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Fine Scale Patterns and Drivers of Plant Species Richness on a Sub-Antarctic Island

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ABSTRACT

Aims: Cold environments, such as polar systems, are highly vulnerable to global change drivers such as climate change and invasive species. Therefore, it is essential to assess what drives the diversity of native and invasive species in these systems.

Location: We investigated what drives native and alien plant species richness on sub-Antarctic Marion Island and determined the scale-dependence of these drivers.

Methods: Native and alien plant species richness was surveyed at “small” ($1\,m^2$) and “large” ($9\,m^2$) sampling grains. Difference in richness between the two sampling grains was calculated to assess how local turnover contributes to species assemblage. The factors driving richness at both grains, and the differences in richness between the two grains, were analysed using simultaneous auto-regressive models. Drivers related to energy and environmental heterogeneity were correlated with native richness, whilst drivers related to productivity were related to alien richness.

Results: Biotic interactions with a cushion plant facilitated native richness, but restricted alien richness at low elevations. Further, some drivers of richness depended on spatial grain. Native richness was positively related to northness at large, but not small grain size, suggesting that higher northness increases local turnover at a grain size $>1\,m^2$. On the other hand, topographical wetness index (TWI) boosted native richness at small but not large grains, implying that competition for water limits coexistence at low TWI (i.e., low moisture availability) only at small grain. Differences in native species richness between large and small grain sizes were more pronounced at low elevations, suggesting higher compositional heterogeneity at low altitudes.

Conclusions: Our study highlights that drivers of plant species richness in a polar ecosystem differ between native and alien plant species. Additionally, the effects of some drivers on richness differ between sampling grains, and considering these differences provides insight into drivers of local patterns of species assemblage.

1 | 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 an indicator of the conservation value of ecosystems (Shokri and Gladstone 2013; Capmourteres and Anand 2016). Understanding the ecological processes and drivers associated with species richness patterns 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).

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Several drivers have been proposed to explain patterns of species richness. Good support exists for the water-energy hypothesis (Hawkins et al. 2003; Currie et al. 2004; Field et al. 2005; Kreft and Jetz 2007) which states that richness increases with energy, specifically through greater water availability and heat. Under this hypothesis, ambient temperature restricts species richness at high latitudes, 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 some species' distributions and thus richness (Hawkins et al. 2003; Currie et al. 2004). 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 in cold climates often shows a hump-shaped relationship with species richness: few species can survive low-nutrient conditions, richness peaks at intermediate levels, and competitive species dominate, reducing diversity at high nutrient levels (Mittelbach et al. 2001; Graham and Duda 2011), although this is debated (Fraser et al. 2015). Further, the intermediate disturbance hypothesis predicts a unimodal relationship between disturbance and species richness, particularly for plant species (Moi et al. 2020; Downey et al. 2023). Biotic interactions, such as competition, mutualism, and facilitation, can also limit or increase species richness (Stachowicz 2001; Van Dam 2009; le Roux et al. 2012; Marques Dracxler and Kissling 2022).

Understanding the patterns and drivers of species richness is critical in cold regions, including polar areas, tundra, and alpine environments. Cold ecosystems are important areas for conservation, largely due to their vulnerability to changing environmental conditions (Olson and Dinerstein 2002; Bennett et al. 2015). Cold systems generally support fewer species than warmer systems (Hawkins et al. 2003) and thus possess weaker ecosystem resilience to changes (Boelter and Mueller 2016) and poorer biotic resistance to invasions (Pertierra et al. 2022). Consequently, species adapted to colder climates face heightened vulnerability to habitat change and the threat of extinction (Crawford 2008; Urban 2015; Stubbs et al. 2018).

Similar to other environments, abiotic factors such as energy and water dynamics largely determine richness patterns in cold climates, with plant species richness usually following a simple energy–water relationship gradient (Walker et al. 2001; Hawkins et al. 2003; Marini et al. 2008; Mucina 2023). Additionally, resource and environmental heterogeneity, including variations in microclimate brought about by topographic heterogeneity (e.g., variations in snow depth and snow duration) and heterogeneity in soils (e.g., variation in stability due to freeze-thaw processes), increase richness at fine scales (Valentine and Binkley 1992; Gough et al. 2000; le Roux, Aalto, et al. 2013; Suvanto et al. 2014; Niittynen et al. 2020). Moreover, biotic interactions can provide valuable resources in determining plant species richness in cold environments. For instance, biotic interactions such as facilitation or competition can shape the species distributions and assemblages in these systems (Kikvidze et al. 2011; Lee et al. 2019). Biotic interactions between species of a community can shift from competitive to facilitative along environmental gradients (Raath-Krüger et al. 2019), significantly impacting species ranges and, as a result, richness patterns in colder environments (Choler et al. 2001). Therefore, a wide suite of biotic and abiotic factors must be considered when examining spatial variation in species richness in cold, high latitude and/or altitude sites.

One of the biggest threats to polar systems are invasive species (Frenot et al. 2005; Leihy et al. 2023). Native plants in cold climates have evolved specialised adaptations—such as frost tolerance, resistance to desiccating winds, and survival in highly seasonal light, intermittent water, and short growing seasons—to endure cold climates (Billings and Mooney 1968; Alberdi et al. 2002; Chwedorzewska 2009; Cavieres et al. 2016), whereas many alien plants in polar regions originate from milder temperate zones (Convey et al. 2006; Greve et al. 2017, 2020). Consequently, alien species often possess traits that differ from those of native species (Mathakutha et al. 2019), enabling them to exploit unoccupied niches within cold climates, facilitating their successful proliferation in such regions. Given the physiological differences between native and alien plants, it is probable that the factors influencing the richness patterns of native and invasive species in cold climate regions differ. For example, whilst native species richness may be better adapted to withstand the harsh environment of cold regions, alien species—often more ruderal—may be more limited by resource availability (Galera et al. 2018; Mathakutha et al. 2019; Rew et al. 2020). Therefore, understanding the patterns and drivers of both native and alien species in polar regions is crucial for managing and preserving ecosystem integrity, especially in the face of climate change and the potential spread of alien plants, which could disrupt the delicate balance of these ecosystems (Convey 2010; Greve et al. 2020).

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 spatial scale, particularly grain size, i.e., the measurement unit or area within which species occurrences are quantified (Whittaker et al. 2001), at which species richness is quantified. 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). Because the choice of grain size affects estimation of species richness (Tuomisto et al. 2017; Bhatta et al. 2018), it can also affect which environmental factors are identified as drivers of species richness (and the strength and nature of their influence on species richness; Chase and Knight 2013). The underlying processes that shape the 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 diminished at larger grains. Additionally, the importance of biotic interactions for species richness is typically stronger at smaller grain sizes (Huston 1999; Willig et al. 2003; McGill 2010). 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). Therefore, to enhance our understanding of the drivers of species richness, some studies argue for adopting a multi-scale approach, recognising the multidimensional nature of biodiversity (Chase et al. 2018; Spake et al. 2021). Furthermore, performing ecological studies at different sampling grains can also increase our understanding of spatial variation in the underlying drivers of species richness (He et al. 2002; Otypková and Chytry 2006).

