

# REVIEWS

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## The spatial structure of Antarctic biodiversity

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*Abstract.* Patterns of environmental spatial structure lie at the heart of the most fundamental and familiar patterns of diversity on Earth. Antarctica contains some of the strongest environmental gradients on the planet and therefore provides an ideal study ground to test hypotheses on the relevance of environmental variability for biodiversity. To answer the pivotal question, “How does spatial variation in physical and biological environmental properties across the Antarctic drive biodiversity?” we have synthesized current knowledge on environmental variability across terrestrial, freshwater, and marine Antarctic biomes and related this to the observed biotic patterns. The most important physical driver of Antarctic terrestrial communities is the availability of liquid water, itself driven by solar irradiance intensity. Patterns of biota distribution are further strongly influenced by the historical development of any given location or region, and by geographical barriers. In freshwater ecosystems, free water is also crucial, with further important influences from salinity, nutrient availability, oxygenation, and characteristics of ice cover and extent. In the marine biome there does not appear to be one major driving force, with the exception of the oceanographic boundary of the Polar Front. At smaller spatial scales, ice cover, ice scour, and salinity gradients are clearly important determinants of diversity at habitat and community level. Stochastic and extreme events remain an important driving force in all environments, particularly in the context of local extinction and colonization or recolonization, as well as that of temporal environmental variability. Our synthesis demonstrates that the Antarctic

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continent and surrounding oceans provide an ideal study ground to develop new biogeographical models, including life history and physiological traits, and to address questions regarding biological responses to environmental variability and change.

*Key words:* adaptation; biogeography; environmental gradients; historical contingency; marine; spatial scale and variation; terrestrial environments.

## INTRODUCTION

### *Spatial structure*

Spatial structure is one of the most fundamental characteristics of the planet. Early natural historians and geographers realized that the environment varies systematically over a range of spatial scales, and following the 19th-century voyages of discovery, widespread recognition developed that this variation extends to global scales in the form of a diversity gradient. As the fields of ecology and biogeography developed over the 20th century, much progress was made in understanding the form of spatial variation and the likely factors underlying it. Several key developments stand out from a biodiversity perspective. First is the early description and analysis of gradients in the abiotic environment, and species responses to them (Andrewartha and Birch 1954, Whittaker 1967). Such work remains important in modern investigations of species distribution and abundance, including recognition of the significance of direct, indirect, and resource gradients (Austin 1980). Second, geographers realized early on that closely located features are most likely to be similar, a feature known as spatial autocorrelation. The significance of autocorrelation for understanding variation in biodiversity remains the subject of intense interest (e.g., Beale et al. 2010, Hawkins 2012). Third, exploration of variation in features at different spatial scales has led to wide appreciation that different processes are likely to underlie patterns at each scale (Ricklefs 1987). Scale-related thinking now permeates almost every area of ecology and evolutionary physiology.

Growing integration among these areas has led to recognition that environmental spatial structure may lie at the heart of the most fundamental and familiar patterns of diversity (Storch et al. 2008). Moreover, it is now widely appreciated that to understand how biodiversity changes through time, as a consequence of dispersal, extinction, speciation, and evolution, and how it may respond to environmental change driven by humans, requires a spatially explicit approach (Blackburn and Gaston 1998, Soberón 2007, Gaston et al. 2008, 2009, McRae et al. 2008, Thuiller et al. 2008, Storfer et al. 2010, Ellner et al. 2011, Bellard et al. 2012). In consequence, much attention is now being given to the collection of spatially explicit data and the description of variation at several scales as the starting point for investigating biodiversity.

Such a perspective is also being brought to bear on the Antarctic. Antarctica contains some of the strongest environmental gradients on the planet (e.g., from extreme hypersalinity to almost zero salinity, exempli-

fied by soils and water bodies in the McMurdo Dry Valleys and the McMurdo Ice Shelf, respectively [Fernández-Valiente et al. 2001, Barrett et al. 2007]), is the terminus of many global gradients (Usher and Booth 1986, Peck et al. 2006), and its biota has formed the focus of many biogeographic investigations (reviewed in Convey et al. 2012a, Fraser et al. 2012, Terauds et al. 2012). Explicit attention to spatial variation in Antarctic diversity and its mechanistic underpinnings is growing apace (e.g., Chown et al. 1998, Adams et al. 2006, Chown and Convey 2007, Peat et al. 2007, Verleyen et al. 2009, Griffiths 2010, Cowan et al. 2011, Mortimer et al. 2011a, b, Schiaparelli and Hopcroft 2011, Allcock and Strugnell 2012, Born et al. 2012). However, few attempts have been made to draw together the conclusions from this work. Doing so would not only provide substantial insight into the biodiversity implications of spatial variation in a physically extreme system, but would also indicate the extent to which spatial frameworks developed elsewhere apply to the region. In turn, this would test their validity and reveal the extent to which the variety encompassed by Antarctic systems can serve further to establish ecological generalities.

As examples of the insights such an approach can deliver, consider two key ecological predictions at different spatial scales. First, diversity at high latitudes should typically show a decline as a consequence either of declining energy (Hawkins et al. 2003, but see Clarke and Gaston 2006) or the change in the seasonal availability of that energy (Archibald et al. 2010). The extent to which such declines are found varies among terrestrial and marine systems in the region (Peck et al. 2006) and among taxa within the marine system (Clarke and Johnston 2003). In consequence, considerable scope exists for testing unified theories to explain biodiversity variation (e.g., Price et al. 2012). Second, much ecological theory suggests that predominantly abiotic factors should influence the distribution and abundance of organisms in low-diversity systems (MacArthur 1972, Southwood 1988, Ricklefs 2011). If this is the case, then models seeking to explain variation in abundance and distribution, as well as in species richness, should be dominated by abiotic terms and by those describing their spatial structure. In turn, the outcomes of mechanistic and environmental niche models (Kearney and Porter 2009) should coincide, so assumptions about the extent to which each of these species distribution modeling approaches deals with fundamental and realized niches should be substantiated.

