table 1c). Furthermore, distance to nearest drainage positively influenced, whilst northness negatively influenced, alien species richness at large grains (Figure 4, Table 1c). Alien species richness in grey-bedded ash geology was significantly higher than in other geologies (Figure 4, Tables 1c, A5). However, since there were very few plots in this geology (N = 5), the effect of geology on alien species richness can be considered negligible.

At small grain, the presence of $A.\ selago$, northness and elevation negatively affected alien species richness whilst distance to nearest drainage positively affected alien species richness (Figure 4, Table 1c).

When analyses were repeated for only plots with at least one alien species (i.e., alien species richness [?] 1), only northness was a significant driver at large grain, having a negative impact on alien species richness. At small grain, A. selago and northness became unimportant when alien richness was at least one, while elevation and distance to the nearest drainage exhibited similar effects as those observed in the main dataset (Table A6).

Both elevation and temperature negatively affected alien Δ_{9-1} , and the rare, grey-bedded ash geology had a significantly higher alien Δ_{9-1} for the full dataset (Figure 4, Table 1d).

Elevation had a similar effect on alien Δ_{9-1} in the subset of the data with at least one alien species present in each plot (Table A6). Distance to nearest drainage had a negative effect on alien Δ_{9-1} in the dataset of plots with at least one alien species present, despite not having an effect in analyses of the full dataset (Table A6).

Table 1: Results from simultaneous auto-regressive models with a Poisson distribution showing the predictors of vascular plant species richness at the large (9 m²) and small (1 m²) grain sizes and at the difference in richness between the two grain sizes (Δ_{9-1}) for both native and alien species.

a. Native species

9 m ² grain	9 m² grain
Variable	Estimate
Intercept	2.938
Presence of A. selago	0.654
Distance to nearest drainage	-0.001
Elevation	-0.002
Northness	0.283
Slope	0.015
A. $selago^*$ Elevation	-0.002
β. Διφφερενςε ιν σπεςιες ριςηνεσς βετωεεν γραινς φορ νατιε σπεςιες (νατιε $\Delta_{9\text{-}1})$	β. Διφφερενςε
Variable	Estimate
Intercept	1.088
Presence of A. selago	0.171
Elevation	-0.001
Northness	0.135
Topographical wetness index	-0.047
c. Alien species	c. Alien species
9 m^2 grain	$9 \text{ m}^2 \text{ grain}$
Variable	Estimate
Intercept	-0.512
Presence of A. selago	-0.996
Distance to nearest drainage	0.001
Elevation	-0.009
Geology	N/A
Northness	-0.238
A. $selago^*$ Elevation	0.005
δ. Διφφερενςε ιν σπεςιες ριςηνεσς βετωεεν γραινς φορ αλιεν σπεςιες (αλιεν $\Delta_{9-1})$	δ. Διφφερενςε
Variable	Estimate
Intercept	0.144
Elevation	-0.001
Mean Temperature	-0.260
Geology	N/A





Discussion

In this study, we demonstrate that plant species richness on Marion Island is related to ecological variables that are recognised to be associated with richness elsewhere, while also showing that the patterns and drivers of richness vary with spatial grain. The drivers of the *difference* in species richness between the two considered grains provide insight into the role of local species turnover in community assemblage patterns.

Native species

Elevation was negatively correlated with native species richness at both grains on Marion Island. Highaltitude environments, both on Marion Island and elsewhere, typically harbour fewer native species and are unable to support non-native species that originated from warmer climates (Chown et al., 2013, Lembrechts et al., 2016). Furthermore, the windy conditions prevalent in these high-altitude areas may limit some species (Momberg et al., 2021). Additionally, the soils at higher altitudes are shallower (or absent) and generally more nutrient poor on this geologically young volcanic island, due to lower biotic inputs (Haussmann et al., 2013).

The effect of elevation on richness was dependent on the presence of the keystone cushion plant, Azorella selago, at the large grain. Cushion plants are common in cold and windy regions, where they modify microhabitats to the benefit of other species growing within them (le Roux and McGeoch, 2010, Badano et al., 2010, Van der Merwe et al., 2021, Reid et al., 2010). At low altitudes ($c \cdot < 250$ m a.s.l.), richness was higher where A. selago occurs. Conversely, at high altitudes where A. selago is often the dominant or even only plant species, fewer species occurred in the presence than the absence of this species. The results of our study align with those of Raath-Krüger et al. (2019), who observed a positive impact of A. selago on the occurrence and cover of some native species at low altitudes. This suggests that, as environmental stressors become increasingly severe, biotic interactions become less important and environmental factors emerge as primary limiting factors (e.g. Raath-Krüger et al., 2019, Louthan et al., 2018).