When patterns and drivers of richness differ between spatial grains, this is due to the occurrence of local spatial turnover in species composition. Spatial turnover refers to change in species composition between neighbouring locations in a geographic area (Yuan et al. 2016). Where local turnover is high, even a small reduction in grain size can lead to a reduction in species richness per sampling unit (Tuomisto et al. 2017). In contrast, where local turnover is low, higher stability and consistency in species composition exists across different grain sizes (Figure 1). By assessing what drives *differences* in richness between grain sizes, we can thus obtain insight into the drivers of local species turnover, i.e., turnover within the larger grain size. This, in turn, can provide information on which factors allow coexistence of species at large grain size but prevent it at small grain sizes. Thus, in environmentally heterogeneous landscapes, which often exhibit higher turnover, there is a notable advantage to adopt a multi-scale approach to understand biotic and abiotic factors shaping species richness.

Most research on terrestrial species richness patterns and drivers in cold environments has been conducted in the northern hemisphere, with temperate forest biomes in North America and Europe being the primary focus of most publications (Lawler et al. 2006; Mott and Clarke 2018; Bennett and Classen 2020; Wells et al. 2022). Less is known about 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 some exceptions (e.g., Chown et al. 1998; Rozzi et al. 2008; Griffiths and Waller 2016). Therefore, in this study, we assess at a local scale the patterns and drivers of native and alien vascular plant species richness on sub-Antarctic Marion Island to assess how drivers of species richness vary with sampling grain size and to understand what drivers of local turnover drive differences in richness between grain size. To address this, the richness of both native and alien plant species on sub-Antarctic Marion Island was assessed at two nested sampling grains, and the factors influencing richness at both grains, as well as the differences in richness between the two grains (as a proxy of turnover), were evaluated.

2 | Materials and Methods

2.1 | Study Area

Marion Island (46°54′ S, 37°45′ E; area: *c.* 270 km^2) is located in the Southern Indian Ocean. The island is of volcanic origin and is believed to be approximately half a million years old

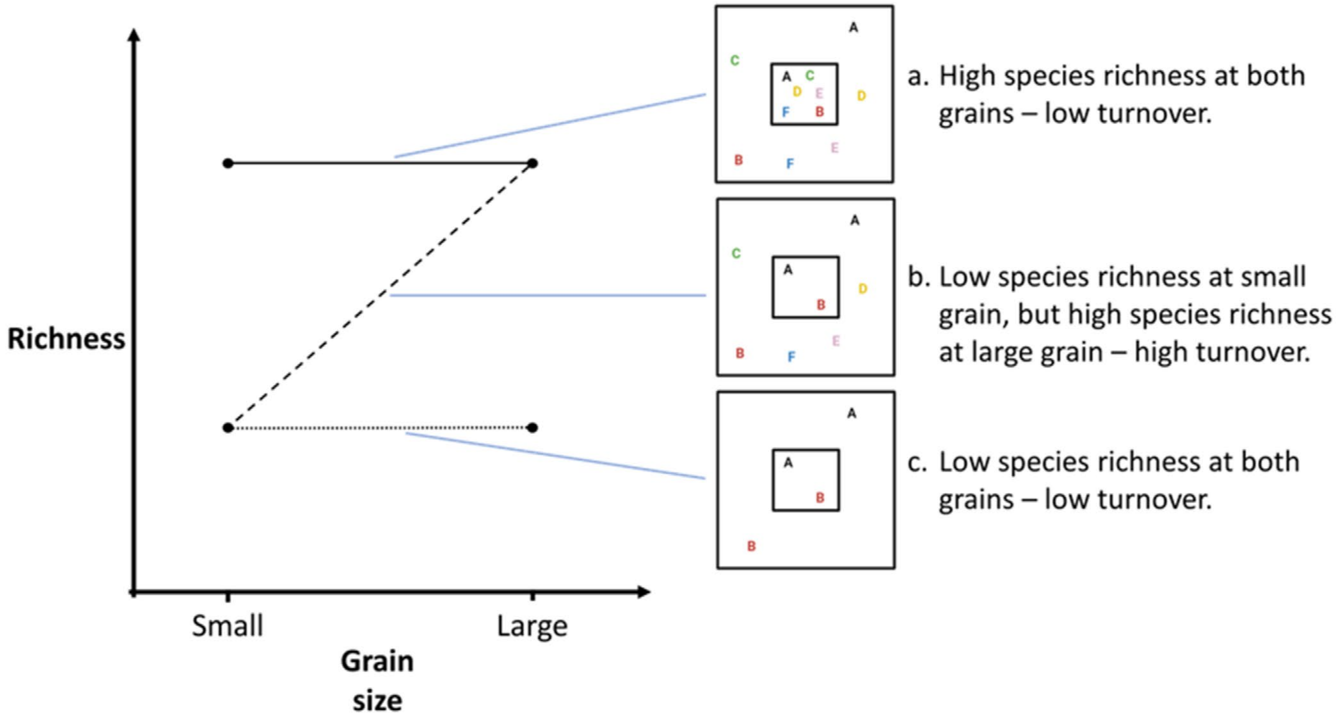


FIGURE 1 | A schematic illustrating the relationship between grain size and species richness across different turnover scenarios. (a) High richness at both small and large grains with low local turnover between the small and the larger grain; (b) low richness at small grains but high richness at large grains due to high local turnover (i.e., new species are added when increasing the sampling grain) between the small and the large grain; and (c) low richness at both small and large grains with no local turnover between the small and the larger grain. Each letter represents a different species. Whilst richness for the large grain size includes both the species in the large and small grain plot, we represent all species that occur only in the small plot within the confines of the small plot, and all the species that occur in the large plot (including the nested small plot) in the space between the small and large plot.

(Chown and Froneman 2008). It reaches an altitude of 1230 m a.s.l (Chown and Froneman 2008). Marion Island is home to a large 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). It supports 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).

Marion Island has an oceanic climate with average annual temperatures of approximately 6.5°C, annual precipitation of around 2000 mm, high humidity, and strong winds (Chown and Froneman 2008). Climatic conditions on the island are changing rapidly in step with global climate change, with temperatures having increased by 1.2°C and precipitation decreased by 25% since the 1960s (Smith 2002; le Roux and McGeoch 2008). Additionally, invasion by plant and animal species is transforming some of this island's landscapes (Gremmen et al. 1998; McGeoch et al. 2015; Houghton et al. 2019). Biologically, Marion Island constitutes a fairly simple system, with few vascular plant species (of which 21 are native and six persistent invasive aliens; Greve et al. 2017; Chau et al. 2020). The keystone plant, *Azorella selago* is widespread across the island; it is also a nurse plant for several insect and epiphyte species and is thought to play a facilitative role in supporting other plant species (le Roux and McGeoch 2004, 2010). Because of the biological simplicity of Marion Island, its well-understood biota, and its isolation, it is a good model system for studying ecological processes.