Our aims here are therefore to provide an overview of spatial variation in the Antarctic terrestrial, limnetic, and marine environments, and to see what lessons for broader understanding of biodiversity variation generally have emerged from work in this area. We then provide a synthesis of current knowledge in these areas. Because biodiversity has an explicitly historical context (Ricklefs 1987, Clarke and Crame 1989), we commence with a brief discussion of the history of the region, making reference to more comprehensive reviews for further information. Throughout, we draw on specific examples to illustrate our broader understanding, recognizing that as a consequence, some significant areas of work have to remain less fully covered. The latter include the roles of polar oceanic fronts, mesoscale features, and seabed topography in determining variation in pelagic biodiversity (see, e.g., Murphy et al. 2007, Tittensor et al. 2010, Louzao et al. 2011, Wakefield et al. 2011, Ainley et al. 2012, Strugnell et al. 2012), the complexities of diversity–environment interactions in the many streams that are a feature of the terrestrial Antarctic in the summer (e.g., Laybourn-Parry and Pierce 2007), and detailed discussion of the functioning of sub-Antarctic terrestrial systems (e.g., Chown and Froneman 2008).

#### *The Antarctic environment*

The “Antarctic” is defined here in its widest sense. For terrestrial and nonmarine aquatic environments, this means the Antarctic continent and Peninsula, the various archipelagos of the Scotia arc, and the sub-Antarctic islands. The marine environment encompasses the entire Southern Ocean, formed by southern provinces of the Atlantic, Indian, and Pacific Oceans (Fig. 1), and is delineated to the north by the mean position of the Antarctic Polar Front. Antarctic ecosystems vary on land from polar deserts, including the continent’s ice itself, freshwater to hypersaline lakes and their ice covers, to lush grasslands and eutrophic ponds (Thomas et al. 2008) (Fig. 2). Marine ecosystems range from shallow coastal regions to abyssal depths of the open ocean, ice-free to permanently ice-covered areas, and highly diverse to very simple, featureless habitats.

The Southern Ocean is dominated by the deep sea (depth >3000 m). However, very little is known about Antarctic deep-sea biodiversity (Kaiser and Barnes 2008), other than that it appears to be rich in some groups and undescribed species (Brandt et al. 2007, Rogers et al. 2012b), and that this richness is patchy across spatial scales (Kaiser et al. 2007, Griffiths et al. 2009, Convey et al. 2012a). The continental slope (shelf break to 3000 m) is also poorly sampled and known, although it would appear to be central to a cline from species-rich and abundant shelf faunas to generally poorer abyssal depths. The majority of sampling, recorded diversity, and knowledge of biological structure concerns the fauna of the continental shelf depths (generally shallower than 1000 m, accounting for 8% of

the shelf area on the planet) (Arntz et al. 1994, Clarke and Johnston 2003, Schiaparelli and Hopcroft 2011).

Unlike the Arctic, Antarctic marine and terrestrial ecosystems are largely isolated, rather than forming a continuum from those at lower latitudes, a process that commenced with the last stages of the breakup of Gondwana, and was enhanced and then maintained by the development of the atmospheric Polar Vortex and oceanic Antarctic Polar Front (Clarke et al. 2005, Barnes et al. 2006b, Bergstrom et al. 2006). In the deep oceans surrounding Antarctica, the isolating influence of the Antarctic Circumpolar Current extends to about 1000 m depth. Below this, connectivity with the other global ocean basins is more significant, exemplified by the northwards flow of cold Antarctic Bottom Water that forms a major driver of the global overturning circulation or “ocean conveyor belt.” In marine pelagic or planktonic ecosystems, the distribution of organisms in time and space is determined by complex interactions among trophodynamics, population dynamics, physical mixing, and circulation processes (Cullen et al. 2002, Wakefield et al. 2011). At the mesoscale and larger scales, distributions correspond to circulation features ranging from eddies and rings to basin-scale frontal boundaries separating major water masses (Knox 1994, Longhurst 1998, Ainley et al. 2012, Rogers et al. 2012a).

Terrestrial ecosystem development is limited to areas that are seasonally or permanently snow- and ice-free, and have appropriate environmental conditions. Ice-free ground is currently limited to ~0.34% of the area of the Antarctic continent, equating to ~45 000 km<sup>2</sup>, while visible life is largely but not completely restricted to lower-altitude exposures in coastal regions (Convey et al. 2009, Convey 2013). In contrast with much of the marine environment, typically island-like terrestrial ecosystems are isolated from each other across a range of scales, from meters to many hundreds of kilometers. The ice of Antarctica is also not devoid of life. Considerable biomass is associated with snow and ice algal communities that develop in summer, especially in coastal regions, although these have received relatively little research attention (Bagshaw et al. 2007, Stibal et al. 2012; see Hodson et al. 2008 for discussion of Arctic parallels). The existence of subglacial microbial communities, increasingly recognized in alpine regions, is now being examined in Antarctica (Tranter et al. 2005, Lanoil et al. 2009), while much attention is focused on the potentially exceptional biota to be found in the many lakes now known to lie beneath the continent’s ice sheets or in its permafrost (Skidmore 2011).

#### HISTORY

##### *Cenozoic climate change and glaciations*

Understanding current biological processes, particularly those relating to diversity, requires sound knowledge of the regional history of the biota. On the longest timescales, Antarctica has shifted from being warm, ice-free, and broadly connected to other land masses, to