Higher native richness in north-facing slopes could be due to that aspect receiving the most potential direct sunlight (Måren et al., 2015). Higher richness on warmer north-facing surfaces is likely necessitated by the high precipitation levels on Marion Island (c. 2000 mm annually, (le Roux and McGeoch, 2008)). In more arid regions where soil moisture is limiting, higher incident radiation can result in lower soil moisture and, as a result, lower richness (Najafifar et al. 2019). These findings further support the water-energy hypothesis, indicating the importance of energy over water in moist high latitude and high altitude areas (Hawkins et al., 2003, Hufnagel and Mics, 2022).

Most vascular plants' ecological limits are influenced by water availability; even in wet environments like Marion Island, plant distributions can be affected by water (le Roux et al., 2013a). As such, in our study, plots with high TWI at small grain, and plots closer to drainage lines (i.e., wetter plots) at both grains, contained more native species. Although TWI is typically only modestly correlated with actual soil moisture, it is a good proxy in the absence of field measurements (le Roux et al., 2013a, Riihimäki et al., 2021). Similarly, distance to nearest drainage is a useful proxy for plant-available water because the draining potential of the soil is a function of vertical rise and horizontal flow (Marshall et al., 1996). Our study, therefore, underscores the importance of soil moisture for plant species richness, which has sometimes been considered less essential in cold and wet environments.

Native richness was higher for both grains on steeper slopes. High environmental heterogeneity, as found on steeper slopes, can increase habitat complexity. Complex habitats offer a variety of microhabitats, refuges, and opportunities for species to specialise in different ecological roles or exploit specific resources, resulting in higher species richness (Tuomisto et al., 2017, Stein et al., 2014, Kreft and Jetz, 2007, Stein and Kreft, 2015).

Alien species

Alien plant richness, which is considerably lower than native plant richness on Marion Island at the scales studied here, was partly affected by energy availability. Positive correlations between northness and alien species richness at both grains provide additional evidence of the importance of sunlight and warmth availability for plant growth (Måren et al., 2015). Furthermore, alien species richness was higher in low elevation areas, characterised by warmer temperatures, nutrient-rich conditions, and pronounced animal and human activities (Haussmann et al., 2013, le Roux et al., 2013b, Greve et al., 2017). However, richness increased with distance to drainage areas, likely due to the island's high precipitation levels being sufficient to support the island's alien species.

Biotic interactions seem to play a minor role in alien species richness on the island. At the large grain, alien species appeared to compete with *A. selago* at low elevations but were facilitated at high elevations. However, with alien species rare at high elevations, there is much uncertainty around the facilitative effects of *A. selago* on alien species at high altitudes. Studies in similar climates have shown cushion plants facilitating non-native species at higher elevations where they would not be able to occur in the absence of this interaction (e.g., Badano et al., 2015, Cavieres et al., 2008, Arredondo-Núñez et al., 2009).

Most alien species on Marion Island still have localised distributions, suggesting they are still in a lag phase and could potentially extend their ranges in future (Greve et al., 2017, Crooks et al., 1999, le Roux et al., 2013b). If this is the case for many of the non-native species, then the patterns of alien richness observed in this study could be expected to change in the future, particularly as warming temperatures may remove some climatic barriers to the spread of localised alien species.

Effects of grain size on patterns and drivers of species richness

The differences in drivers between small and large grains provide insight into the manner in which the plant communities on Marion Island assemble.

Higher elevations supported lower native plant richness at both large and small grain. This suggests that at both grains, elevation restricts the number of species that can coexist, and that as altitude decreases, more species coexist at both grains (Figure 5a). Because richness increases for both grain sizes with decreasing elevation, higher values of native Δ_{9-1} at low than high elevations is probably due to the higher overall number of species at low elevations (Gremmen and Smith, 2008). High altitude environments, characterised by colder temperatures, support a limited range of plant species (Figure A3), and therefore have limited potential for turnover.

Northness increased species richness at the large but not small grain in our study. Native Δ_{9-1} was higher in warmer north-facing plots than cooler south-facing plots. This suggests that, while greater northness creates warmer and more sunny environments that may benefit plants, and thus increasing the local species pool, it only leads to increased species coexistence at large grains (Figure 5b). Therefore, higher sun exposure does not lead to more species coexisting within 1 m², possibly due to the influence of other limiting factors such as competition for nutrients (e.g., Cramer et al., 2022) restricting the number of species that can coexist per unit area. However, at higher northness, more species accumulate within the 9 m² plot, indicating species turnover between small and large grains.