2.2 | 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 (Rudolph et al. 2021). Plant species richness was quantified in 3×3 m plots and in the centrally nested 1×1 m plots (Appendix S1). These grain sizes were selected because “small” grains, ranging from 1 and 4 m^2, and “large” grains, up to 9 m^2, have also been used in herbaceous surveys of tundra vegetation surveys (Theodose and Bowman 1997; Gough et al. 2000; Pajunen et al. 2008; Salminen et al. 2023). Because of the low species richness of the island, the grain sizes captured sufficient richness for both native and alien species (Appendix S2). The identity of all vascular plant species was recorded in all plots. In addition, the percentage cover of all alien species was recorded. Though the presence of *A. selago* was recorded, it was excluded from the vascular plant species richness count in each plot. This is because *A. selago* is a keystone species on Marion Island which can facilitate but also outcompete other species (Hugo et al. 2004; le Roux and McGeoch 2004, 2010; Raath-Krüger et al. 2019) and its occurrence was therefore used as a predictor of species richness in analyses.

A number of predictor variables for vascular plant species richness were obtained. A digital elevation model (DEM, produced at 1 m resolution but resampled to 20 m using the bilinear technique) was obtained from Rudolph et al. (2021). DEMs describe terrain and elevation for a given area, enabling studies of habitat suitability, landscape connectivity, hydrological processes, and climate-related ecological patterns. They are especially valuable in providing geo-spatial information in challenging, inaccessible locations such as Marion Island, where physical measurements are difficult to obtain across the entire extent of the island. Using this DEM, the following parameters were extracted for each plot: elevation, topographical wetness index (TWI), hillshade, slope, northness, distance to the nearest drainage line, distance to the coast, and elevation. TWI was calculated using the SAGA GIS tool (Böhner and McCloy 2006): $\text{TWI} = \ln(\text{AS}/\tan\beta)$, where AS is the drainage area (in m^2) and β is the local slope gradient (in %; Beven and Kirkby 1979). TWI is a proxy for soil moisture (Riihimäki et al. 2021). Slope and hillshade were calculated with the tools Slope and Hillshade, respectively, in ArcMap 10.8.1. The slope tool identifies the steepness of a terrain, with lower values indicating flatter terrains, and higher values steeper areas. Steep slopes tend to have lower water retention than flatter terrains but exhibit greater habitat heterogeneity, providing numerous niches for species (see Cramer et al. (2022) for evidence from Marion Island). Hillshade function is a proxy for potential incident solar radiation (Najafifar et al. 2019) and therefore is expected to correlate with local temperature and evaporation, both important factors influencing plant composition and richness patterns (Najafifar et al. 2019). Northness was calculated using the formula $\text{northness} = \cos(\text{aspect})$, where aspect was calculated with the function Aspect in ArcMap from the DEM. Northness quantifies a slope's orientation, with high values of northness representing north-facing slopes. In the southern hemisphere, north-facing plots receive more direct sunlight and are therefore typically warmer than south-facing plots. The distance to the nearest drainage line was calculated using the topographic database from the DEM. Distance to nearest drainage line was used as 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). Distance to the coast was calculated using the Euclidean Distance tool in ArcMap. Plots closer to the coast serve as indicators of nutrient availability, as coastal areas receive greater biotic inputs from marine mammal and bird species (Smith 2008; Haussmann et al. 2013).

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 resampled using the bilinear technique to a 20×20 m resolution.

Geology was extracted from a geo-rectified spatial geodatabase and map of Marion Island's glacial geomorphology which was mapped from high-resolution satellite imagery onto a digital surface model (DSM) with a 1×1 m cell resolution from Rudolph et al. (2021) and resampled to 20×20 m using the majority technique. The island's three primary geological formations—black lava, grey lava, and red scoria—exhibit distinct properties that can impact plant richness: black lava, being more nutrient-rich, contrasts with the less fertile and shallower grey lava, whilst scoria, characterised by its porous nature, is unstable and exhibits the lowest water retention properties (Boelhouwers et al. 2008).

Distance of plots to the nearest research base or field hut was calculated using the Euclidian Distance tool in ArcMap as a surrogate for the intensity of human activities.

The above predictor variables were selected as proxies for groups of variables known to drive species richness (Hawkins et al. 2003): mean temperature, elevation, distance to coast, northness and hillshade as proxies for temperature and solar energy inputs; TWI and distance to nearest drainage line as proxies for water availability; slope and geology as proxies for topographical and environmental heterogeneity; distance to nearest base/hut as a proxy for human activity (likely particularly important for alien species); and the occurrence of *A. selago* as an important biotic interaction. 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: it influences habitat structure, with higher elevations likely to feature rockier terrain and sparse vegetation (Smith and Mucina 2006); and soil characteristics, with low elevation areas typically having deeper, nutrient-rich soils due to a high influx of biotic inputs from mammal and bird species compared to higher elevation areas (Smith 2008). These factors can impact species richness independently of temperature.

2.3 | Statistical Analysis

The native species richness and alien species richness per plot at grain sizes of $9\,\mathrm{m}^2$ and of $1\,\mathrm{m}^2$ were response variables in statistical models. An additional response variable, the *difference* in species richness between the large ($9\,\mathrm{m}^2$) and small ($1\,\mathrm{m}^2$) spatial grains (henceforth '$\Delta_{9\text{-}1}$') was calculated for both native and alien species by subtracting the species richness of the nested central $1\,\mathrm{m}^2$ subplot from that of the larger $9\,\mathrm{m}^2$ plot. $\Delta_{9\text{-}1}$ is a measure of the local species turnover, i.e., how many new species are added from small to large grain size. Thus, by assessing what drives $\Delta_{9\text{-}1}$, we could assess what variables could be contributing to local turnover. Large values of $\Delta_{9\text{-}1}$ indicate high local turnover, whilst small values indicate little to no turnover.

Predictor variables were tested for collinearity. Distance to coast, which was highly correlated with elevation ($r = 0.75$), was excluded from further analyses (Appendix S1). We included ecologically-relevant interaction terms in our statistical models. Underlying geology can influence soil moisture (Kopec 1995; Huang et al. 2016), and the effect of elevation on species (Gerdol et al. 2017). Furthermore, 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 coexisting 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 tested for spatial autocorrelation in the response variables using Moran's *I*. Moran's *I* values were small but significant, suggesting some spatial autocorrelation (Appendix S2). Therefore, to account for spatial autocorrelation, we opted for simultaneous auto-regressive models (Kissling and Carl 2008). For all six response variables, a full model was run with all predictor variables (mean temperature, slope, TWI, northness, hillshade, elevation, distance to the nearest drainage line, distance to nearest base/hut, presence/absence of *A. selago*, geology, geology*elevation, hillshade*TWI, northness*elevation, presence/absence of *A. selago**elevation, and geology*TWI). These statistical analyses were run assuming a Poisson distribution. Best subset models 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). Therefore, our final models only included the best subset of predictors, with all the selected predictors considered to be strongly related to response variables.