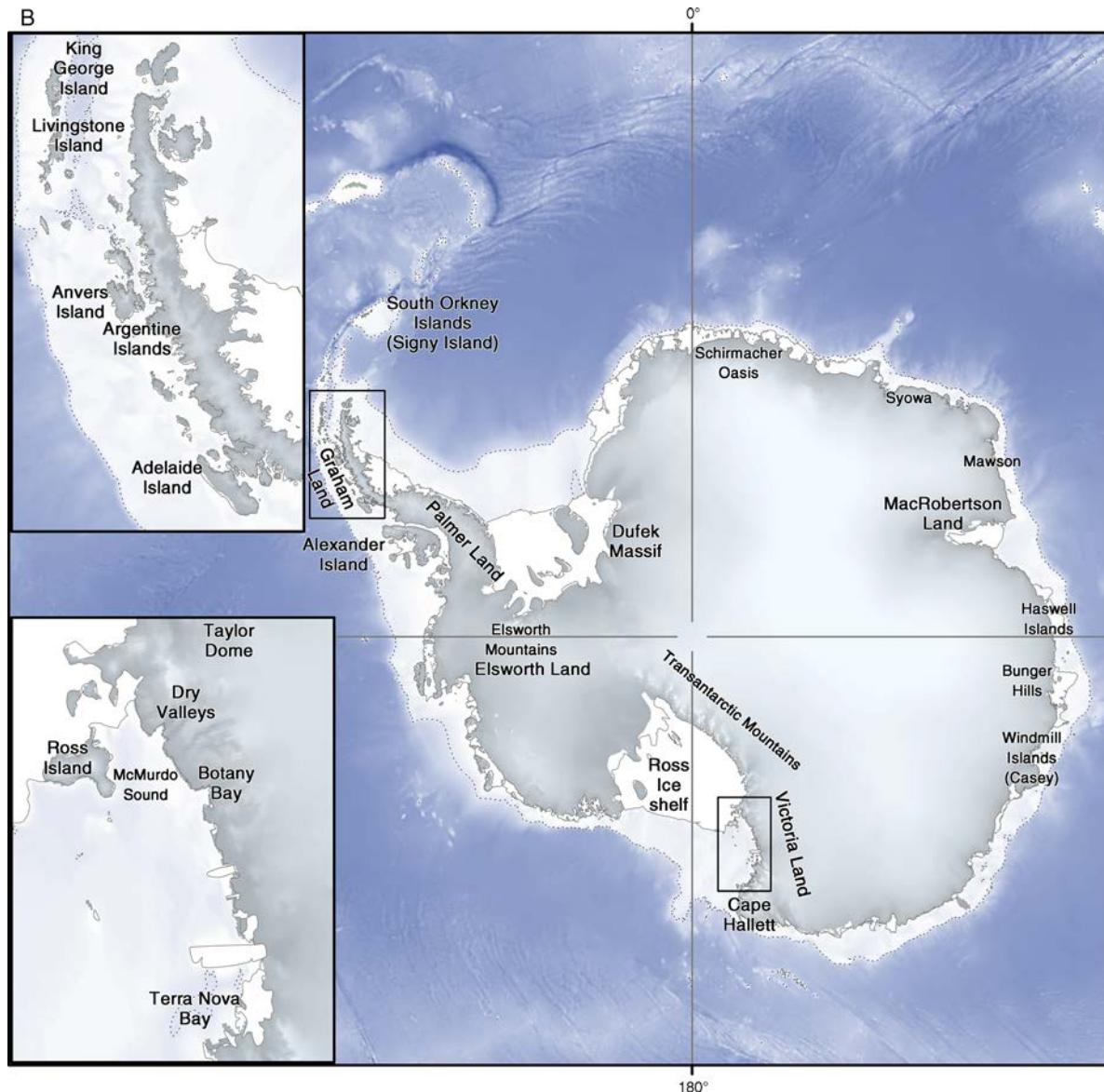


FIG. 1. Continued.

dropped temperatures by  $\sim 4^{\circ}\text{C}$ . After 10 kyr BP there was a gradual cooling of  $\sim 5^{\circ}\text{C}$ , with sharp cooling events 9.5 and 6.5 kyr BP. Finally, over the last 1000 years, there has been a warming of  $\sim 2^{\circ}\text{C}$ . A similar climatic history is evident on the sub-Antarctic islands, although it varies with their spatial location (e.g., Hall 2002, Fraser et al. 2012).

This historical background has left traces detectable in modern terrestrial and aquatic habitats. For example, molecular signals are present in populations of McMurdo Dry Valley springtails that indicate the influence of ancient shorelines (Nolan et al. 2006). Lakes can preserve clear records of change over long timescales. In Victoria Land, lakes reached their maximum extent 10–

12 kyr BP (Webster et al. 1996). As the Ross Ice Shelf then retreated, these drained, leaving a series of smaller lakes. Cooling up to about 1 kyr ago was accompanied by lake evaporation to a minimum volume (Wilson 1964, Lyons et al. 1998), and the lakes have since partially refilled as temperatures have warmed. During the high lake stands, previously deposited salts were solubilized, now underlying structurally important salinity gradients (Vincent et al. 1981), and providing nutrients for chlorophyll maxima at depth (Priscu 1995).

The ecological history (or legacy) of a given area is important in the understanding of inland ice-free ecosystems such as the McMurdo Dry Valleys, Vestfold Hills (Pickard 1986, Zwart et al. 1998, Moorhead et al.

1999, Lyons et al. 2001, Hodgson et al. 2004), Larseman Hills (Burgess et al. 1994), and Schirmacher Oasis (Bormann and Fritzsche 1995). Soils in the McMurdo Dry Valley region have been produced by the successive movements of the East Antarctic and West Antarctic Ice Sheets through the Valleys as climate has fluctuated (Hall et al. 2000, Hendy 2000). Thus the soils in the eastern end of the Taylor Valley are young (~24 kyr and less), while those in the western part of the valley are much older (~75–130 kyr), indicating that even at the last glacial maximum the Antarctic terrestrial environment was not completely covered by ice. The younger soils have much lower N:P ratios (Barrett et al. 2007), as they have more soluble P (low weathering loss), while the older soils have higher total nitrogen content due to longer exposure to atmospheric nitrate input. The oldest soil surfaces have higher conductivities because they have accumulated atmospheric aerosols, leading to lower soil invertebrate abundance (Virginia and Wall 1999). Some of the soil organic carbon in the Taylor Valley is of earlier lacustrine origin, and is now a major energy source for the terrestrial invertebrate community (Burkins et al. 2000). The soil stoichiometry gradient is also reflected in the lakes within the basins (Priscu 1995). Older soil surfaces also exist in this area (mostly at higher elevations) and have been exposed for up to several million years, having an order of magnitude higher N:P ratio again (Barrett et al. 2007). Barrett et al. (2007) hypothesized that, in general, the input elemental composition (i.e., C, N, P) not only constrains productivity within the ecosystem, but is modified by the biological processes occurring there by changing the stoichiometry “downstream.” As an example, the N:P ratio changes from 21:1 for glacial snow/ice, to 15:1 for cryoconite water, to 12:1 for stream water, to 25:1 for lake water. Over longer time periods, as lake levels fluctuate with climate change, soil and lake nutrients can be redistributed between the terrestrial and aquatic systems, providing legacy subsidies for both systems (Moorhead et al. 1999, Lyons et al. 2000). The drawdowns have concentrated nutrients in the hypolimnia of older lakes (Priscu 1995). This cryoconcentration of nutrients in the deeper, saline portions also creates important nutrient gradients within the lakes themselves. The diffusion of nitrate, ammonium, and phosphate across the chemoclines drives production in the deep chlorophyll maxima of the lakes in the McMurdo Dry Valleys.