Native richness increased with TWI at small, but not large, grains; and native Δ_{9-1} decreased with increasing TWI. Therefore, increasing TWI allowed more species to co-exist, but only at small grain. At large grain, higher TWI did not result in higher richness, suggesting that the species that are added at smaller grain in high TWI environments already occur at the large grain. As a result, when TWI is low, increasing the grain size increase species richness, indicating local turnover within the 9 m² grain. However, when TWI is high, this trend is not observed as more species already coexist at the smaller grain; increasing grain size does not introduce new species (Figure 5c). Thus, in drier plots richness may be limited by competitive exclusion at small grain size, but the effects of competitive exclusion do not act (or are diluted) at the large grain size, allowing for more species to coexist and exploit a broader range of available resources.

Finally, native Δ_{9-1} was higher (i.e., more species at large than at small grain) in the presence of *A. selago* than in its absence. This may be because *A. selago* increases the complexity of the plot as conditions on and at the edge of the cushion differ to those in the adjacent open habitat, but this effect is only obvious

at large grain. Alternatively, at small grains, the cushion plant's expansive growth form, which can cover most of or an entire plot, may limit other plants through competition, but only at small grain (Nyakatya and McGeoch, 2008). Another possible explanation could simply be that the environment that is suitable for *A. selago* is also suitable for other species, and these species thus co-exist at large grains, but less so at small grains where *A. selago*outcompetes other plants with its cushion growth form.

Possibly due to most alien species in this study being in their lag phase with the potential for increased spread, the effect of grain size on environmental drivers of alien richness is less pronounced. Given the unfavourable conditions for alien species at high elevations, resulting in lower alien richness, alien Δ_{9-1} was also lower there. In addition, grey-bedded ash geology significantly increased alien Δ_{9-1} , but only five plots had this geology. Therefore, the effect of geology on alien Δ_{9-1} is considered negligible in this system.



Figure 5: A representation of the effect of grain size on drivers of native plant species richness on Marion Island: a.elevation, b. northness, and c. topographical wetness index (TWI). Effect of each of the significant predictors of Δ_{9-1} for native species is shown: the green and yellow lines show the effect of the predictor variable on species richness at large and small grains respectively. The effect of grain size on richness is further illustrated in schematics showing how richness changes in large and associated nested small plots along gradients of each of the significant predictors of Δ_{9-1} . Coloured letters represent different species. Only species that do not occur in the small plot but occur in the large plot are added to the area of the large plot.

Conclusion

The results of this study show that assessing species richness patterns at multiple grains provides insight into community assembly processes. Variables can exhibit scale-dependent relationships with plant species richness, with some variables having detectable effect on species richness at finer grain sizes, while the influence of others may only become more apparent at coarser grain. Ultimately, using several grains increases understanding of the spatial component of species assemblage patters in response to underlying drivers of species richness.

Author Contributions

Joshua Tsamba: Conceptualization (equal); data curation (equal); formal analysis (lead); investigation (equal); methodology (equal); writing – original draft (lead); writing – review and editing (lead). Michelle Greve: Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (lead);

investigation (equal); methodology (equal); project administration (lead); supervision (lead); writing – original draft (supporting); writing – review and editing (supporting). Peter C. le Roux: Investigation (supporting); project administration (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (supporting). Luis R. Pertierra: Formal analysis (supporting); methodology (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (supporting). Bongekile S. Kuhlase: Investigation (supporting); data curation (equal); writing – review and editing (supporting).

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Data Availability Statement

The data that supports the findings of this study are available in the supplementary material of this article.

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Appendix



Figure A1 : Layout of the main plot $(9m^2)$ and nested plot $(1m^2)$. Species richness was measured for the central 1 x 1 m, and for the larger 3 x 3 m grain size. Additionally, the difference in richness between large and small grain size was calculated (Δ_{9-1}) .



Figure A2: The effect of northness at changing elevation on native species richness at the small (1 x 1 m) grain in plots in which alien species cover was less than 10 %. (The long-dashed line "Mean" signifies the mean species richness for each combination of northness and elevation). Model parameters are shown in Table A4.



Figure A3: The upper limit of elevation for native and alien vascular plants recorded for Marion Island in the study. The red dotted line represents the maximum elevation sampled where vascular plants were present.

Table A1: Pearson correlation matrix of continuous predictor variables initially considered for analyses. Distance to coast was excluded from analyses due to high correlation with elevation (bold font).

Variable	Aspect	Elevation	Distance to coast	Distance to drainage line	Hillshade	I
Aspect	1	-0.03	-0.22	-0.03	0.28	_
Elevation		1	0.75	-0.02	-0.12	(
Distance to coast			1	-0.14	-0.11	(
Distance to drainage line				1	0.02	(
Hillshade					1	-
Mean Temperature]
Northness						
Slope						
TŴI						
Distance to base						

Table A2: Moran's I test of spatial autocorrelation for the response variables.