Initial models were run on the full dataset of all plots, separately for native and alien species. However, 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 initially consider repeating the analyses of native richness and $\Delta_{9\text{-}1}$ 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 2); therefore, this analysis was not run. Instead, we repeated these analyses using a subset of the data where alien cover was less than 10% in the plots, assuming that such low alien cover is unlikely to strongly affect patterns of richness of native plants.

For models assessing alien richness and $\Delta_{9\text{-}1}$, we analysed a subset of plots where 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, Ramaswiela, et al. 2013) and that if there is at least one alien species in a plot, it is likely that other alien species would have had time to colonise the plot.

The same predictor variables were used for analyses at both grain sizes (1 and $9\,\mathrm{m}^2$). The reason for this was because most data, which were largely obtained from spatial datasets that have been issued at a resolution coarser than that at which vegetation plots were surveyed, were not available at both grain sizes, but also because drivers of species richness are often obtained from spatial datasets that are available at grain sizes that are coarser than the grain size at which sampling is conducted and yet are still considered informative.

All statistical analyses were run in R, version 4.2.0 (R Core Team 2020), using functions from the spdep (Bivand et al. 2006), car (Fox et al. 2012), mass (Ripley et al. 2013), nlme (Pinheiro

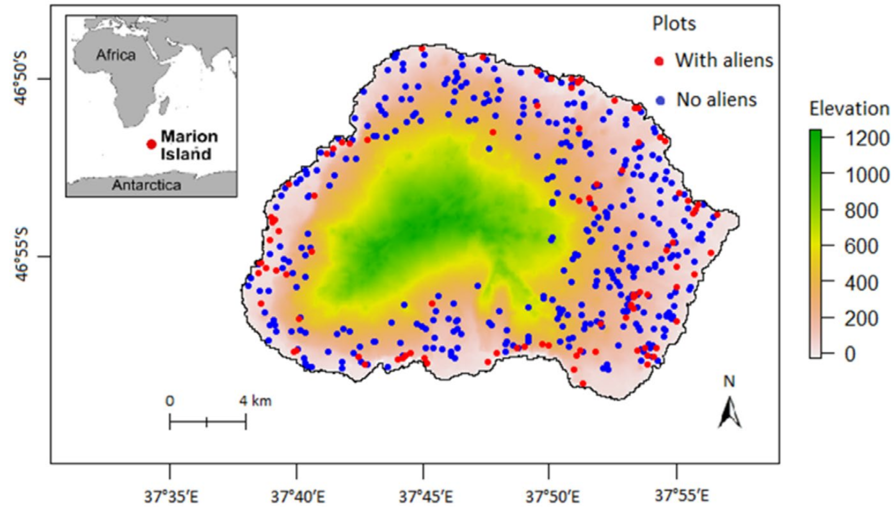


FIGURE 2 | The location of Marion Island (inset) and the island's elevation map showing the position of sampling plots ($n = 464$). Plots in which only native species (blue) and plots in which native and alien species (red) were recorded are shown.

et al. 2017), ape (Paradis and Schliep 2019), MuMIn (Barton and Barton 2015), and ggplot2 (Wickham et al. 2021) packages.

3 | Results

A total of 20 vascular plant species were observed in our study, of which five were alien. Out of the 464 plots sampled, 95 contained alien species (Figure 2). At the large grain, maximum native species richness was six species per plot (mean ± SD = 2.81 ± 1.33), whilst at the smaller grain it was five native species per plot (mean ± SD = 1.99 ± 1.03). The maximum native $\Delta_{9\text{-}1}$ was four species per plot (mean ± SD = 0.82 ± 0.87). Maximum alien species richness per plot was three species at the large grain (mean ± SD = 0.23 ± 0.49) and two species at the small grain (mean ± SD = 0.13 ± 0.35). The maximum alien $\Delta_{9\text{-}1}$ was two species (mean ± SD = 0.10 ± 0.34; Appendix S3), and most of the plots ($n = 424$) had alien cover < 10% (Appendix S4).

3.1 | Drivers of Native Species Richness

For the full dataset, at a large grain ($9\,\text{m}^2$), northness and slope were positively related to native species richness, and distance to the nearest drainage line negatively influenced species richness. The interaction between elevation and *A. selago* presence was included in the best subsets model: 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 ($1\,\text{m}^2$), species richness decreased with elevation, whilst the presence of *A. selago*, slope, and TWI were positively related to species richness (Figure 3, Table 1a).

Results were similar at both large and small grains for native richness when only plots with alien cover < 10% were considered, with some exceptions (highlighted in Appendix S3, Appendix S5); e.g., richness decreased with hillshade at both large and small grains and the effect of northness on richness was dependent on elevation at small grain.

Both elevation and TWI were negatively correlated with native $\Delta_{9\text{-}1}$, whilst northness and presence of *A. selago* positively influenced native $\Delta_{9\text{-}1}$ (Figure 3, Table 1a).

Similar results to the full dataset were obtained for the dataset of plots with alien cover < 10%. However, higher native $\Delta_{9\text{-}1}$ occurred at distances closer to drainage lines only when alien cover was below 10% (Appendix S3).

3.2 | Drivers of Alien Species Richness

For the full dataset, at large grains, alien species richness declined with increasing elevation, but at low elevation richness was higher in the absence of *A. selago*, whilst at high elevations richness was similar in the presence and the absence of *A. selago* (Figure 4, Table 1b). Distance to nearest drainage was positively correlated with alien species richness at large grains (Figure 4, Table 1b). Alien species richness in grey-bedded ash geology was significantly higher than in other geologies (Figure 4, Table 1b; Appendix S4). 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, alien species richness declined with elevation, but elevation interacted with the presence of *A. selago*: at low elevations richness was higher in the absence of *A. selago* than in the presence of *A. selago* (Figure 4, Table 1b). Northness was negatively correlated with alien species richness whilst distance to nearest drainage line positively affected alien species richness (Figure 4, Table 1b).