In the Windmill Islands region the best-developed vegetation communities are found in sites where nutrients were deposited in penguin colonies abandoned thousands of years ago (Goodwin 1993). The vegetation changes from extensive moss beds in the lower-lying regions to lichen-dominated communities toward the summits (Melick and Seppelt 1997). Opposing resource gradients accompany the vegetation change, with water decreasing and plant nitrogen content increasing with elevation (Wasley et al. 2006a, 2012).

### *Refugia and isolation*

Signals of spatial regionalization and temporal isolation are apparent in both terrestrial and marine environments of Antarctica (Griffiths et al. 2009, Terauds et al. 2012). In the sea, the overwhelming cause of isolation is that of the Antarctic Circumpolar Current (ACC) and Polar Front (Clarke et al. 2005). This eastwards flowing current, formed between 24 and 41 mya, creates a steep temperature gradient of 3°–4°C over a distance of tens of kilometers, and forms a strong biogeographic discontinuity. Subsequent evolution in the cold Antarctic marine environment has selected for stenothermal (Somero and DeVries 1967, Peck et al. 2010b) and eurybathic taxa (Brey et al. 1996), and led to high species-level endemism (50–70%) (Griffiths et al. 2009, Convey et al. 2012a). At glacial maxima, most of the continental shelf was covered by ice, restricting fauna to isolated refugia or forcing them into deeper water (Thatje et al. 2005, Convey et al. 2009). Cycles of contraction to refugia followed by re-expansion are likely to have been a major influence on evolution in the Antarctic marine fauna (Clarke and Crame 1989, 1992, 1997, Fraser et al. 2012), and increasingly it appears also on the Antarctic and sub-Antarctic terrestrial biota, which also shows substantial endemism (Greve et al. 2005, Stevens and Hogg 2006, Stevens et al. 2006, Pugh and Convey 2008, McGaughan et al. 2010, Grobler et al. 2011, Mortimer et al. 2011a, b).

### SPATIAL VARIATION IN TERRESTRIAL SYSTEMS

Terrestrial Antarctica is characterized by limited and insular exposure of ice-free ground as well as patchy and discontinuous substrates. Thus, the potential to link biological features with “continuous” physical environmental gradients such as temperature or water availability is limited. The sub- and maritime Antarctic islands experience less extreme daily and seasonal temperature variations than do locations within the main body of the continent, but show more variation in other variables such as precipitation (Convey 2013). In consequence, investigations of biodiversity at a wider range of spatial scales are possible (e.g., Terauds et al. 2011). A spatial approach, based on latitude, elevation, and distance from the coast (see Table 1), was first proposed as a means to investigate variation in the Antarctic terrestrial fauna by Janetschek (1970). In the last decade interest in this approach has increased both for fundamental theoretical reasons (e.g., le Roux and McGeoch 2008a) and to address complex questions related to climate change impacts in the polar regions (Chown et al. 2012b).

Antarctic terrestrial organisms typically have patchy local distributions (Usher and Booth 1984, 1986, Caruso and Bargagli 2007, Caruso et al. 2007, 2009, 2012a), as do the microbiota (Caruso et al. 2011, Chong et al. 2011). Various biotic factors, such as productivity and chlorophyll *a* content (Sinclair and Sjørnsen 2001), macroscopic vegetation (Sinclair 2001), and food