Grain size	Species	P-value
$3 \ge 3 \le (9 \le m^2)$	Native	< 0.001*
$1 \ge 1 \le (1 \le m^2)$	Native	< 0.001*
$3 \ge 3 \le (9 \le m^2)$	Alien	$< 0.001^{*}$
$1 \ge 1 \le (1 \le m^2)$	Alien	< 0.001*
Δ_{9-1}	Native	0.007^{*}
Δ_{9-1}	Alien	0.138

Table A3: Results from simultaneous autoregressive models with a Poisson distribution showing the predictors of vascular plant species richness at the large (9 m²) and small (1 m²) grain sizes, and at the difference in richness between the two grain sizes (Δ_{9-1}) for native species in plots in which alien species are absent.

a. 9 m^2 grain

Estimate
4.691
-0.001
-0.004
-0.007
0.350
0.017
b. 1 m^2 grain
Estimate
2.980
-0.001
-0.004
-0.006
0.028

Slope	0.018
Topographical wetness index	0.074
Elevation*Northness	0.001
ς. Διφφερενςε ιν σπεςιες ριςηνεσς βετωεεν γραινς (νατιε $\Delta_{9-1})$	ς. Δ ιφφερενζε ιν σπεζιες ριζηνεσ
Variable	Estimate
Intercept	1.108
Distance to nearest drainage	-0.001
Northness	0.123
Topographical wetness index	-0.035

Table A4: Results from simultaneous autoregressive models with a Poisson distribution showing the predictors of vascular plant species richness at the large (9 m^2) and small (1 m^2) grain sizes, and at the difference in richness between the two grain sizes (Δ_{9-1}) for native species in plots in which alien species cover was less than 10 %.

a. 9 m² grain

Variable	Estimate
Intercept	Intercept
Presence of A. selago	Presence of A. selago
Distance to nearest drainage	Distance to nearest drainage
Elevation	Elevation
Hillshade	Hillshade
Northness	Northness
Slope	Slope
b. 1 m ² grain	
Variable	Estimate
Intercept	Intercept
Elevation	Elevation
Hillshade	Hillshade
Northness	Northness
Slope	Slope
Topographical wetness index	Topographical wetness index
Elevation*Northness	Elevation*Northness
ς. Διφφερενςε ιν σπεςιες ριςηνεσς βετωεεν γραινς (νατιε $\Delta_{9-1})$	ς. Δ ιφφερενςε ιν σπεςιες ριςηνεσ
Variable	Estimate
Intercept	Intercept
Distance to nearest drainage	Distance to nearest drainage
Elevation	Elevation
Northness	Northness
Topographical wetness index	Topographical wetness index

Table A5: Tukey multiple comparisons of means post hoc tests at 95% family-wise confidence level for geology at the large 9 m^2 grain for alien species.

Geology Type	Difference in means	Lower confidence interval	Upper confidence int
Grey-bedded Ash - Black Lava	1.043	0.276	1.809
Grey Lava - Black Lava	0.059	-0.074	0.193
Recent (Post 1980) - Black Lava	-0.024	0.698	0.641
Scoria - Black Lava	0.101	-0.146	0.348

Geology Type	Difference in means	Lower confidence interval	Upper confidence inte
Wind-blown Ash - Black Lava	0.035	-0.561	0.631
Grey Lava - Grey-bedded Ash	-0.984	-1.753	-0.214
Recent (Post-1980) - Grey-bedded Ash	-1.067	-2.075	-0.058
Scoria - Grey-bedded Ash	-0.942	-1.740	-0.145
Wind-blown Ash – Grey-bedded Ash	-1.008	-1.972	-0.044
Recent (Post-1980) - Grey Lava	-0.083	-0.752	0.586
Scoria - Grey Lava	0.041	-0.215	0.298
Wind-blown Ash - Grey Lava	-0.024	-0.624	0.576
Scoria - Recent (Post-1980)	0.124	-0.576	0.824
Wind-blown Ash - Recent (Post 1980)	0.059	-0.827	0.944
Wind-blown Ash - Scoria	-0.066	-0.701	0.569

Table A6: Results from simultaneous autoregressive models with a Poisson distribution showing the drivers of vascular plant species richness at the large (9 m^2) and small (1 m^2) grain sizes, and at the difference in richness between the two grain sizes (Δ_{9-1}) for alien species in plots in which at least one alien species richness was present.

a. 9 m^2 grain

Variable	Estimate
Intercept	1.1492
Northness	-0.102
b. 1 m ² grain	
Variable	Estimate
Intercept	0.604
Distance to nearest drainage	0.001
Elevation	-0.001
ς. Διφφερενςε ιν σπεςιες ριςηνεσς βετωεεν γραινς φορ αλιεν σπεςιες (αλιεν $\Delta_{9\text{-}1})$	ς. Δ ιφφερενςε
Variable	Estimate
Intercept	0.601
Distance to nearest drainage	-0.001
Elevation	0.001