When analyses were repeated for only plots with at least one alien species present (i.e., alien species richness ≥ 1), only northness was included in the best subset model at a large grain, having a negative correlation with alien species richness. At small grain, richness was higher in the presence of *A. selago*, whilst

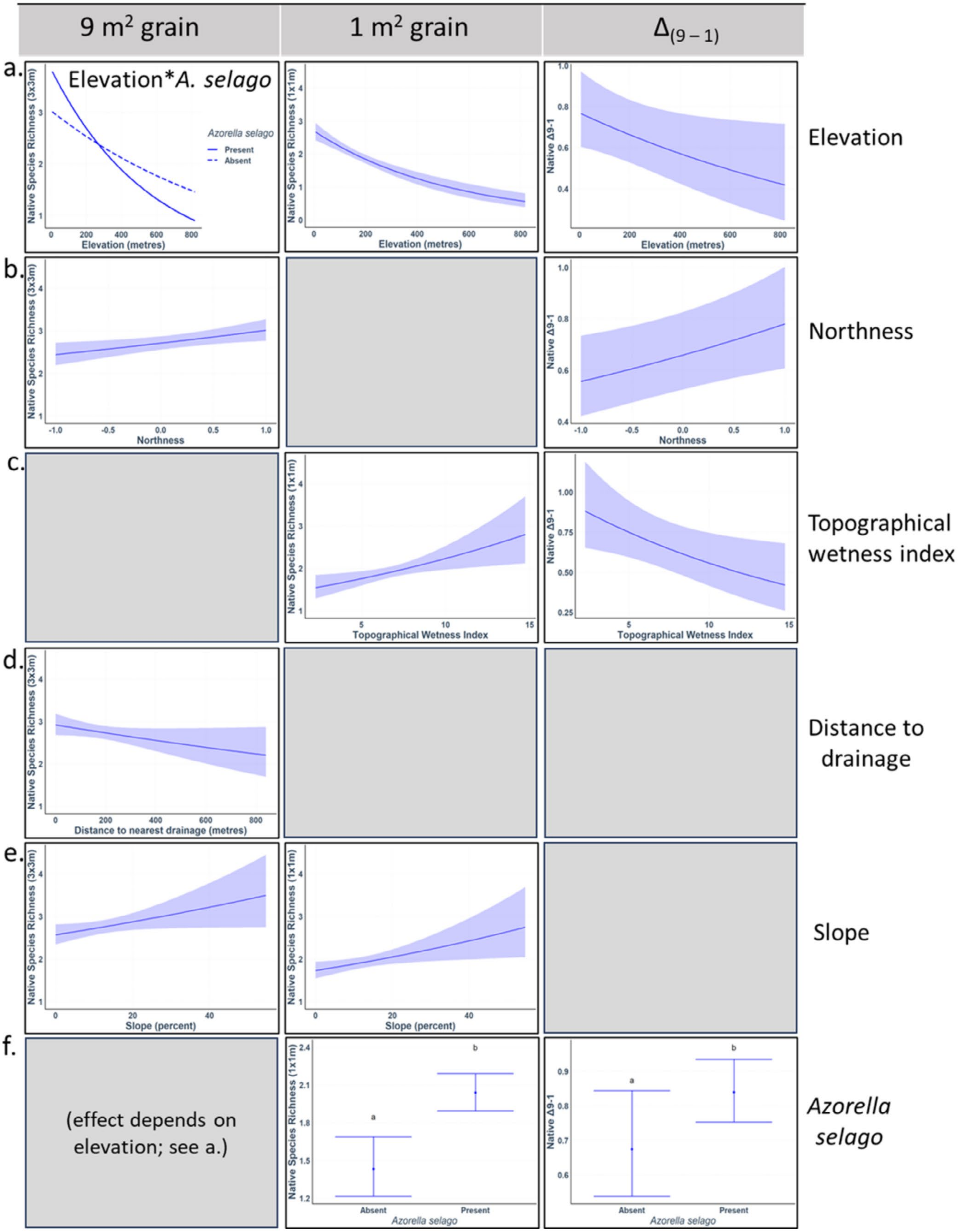


FIGURE 3 | The drivers of native species richness at large (9 m^2) and small (1 m^2) grain, and the difference in native species richness (Native $\Delta_{9\text{-}1}$) between large and small grain. (a) Elevation, (b) northness, (c) topographical wetness index (TWI), (d) distance to nearest drainage line, (e) slope, and (f) presence/absence of *Azorella selago*. The graphs show the effect of predictors on the response variable after the effect of all the other predictor variables have been considered. Only effects of predictors retained by best subset modelling are shown. Model parameters are shown in Table 1a.

TABLE 1 | Results from simultaneous auto-regressive models with a Poisson distribution showing the predictors of (a) native, and (b) alien vascular plant species richness at large ($9\,\mathrm{m}^2$) and small ($1\,\mathrm{m}^2$) grain sizes and of the difference in richness between the two grain sizes ($\Delta_{9\text{-}1}$) for both native and alien species using the full dataset.

(a) Native species					
Native richness $9\,\mathrm{m}^2$ grain			**Native richness $1\,\mathrm{m}^2$ grain**		
Variable	**Estimate**	***p***	**Variable**	**Estimate**	***p***
Intercept	2.753	<0.001	Intercept	1.404	<0.001
Presence of *A. selago*	1.007	<0.001	Presence of *A. selago*	0.591	<0.001
Distance to nearest drainage	−0.001	0.035	Elevation	−0.003	<0.001
Elevation	−0.004	<0.001	Topographical wetness index	0.086	<0.001
Northness	0.272	<0.001	Slope	0.017	<0.001
Slope	0.015	<0.001			
*A. selago**Elevation	−0.001	0.164			
Difference in native species richness between grains (native $\Delta_{9\text{-}1}$)					
Intercept	1.034	<0.001			
Presence of *A. selago*	0.265	0.009			
Elevation	−0.001	0.013			
Northness	0.137	0.012			
Topographical wetness index	−0.047	0.018			

(b) Alien species					
Alien richness $9\,\mathrm{m}^2$ grain			**Alien richness $1\,\mathrm{m}^2$ grain**		
Variable	**Estimate**	***p***	**Variable**	**Estimate**	***p***
Intercept	−0.347	0.320	Intercept	−0.428	0.325
Presence of *A. selago*	−1.397	<0.001	Presence of *A. selago*	−1.217	0.002
Distance to nearest drainage	0.001	0.057	Distance to nearest drainage	0.002	0.003
Elevation	−0.031	<0.001	Elevation	−0.023	0.007
Geology	N/A	0.007	Northness	−0.285	0.084
*A. selago**Elevation	0.028	0.001	*A. selago**Elevation	0.020	0.033
Difference in alien species richness between grains (alien $\Delta_{9\text{-}1}$)					
Intercept	−1.066	0.105			
Presence of *A. selago*	−0.897	0.196			
Distance to nearest drainage	−0.002	0.138			
Elevation	−0.030	0.082			
Geology	N/A	0.029			
*A. selago**Elevation	0.028	0.104			

Note: A best subset modelling approach was used to select the most parsimonious set of explanatory variables. Estimates are only given for continuous variables; for categorical variables "N/A" is specified.

distance to the nearest drainage line exhibited similar effects as those observed in the main dataset (Appendix S5).