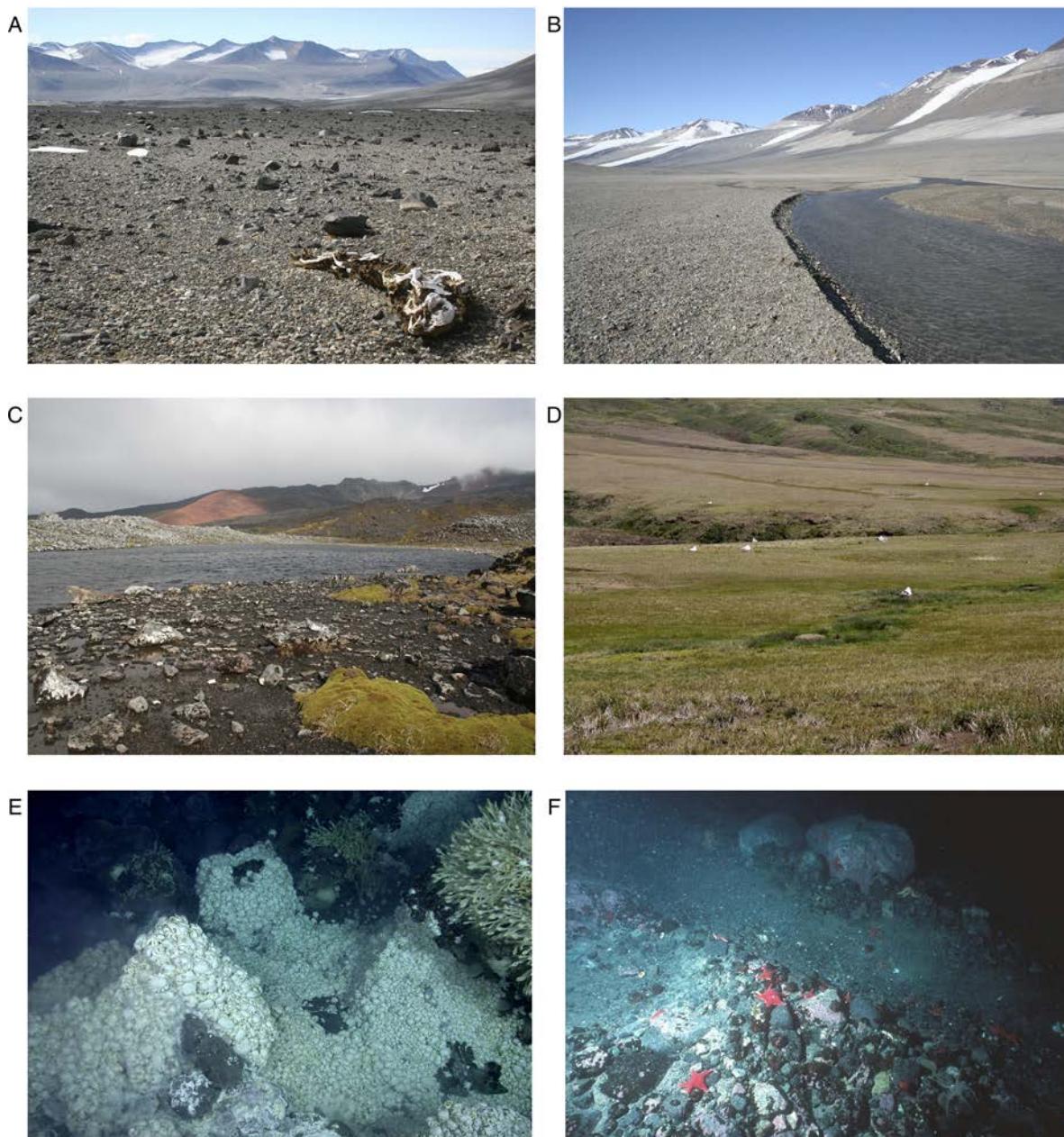


FIG. 2. Terrestrial and marine environments in the Antarctic region. (A) A mummified seal in McKelvey Valley, McMurdo Dry Valleys. (B) Onyx River, Wright Valley, McMurdo Dry Valleys. (C) The cushion plant *Azorella selago* (Apiaceae) alongside a high-altitude lake on sub-Antarctic Marion Island. (D) Wandering Albatross (*Diomedea exulans*) nests, lowland tussock grassland, and mire vegetation on sub-Antarctic Prince Edward Island. (E) Yeti crabs (*Kiwa* sp.) at a Scotia arc hydrothermal vent site >2500 m in depth. (F) The impact of ice scour on the rich benthic diversity near Rothera Research Station, Adelaide Island, Antarctic Peninsula. Photo credits: A–D, S. L. Chown; E, Courtesy of NERCChEsSo Consortium; F, K. Brown, British Antarctic Survey.

preference (Kennedy 1999) influence distributions of the fauna (see also Hogg et al. 2006, Caruso et al. 2012b). Notwithstanding these factors, Antarctic biodiversity variation and ecosystem functioning are predominantly driven by abiotic factors (Convey 1996), including soil structure (Bölter et al. 1997, Wall and Virginia 1998), chemistry (Porazinska et al. 2002a), and, in particular, water availability (Kennedy 1993, Block 1996, Powers et

al. 1998, Bargagli et al. 1999, Porazinska et al. 2002b, Sinclair 2002, Poage et al. 2008) (see Table 2). Similar patterns are manifest in the sub-Antarctic, though here interspecific (i.e., biotic) interactions may become more significant (e.g., Vogel 1985, Frenot 1987, Chown 1994, Bergstrom and Selkirk 1997, Smith et al. 2001, Davies et al. 2011, Lebouvier et al. 2011, Terauds et al. 2011). Thus, any discussion of spatial variation in diversity

TABLE 1. Dependence matrix of terrestrial and marine physical factors vs. latitude, altitude/depth, and distance from the coast in Antarctica (from Peterson and Howard-Williams 2001).

Terrestrial and marine factors	Latitude	Altitude/depth	Distance from coast
Terrestrial physical factor			
Total solar radiation	3	1	0
Temperature	3	2	1
Humidity	2	1	2
Wind	1	1	1
Precipitation (amount)	2	1	1
Precipitation (type)	2	1	1
Ablation (amount)	2	2	2
Ablation (type)	2	2	2
Terrestrial geochemistry	1	1	1
Seasonality	3	1	0
Marine physical factor			
Polynya	2	0	1
Current	2	2	2
Salinity	1	2	2
Sea ice cover	2	0	1
Ice shelf cover	3	0	0

Notes: Key: 0, no dependence; 1, weak dependence; 2, medium dependence; 3, strong dependence. The original measurements for latitude were in degrees, for altitude/depth were per 100 m, and for distance from the coast were in kilometers.

must commence with a treatment of the direct effects of abiotic environmental variation. We do so here, then discuss direct gradients, such as resource gradients (including soils and productivity), followed by indirect gradients, most commonly investigated with latitude or altitude as the independent factor. Although this approach follows, in broad outline, Austin's (1980) classification, the strong influence of solar radiation on water availability means that we accord it initial attention. Usually, or at least in the case of plants, it is considered a resource gradient. Throughout we consider both strictly terrestrial and limnetic environments, which may include a variety of streams, lakes, and smaller water bodies such as cryoconite holes (see Bergstrom et al. 2006).

#### *Solar radiation*

The two physical attributes that have the greatest influence on Antarctic ecosystems are the presence of liquid-phase water on land and of ice cover in marine and freshwater systems. These are both influenced by solar radiation and hence show a latitudinal response. Other important factors include extreme seasonality combined with steep latitudinal gradients of light-dark periodicity (Fig. 3) and exposure to high incident radiation and to damaging wavelengths of the radiation spectrum.

TABLE 2. Environmental stressors for and response patterns by Antarctic terrestrial biota.

Factor	Protection provided by	Negative effects of protection
Radiation (PAR and UV)	screening pigments	lowered light response of photosynthesis; cost of production
	shaded habitat, refraction/reflectance due to plant form and/or overlying snow	lowered PAR and temperature
Temperature (including freeze-thaw consequences)	insulation by snow	lowered PAR; increased respiration cost; potentially shortened growth season
	northern growth aspect	increased desiccation
	wet ground (extracellular freezing of water protects active mosses from subzero temperatures (continent))	surface ice layer can lead to increased soil invertebrate mortality
	button form, low stature	potential to reduce PAR and thus photosynthesis
Wind	dark pigmentation (enhances solar heating)	accelerated desiccation
	ground between rocks, soil crusts, endo- and chasmo-lithic habitats (strong link with water availability), lee location	reduced light availability
Desiccation (note strong linkage with wind, radiation and temperature)	south-facing aspect (continent)	lower temperatures
	endo- and chasmo-lithic habitat, soil crusts	lowered PAR; physical limit to organism size
	sublithic habitat	lowered PAR
	permanent snow bank/drift	lowered PAR and temperature; increased respiration cost; at continental sites insulation prevents warming in early summer
	flowing melt water	substrate instability; abrasion; burial

Notes: Protection against the main environmental stressors (shown in the middle column) for Antarctic terrestrial biota also results in negative consequences for growth and development as shown in the right column.