Elevation was negatively correlated with alien $\Delta_{9\text{-}1}$, and at low elevations more alien species occurred in the absence than the presence of *A. selago*. Further, distance to the nearest drainage line was negatively correlated with alien $\Delta_{9\text{-}1}$, and the rare, grey-bedded ash geology had a significantly higher alien $\Delta_{9\text{-}1}$ for the full dataset (Figure 4, Table 1b).

In the subset of the data using plots with at least one alien species present (Appendix S5), the presence of *A. selago* and distance to nearest drainage line were positively correlated with alien $\Delta_{9\text{-}1}$ (Appendix S5).

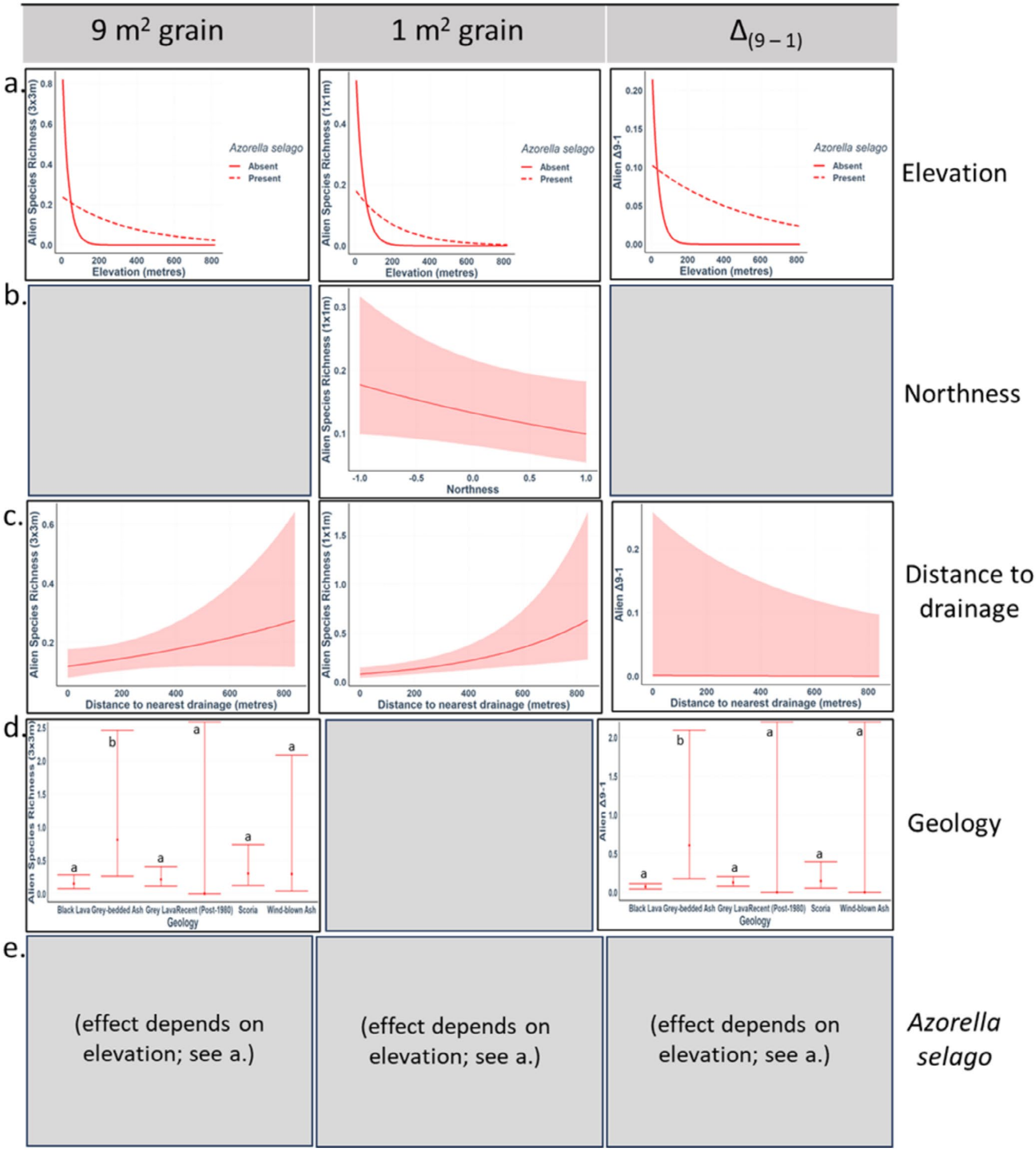


FIGURE 4 | The drivers of alien species richness at large (9 m^2) and small (1 m^2) grain, and the difference in alien species richness (Alien $\Delta_{9\text{-}1}$) between large and small grain. (a) Elevation, (b) northness, (c) distance to nearest drainage, (d) geology (different letters above plots indicate significant differences in mean values between the geologies at $p \leq 0.05$), and e. presence/absence of *Azorella selago*. The graphs show the effect of predictors on the response variable after the effect of all the other predictor variables have been considered. Only effects of predictors retained by best subset modelling are shown. Model parameters are shown in Table 1b.

4 | Discussion

This study provides the first empirical demonstration of plant species richness drivers in a sub-Antarctic ecosystem. We demonstrate that some of the drivers of native and alien species richness differ and that the effects of drivers vary with spatial grain. The presence of a keystone plant species was the most important predictor of both native and alien plant species richness on Marion Island. Though the keystone species is a strong facilitator of native species, it appears to compete with alien plant species. By quantifying the drivers of the *difference* in species richness between the two considered grains, we could provide insight into the role of local species turnover in community assemblage patterns.

4.1 | Drivers of Native Species Richness

Support for the energy hypothesis driving native plant richness on Marion Island was found, with warmer north-facing slopes and lower elevations harbouring higher richness. The higher richness in warmer north-facing and coastal sites is likely facilitated by the high precipitation levels on Marion Island (le Roux and McGeoch 2008). In more arid regions where soil moisture is limiting, higher incident radiation can result in lower soil moisture and thus limit richness (Najafifar et al. 2019). Additionally, plots with high TWI at small grain and plots closer to drainage lines (i.e., wetter plots) at large grain, contained more native species. Whilst we expected water to be less important in limiting richness in this wet and cold environment, these findings corroborate other studies which find that even in wet environments, like Marion Island, plant distributions can be limited by water (le Roux, Aalto, et al. 2013). Our study, therefore, underscores the importance of soil moisture for influencing plant species richness, which has sometimes been considered less essential in cold and wet environments.

The decrease in native species richness with elevation at both grains could also be driven by factors other than temperature. The windy conditions at high altitudes may limit some species (Momberg et al. 2021); and soils at higher altitudes are shallower (or absent) and generally more nutrient-poor on this geologically young volcanic island, due to lower biotic inputs (Smith 2008). Therefore, the decrease of species richness with altitude could also provide support for the productivity hypothesis which states that more productive environments support more species (Mittelbach et al. 2001).