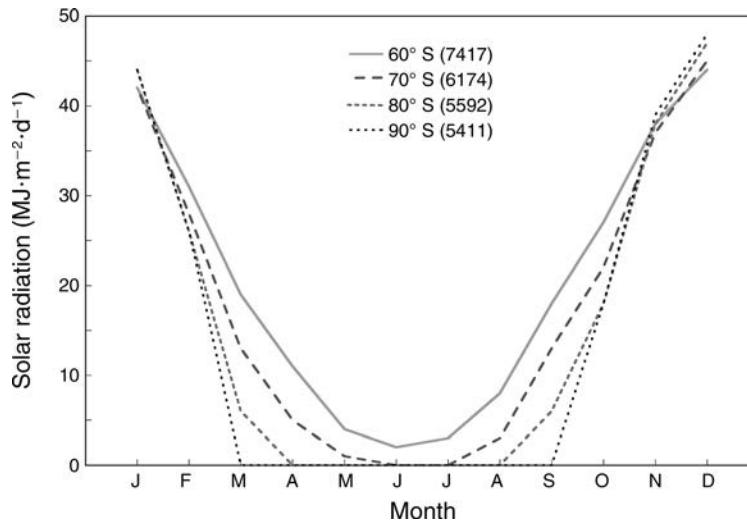


FIG. 3. Solar radiation at the top of the atmosphere as a function of latitude and time of year for the zone 60°–90° S (adapted from Vincent 1988). Values following the latitude values are total annual radiation (MJ/yr).

The existence of gradients in exposure to solar radiation is implicit in many studies of terrestrial vegetation distribution, ecophysiology, and photosynthetic biochemistry. These include photosynthetically active radiation (PAR), ultraviolet radiation (UV-A) and seasonally anthropogenically enhanced levels of biologically harmful UV-B radiation. On an annual basis there is a latitudinal decline in total radiation incident on the Earth's atmosphere, from a monthly average of about 22 MJ/m<sup>2</sup> in the northern Antarctic Peninsula to around 9 MJ/m<sup>2</sup> at the South Pole. PAR comprises only part of the radiation spectrum (400–700 nm, typically 43% of the total radiation energy), and the fraction that reaches ecosystems at Earth's surface is influenced by large-scale patterns in cloudiness as well as reflectance through albedo, with the result that the radiation gradient experienced at ground level can be reversed.

In summer the integrated daily radiation is as high, or even higher, in continental Antarctica than in many temperate areas. Geography, however, can also strongly influence local weather conditions, consequently affecting the proportion of radiation reaching ecosystems. For example, as a result of different cloud cover and path length, islands off the Antarctic Peninsula receive about 10% of radiation incident on the Earth's atmosphere, while on the polar plateau this can reach 90%. The almost continuous cloud in the northwestern Antarctic Peninsula means that radiation levels at ground level are low and even, and temperatures relatively stable compared to elsewhere in Antarctica. As a result the active times of lichens are mainly confined to the two summer months at Botany Bay (77° S) compared to the whole year at Livingston Island (62° S) (Schroeter et al. 2010). However, photosynthesizing organisms in the former region can experience incident PAR exceeding

nominal full sunlight, 2000  $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Pannewitz et al. 2003a, Schroeter et al. 2011).

Little evidence exists that naturally occurring levels of PAR or UV radiation are major limiting factors for autotrophs in Antarctica (Kappen et al. 1998a, Clarke and Robinson 2008, Schroeter et al. 2012). UV radiation generally is lower in Antarctica than in tropical and temperate areas; the mean UV index for January is ~3 at Ross Island and ~4 at Anvers Island, compared to 7–12 in New Zealand. Increased UV-B radiation as a result of the ozone hole occurs between September and early December, so has little effect within the main Antarctic continent, as vegetation activity occurs mainly within the period December to early February. Enhanced levels do occur on the Antarctic Peninsula, but there is evidence that the bryophytes at least can rapidly acclimate to changes in UV radiation (Newsham 2003, Green et al. 2005, Newsham and Robinson 2009, Turnbull et al. 2009). Exposure does result in damage to biochemical constituents of cells (e.g., DNA and photosystems [Green et al. 2000, George et al. 2002, Lud et al. 2002, Turnbull and Robinson 2009, Robinson and Waterman 2013]), but these effects are transient. The dynamic behavior of the protective pigments, which are typically lost if the plants are shaded, suggests that there is a metabolic cost to their presence. However, their production costs are small, estimated at 2% of daily net photosynthesis (Snell et al. 2009). While protective “sunscreen” pigments are found across many mosses, lichens, and microbes, and there is clearly greater production in more exposed locations (Post 1990, Post and Vesik 1992, Lovelock and Robinson 2002, Clarke and Robinson 2008), studies quantifying the energetic or resource investment in these strategies across exposure gradients are still required. Dynamic avoidance strategies such as vertical migrations to avoid high UV have

also been demonstrated in Antarctic microbial mats (Nadeau et al. 1999). Such investment is arguably sufficient to generate a significant selection pressure, suggesting that spatial variation in exposure will be mirrored in biological responses that affect organism energy budgets and life history trade-offs (Convey 2011).

The interaction between insolation and desiccation is important. The mosses and lichens that dominate the limited continental Antarctic flora and survive in extremely xeric environments, such as rock surfaces, can avoid light stress by drying out rapidly, becoming inactive and increasingly tolerant of radiation including UV-B (Schlensog and Schroeter 2000, Kappen and Valladares 2007, Turnbull et al. 2009). Interspecific differences in the response of mosses to desiccation and UV radiation (Smith 1999, Robinson et al. 2003, Dunn and Robinson 2006, Turnbull and Robinson 2009, Wasley et al. 2012), determine both their spatial distribution on small scales, and their likely different future response to changes in the pattern and/or magnitude of stresses experienced. On exposed surfaces that dry quickly, lichen development is limited to crevices, interstitial spaces, or south-facing surfaces that offer shade but also where a reliable water supply is present. One result of this is the development of endolithic and chasmolithic communities, which are completely confined to the north faces of suitable rocks (Friedmann 1982). Mosses and lichens that grow in mesic areas where meltwater is the main supply may face very high light levels when active. However, the specific conditions when biota are active at a given location are important. Temperatures, for example, are practically identical for active lichens in the maritime Antarctic and continental dry valleys, but their periods of activity vary drastically (Schroeter et al. 2010). Interstitial, sublithic, and soil crust communities become relatively more important in drier areas, with translucent rock and soil particles allowing light transmission while protecting from desiccation (Hughes and Lawley 2003, Cowan et al. 2010).

As a result of these activity patterns, there is no relationship at continental scale between light levels or intercepted quantity of light and growth rate. Lichens in the maritime Antarctic have some of the highest growth rates in the world for this group, while those in the continent can be one (Cape Hallett) or two orders of magnitude (McMurdo Dry Valleys) slower (Sancho et al. 2007, Green et al. 2012). The duration of annual metabolic activity, controlled by water availability, appears to be correlated with richness (Green et al. 2011a, Clarke et al. 2012).

#### *Temperature*

Antarctica contains among the most and the least variable thermal environments, with the former being mostly terrestrial and the latter marine. Temperatures on open rock surfaces can vary by  $>75^{\circ}\text{C}$  through the year and by at least  $10^{\circ}\text{C}$  and even up to  $50^{\circ}\text{C}$  within

hours (Peck et al. 2006). Similarly, freshwater pools can vary by  $>50^{\circ}\text{C}$  annually and by  $20^{\circ}\text{C}$  daily. Small, chemically stratified ponds in ice-free areas can have summer temperature differences between surface and bottom waters ( $\sim 40\text{--}70$  cm depth) of  $>10^{\circ}\text{C}$  (Healy et al. 2006). At broader scales, pronounced variation is clear, as might be expected. For example, Howard-Williams et al. (2010) found a significant linear decline in summer temperatures across Victoria Land. As an integrating measure of “probability of melt,” they also calculated degree-days above freezing, finding a wide variation at latitudes above  $80^{\circ}\text{S}$ , with values rapidly dropping toward zero at higher latitudes.

Variability in abiotic conditions is recognized as a key feature affecting organismal responses (e.g., Tufto 2000), and possibly also biodiversity variation (e.g., Archibald et al. 2010). However, the effects of temperature variation and its predictability per se (rather than mean annual temperatures), have not been as widely studied in Antarctic organisms as elsewhere. Most of the work in this area is concerned with the physiological implications of thermal variation at several spatial scales both on the continent and on the sub-Antarctic islands (e.g., Davey et al. 1992, Deere and Chown 2006, Rinehart et al. 2006, Teets et al. 2011). Nonetheless, adaptation to large diurnal temperature variation means that the terrestrial biota may not respond clearly to small local temperature gradients, especially if confounded by other environmental factors (Smith 2003). High natural variability in temperature may also underlie the comparatively small effects of artificial warming often reported in climate manipulation experiments (Sinclair 2002, Bokhorst et al. 2007b, 2008) compared with changes in response to moisture availability and freeze–thaw cycles (Wasley et al. 2006a, b, 2012, Yergeau and Kowalchuk 2008, Lenné et al. 2010).

#### *Water availability*

At a large geographic scale, a strong desiccation (water availability) gradient exists from the sub- and maritime Antarctic into the continent (Walton 1984), the latter including some of the driest sites on Earth. The availability of liquid water to organisms broadly depends on the balance between annual precipitation and losses by evaporation, sublimation, and freezing. In locations such as the McMurdo Dry Valleys, most or even all precipitation falling as snow may sublime, and thus not become available to biota. Precipitation occurs mainly as rain in the warmer sub-Antarctic zones (and increasingly in the maritime Antarctic during summer), and snow on the continent. Additional, though not well quantified, sources are dew (Büdel et al. 2008) and cloud or mist (especially for ridgeline biotas in montane areas). This balance can be modified by snow removal by wind scour or addition by redistribution, or by release of concentrated precipitation during local melt of ice or snow. The concentration of precipitation is particularly

important in extremely dry environments where areal deposition is insufficient to support organisms (Vaughan et al. 1999, Hodgson et al. 2010).

Water availability is regarded as the most important abiotic stress influencing Antarctic terrestrial communities (Kennedy 1993, Howard-Williams et al. 2010, Nielsen et al. 2012). At the broadest scales, this is illustrated by the substantial decline in cryptogamic vegetation abundance and areal extent from the maritime regions of the Scotia arc to the southern part of the Antarctic Peninsula (Smith 1972, V. R. Smith 1988, Peat et al. 2007). Only sporadic changes are then seen within the main body of the Antarctic continent, as the terrestrial organisms become confined to progressively smaller sites with suitable microclimates and substrata (Green et al. 2011a). Similarly, in Victoria Land, at Cape Hallett (73° S), extensive areas of terrestrial moss flush are found (Brabyn et al. 2006), while in the McMurdo Dry Valleys (78° S), moss flush areas are found occasionally (Schwarz et al. 1992), and at 80° S and higher latitudes none have been recorded (Green et al. 2011b). In the Windmill Islands and elsewhere, moss beds and turfs are extensive where summer melt water is abundant. In contrast, in drier areas the same species typically form only small colonies in sheltered niches (Melick and Seppelt 1997).