The effect of elevation on richness was dependent on the presence of the cushion plant *Azorella selago* at the large grain. Indeed, the presence of *A. selago* had the biggest effect on native species richness. Cushion plants are common in cold and windy regions, where they modify microhabitats to the benefit of other species growing within them (Reid et al. 2010; van der Merwe et al. 2021). At low altitudes (*c.* < 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 vascular 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, facilitation decreases and environmental factors emerge as primary limiting factors (e.g., Louthan et al. 2018; Raath-Krüger et al. 2019). Interactions between elevation and *A. selago* were not present at small grain—instead *A. selago* consistently resulted in a decrease in native richness, suggesting that the species outcompetes other native plants at all elevations.

Native richness was higher for both grains on steeper slopes. High environmental heterogeneity, as found on steeper slopes, can increase habitat complexity (Stein et al. 2014). 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 (Kreft and Jetz 2007; Stein et al. 2014; Stein and Kreft 2015; Tuomisto et al. 2017).

4.2 | Drivers of Alien Species Richness

Alien plant richness, which is lower than native plant richness on Marion Island, was not strongly affected by energy availability. This was unexpected because there is evidence for some physiological and trait research that alien species may benefit from warmer temperatures at this site (Mathakutha et al. 2019; Ripley et al. 2020). However, this does not seem to translate into alien richness patterns. The negative relationship between northness and alien species richness at a small grain, indicating higher richness in cooler south-facing slopes, is contrary to what was expected from the energy hypothesis (Måren et al. 2015). However, alien species richness was higher at low elevations, characterised by warmer temperatures but also more nutrient-rich conditions due to pronounced animal activity (Haussmann et al. 2013; le Roux, Ramaswiela, et al. 2013; Greve et al. 2017). Indeed, alien species tend to proliferate in sites which experience high nutrient inputs (Smith 2008; Haussmann et al. 2013); therefore, the increase in richness at low elevations may be driven more strongly by nutrients, i.e., productivity, than by warmer temperatures (Cramer et al. 2022). Additionally, contrary to the energy hypothesis, richness increased with distance from drainage areas (i.e., progressively drier), suggesting that the island's high precipitation levels are sufficient to support the alien species.

A biotic interaction, in the form of the presence of *A. selago*, was the strongest predictor of alien species richness on the island. At both grains, alien species appeared to compete with *A. selago* at low elevations, but at high elevations, where aliens are mostly absent, the presence of *A. selago* had little effect. Studies in similar climates have shown cushion plants facilitating alien species at higher elevations where they would otherwise not be able to occur in the absence of this interaction (e.g., Cavieres et al. 2008; Arredondo-Núñez et al. 2009; Badano et al. 2015); we found no evidence for this. Invasive mice on Marion Island burrow into, and kill, *A. selago* cushions (Phiri et al. 2009), and there has been a systematic decrease of the cushion plant on Marion Island (van der Merwe et al. 2024). Eradication of the invasive mice from the island is currently being planned (Preston et al. 2019), and our findings suggest that if successful eradication of the mice allows *A. selago* populations to recover, additional biotic resistance could be provided by *A. selago* to invasive plants on the island.

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 the future (Crooks et al. 1999; le Roux, Ramaswiela, et al. 2013; Greve et al. 2017). Therefore, the patterns of alien richness observed in this study could be expected to change in the future.

In summary, some commonality in drivers of native and alien richness was found: the strongest predictor of richness for both groups was the presence of the keystone plant *A. selago*. However, this biotic interaction had contrasting impacts on native and alien species. At low elevations, *A. selago* competed with alien species, whereas *A. selago* benefitted native species at low elevations, suggesting facilitation. The opposite was true at high elevations, though the facilitative effect of *A. selago* on alien species was weak at high elevations. This mostly contrasts with other findings that cushion plants are important contributors to alien species' success, with significant implications for the susceptibility of communities to invasion (Cavieres 2021). Another difference between factors influencing native and alien species richness on Marion Island is the role of energy. Whilst energy levels determined the richness patterns of native species, there was limited evidence of energy influencing the richness of alien species. However, there is support for productivity affecting alien species distributions, with aliens mainly being restricted to coastal regions (Figure 2; Smith 2008). Indeed, on Marion Island, alien species possess more acquisitive traits than native species, allowing them to successfully occupy unfilled niches within the ecosystem (Mathakutha et al. 2019).

4.3 | 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). The observed higher values of native $\Delta_{9\text{-}1}$ at low elevations compared to high elevations are likely attributed to the greater overall number of species present at lower elevations. (Gremmen and Smith 2008). High-altitude environments, characterised by colder temperatures and lower soil nutrients, support a limited range of plant species (Appendix S6) and therefore have limited potential for turnover.

Native species richness was correlated with northness at the large but not small grain in our study. Native $\Delta_{9\text{-}1}$ was higher in warmer north-facing plots than in cooler south-facing plots. This suggests that, whilst greater northness creates warmer and more sunny environments that may benefit plants, 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 $1\,\text{m}^2$, 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 $9\,\text{m}^2$ plot, indicating local species turnover.

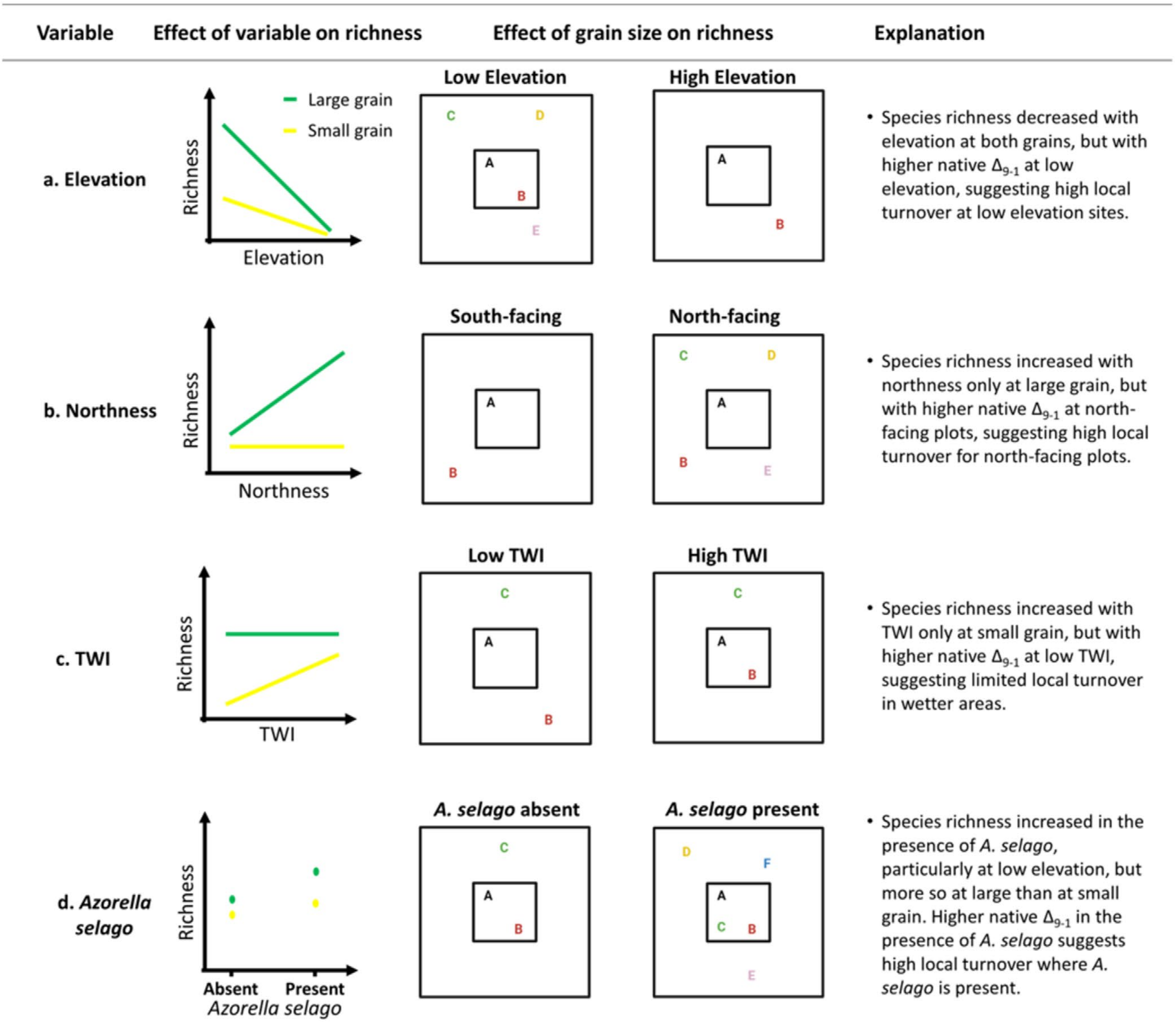
Native richness increased with TWI (i.e., moisture) at small, but not large, grains; and native $\Delta_{9\text{-}1}$ decreased with increasing TWI. Therefore, increasing TWI allowed more species to coexist, but only at small grain. At large grain, higher TWI did not result in higher richness, suggesting 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 increases species richness, indicating local turnover within the $9\,\text{m}^2$ 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 $\Delta_{9\text{-}1}$ 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 from those in the adjacent open habitat (Le Roux 2004), but this effect is stronger at large grain (Figure 5d). Another possible explanation could be that the environment that is suitable for *A. selago* is also suitable for other species, and these species thus coexist at large grains, but less so at small grains where *A. selago* outcompetes other plants with its cushion growth form.

Possibly due to several 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 was less pronounced. Given the unfavourable conditions for alien species at high elevations, resulting in lower alien richness, alien $\Delta_{9\text{-}1}$ was also lower there. However, alien $\Delta_{9\text{-}1}$ did not decrease much with elevation in the presence of *A. selago*, whilst it decreased more with elevation in the presence of *A. selago*, providing some evidence of a slight facilitative role of *A. selago* for alien species at high altitudes, though this effect is weak. In addition, grey-bedded ash geology significantly increased alien $\Delta_{9\text{-}1}$, but only five plots had this geology. Therefore, the effect of geology on alien $\Delta_{9\text{-}1}$ is considered negligible in this system. Alien $\Delta_{9\text{-}1}$ decreased with distance to the nearest drainage, indicating that as the distance to the nearest drainage line decreased, the difference in richness between large and small grains decreased. Therefore, as the distance to the drainage line increases, more local turnover happens within the $9\,\text{m}^2$ grid, although the number of species that are added through this process is not big enough for it to have a strong effect on species richness at large grain size.

5 | Conclusions

The findings of this study underscore the resonance between the drivers of plant species richness observed on Marion Island and those documented in comparable cold climate ecosystems. However, drivers of alien richness differ from those of native species, providing support for previous work suggesting that native and alien species fill different ecological niches on Marion Island (Mathakutha et al. 2019). Therefore, native and alien species are also expected to respond differently to global change drivers on Marion Island. The sub-Antarctic region, including Marion Island, has been experiencing progressively drier and warmer climates (le Roux and McGeoch 2008; Nel et al. 2023). Our findings predict that, on Marion Island, warming could locally increase the richness of native species, though only in wet areas, as drier regions support fewer species. In contrast,



- Species richness decreased with elevation at both grains, but with higher native $\Delta_{9\text{-}1}$ at low elevation, suggesting high local turnover at low elevation sites.
- Species richness increased with northness only at large grain, but with higher native $\Delta_{9\text{-}1}$ at north-facing plots, suggesting high local turnover for north-facing plots.
- Species richness increased with TWI only at small grain, but with higher native $\Delta_{9\text{-}1}$ at low TWI, suggesting limited local turnover in wetter areas.
- Species richness increased in the presence of *A. selago*, particularly at low elevation, but more so at large than at small grain. Higher native $\Delta_{9\text{-}1}$ in the presence of *A. selago* suggests high local turnover where *A. selago* is present.

FIGURE 5 | A representation of the effect of grain size on drivers of native plant species richness on Marion Island: (a) elevation, (b) northness, (c) topographical wetness index (TWI), and (d) presence/absence of *Azorella selago*. Effect of each of the predictors of $\Delta_{9\text{-}1}$ 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 $\Delta_{9\text{-}1}$. 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.

warming will have little effect on alien richness, though drying could increase alien richness.

We also show that assessing species richness patterns at multiple grains provides insight into community assembly processes. Variables can exhibit scale-dependent relationships with species richness, with some variables having a detectable effect on species richness at finer grain sizes, whilst the influence of others may only become more apparent at coarser grains, which is ultimately driven by species turnover within the larger grain size. Ultimately, using several grains increases understanding of the spatial component of species assemblage patterns in response to underlying drivers of species richness. Therefore, we advocate for the use of different grain sizes in assessing patterns and drivers of species richness.

Author Contributions

Joshua Tsamba: conceptualization (equal); data curation (equal); formal analysis (lead); investigation (equal); methodology (equal); writing – original draft (lead); and 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); and writing – review and editing (supporting). **Luis R. Pertierra:** formal analysis (supporting); methodology (supporting); supervision (supporting); writing – original draft (supporting); and writing – review and editing (supporting). **Bongekile S.N. Kuhlase:** investigation (supporting); data curation (equal); and writing – review and editing (supporting).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in Appendices S7 and S8 in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.