Detailed assessments of soil moisture levels at continental scale are lacking. Several smaller-scale studies have assessed soil moisture, and/or its influence on soil chemistry, on the distribution and abundance of soil organisms. For example, frost-heaving of moss turfs creates exposed dry “ridges,” which contrast with the moister shaded environments of the “valleys,” giving large gradients over a few centimeters (Lovelock and Robinson 2002). The abundance of Acari, Collembola, and Nematoda is also highly correlated with a gradient of soil moisture (Kennedy 1999, Treonis et al. 1999, Sinclair 2002, Ayres et al. 2010, Lee et al. 2012). However, temperature may still have important indirect influences, through its effects on the rate of snow- and ice-melt, and eventually, on soil moisture (Convey et al. 2003, Clarke et al. 2012). This implies that global climate change will have indirect effects on abundance and distribution through the modification of the normal water cycle in Antarctica, mediated by small-scale variation in water availability (Nielsen and Wall 2013). Recently, decadal time-scale climate changes have been recorded, along with occasional exceptional years (McKnight et al. 1999, Doran et al. 2002, 2008, Fountain and Lyons 2003), which can have long-standing effects on the soil biota (e.g., Barrett et al. 2008). In the sub-Antarctic, water availability is a significant factor affecting local assemblage structure and species responses to environmental change (e.g., Bergstrom and Selkirk 1997, Smith et al. 2001, Chown et al. 2007, Lebouvier et al. 2011).

### *Ice and snow*

Ice dominates the ecology of terrestrial, marine, and intertidal environments of the polar regions. On land the melting–freezing transition between water and ice is often unpredictable, sometimes occurring over minutes and being crossed daily or more frequently (Walton 1984, Davey et al. 1992). This means that mechanisms to survive freezing periods are essential for terrestrial organisms. Similarly, ice may have profound effects on local diversity through disturbance of the substratum and if substantial melt events occur (Barrett et al. 2008, Engelen et al. 2008).

In freshwater ecosystems (lakes, streams, and ponds), biological activity is strongly influenced by ice phenology (thickness, transparency, and duration) (Rochera et al. 2010, Quesada and Velázquez 2013). Pond systems in early summer can be highly depleted in inorganic carbonate, resulting in pH maxima >9 before ice melt because of CO<sub>2</sub> uptake under ice cover. Later, toward autumn, the reformation of ice cover under diminishing light conditions produces initially low dissolved inorganic carbon and high pH conditions followed by rapid respiration and CO<sub>2</sub> production with anoxia (Hawes et al. 2011a, b). Lake ecosystems may have permanent ice cover or annual ice cover that breaks out for a few weeks each year. There is a latitudinal threshold at ~72° S, after which deep lakes (>4 m) have permanent ice cover. Shallow water bodies may freeze completely each winter, while extremely hypersaline lakes may never develop ice cover (Vincent 1988). These characteristics vary with latitude, exposure, elevation, and aspect.

In the sub-Antarctic and coastal maritime Antarctic, precipitation falls mainly as rain in the summer months, whereas that in the continental and inland maritime Antarctic falls as snow. Snow can be redistributed extensively by the interaction between wind and local topography (Walker et al. 2001, van Lipzig et al. 2004). Therefore deep snow tends to be confined to certain sites where it is constantly present, and gradients from snow-covered to snow-free sites are often fixed in location.

The regular formation of snowbanks at certain locations strongly affects vegetation distribution. In the Antarctic Peninsula, as in alpine areas, snow cover can protect plants and animals from erosion, excessive desiccation, and extreme cold (Winkler et al. 2000, Block et al. 2009). In contrast, snowbanks on the continent, while still providing insulation, can lead to early summer temperatures remaining well below the air temperature, which is significant, as most lichens and mosses do not become metabolically active until temperatures rise above freezing (Pannewitz et al. 2003a). Attenuation of light can further result in vegetation being below the compensation point for photosynthesis. However, at the margins of the snowbanks, there can be a “greenhouse” zone where lichens, mosses, and microbial soil crusts are regularly moistened and active (Kappen et al. 1998b, Cockell et al. 2002, Schroeter et al. 2012). Snow kill and snow loss events may be important in opening areas for

colonization (Green et al. 2011*b*). The gradient from snow-covered to bare ground is therefore one of the strongest for plant life in continental Antarctica.

Deep snow can have profound effects on ice-covered aquatic ecosystems, because light is strongly attenuated even by thin layers of snow (Hawes 1985, Thomas et al. 2008), and snow cover can retard ice melting (Laybourn-Parry et al. 2002). Consequently, primary production in these ecosystems is restricted to species adapted to photosynthesize under extremely low irradiances, with mixotrophs playing an important role (Rocheira et al. 2010, Quesada and Velásquez 2013).

### Soils

The Antarctic terrestrial environment exhibits a strong gradient of soil formation (Allen and Heal 1970, Beyer and Bölder 2002, Thomas et al. 2008). Simple fragmentation of bedrock through mechanical (e.g., freeze–thaw) and chemical weathering (including that caused by epilithic and endolithic biota) is the initial step. The resulting lithosols are often redistributed and compacted into pavements or regosols. Subsequently, chemical processes and biological weathering by microorganisms lead to formation of cold desert mineral soils, where salt transfer and accumulation are important phenomena, resulting in “polar desert soils.” Thereafter, biological processes increase in importance, increasing the humic content and creating “tundra soils.” These processes lead to protoranker soils, characterized by the organic material remaining superficial, as there is no bioturbation by roots of vascular plants or larger soil fauna. Ornithogenic and wallow soils, where the organic matter originates from bird or sea mammal excrement, can also be characterized as protoranker soils.

Cold and aridity slow down these chemical and biological processes, prolonging the period of soil maturation. Biological activity, particularly in the early stages, is often low and sometimes absent (e.g., Tedrow and Ugolini 1966), although recent findings suggest this may be a result of methodological limitations (Cowan et al. 2002, Cary et al. 2010). Accumulating layers of moss material can result in peat banks of up to 2 m depth at a few maritime Antarctic locations (Fenton 1982), and as a consequence of high primary production and low decomposition rates of vascular plants and mosses in lowland systems of the sub-Antarctic islands (e.g., Smith 2008). Where root systems and/or bioturbating soil organisms are present, brown earth formation can occur, largely restricted to certain parts of the sub-Antarctic islands, and larger stands of the two native flowering plants in the maritime Antarctic. Ahumic soils tend to be found in the colder and drier parts of Antarctica, while humic soils occur in moister regions. The complexity of soil communities, soil chemistry, amount and type of organic matter, and degree of soil development vary considerably with latitude, distance to the coast, and geological parent material (e.g., Smith et

al. 2001, Bockheim 2008, Lee et al. 2009, Treasure and Chown 2013).

Temperature effects on the physical phase of water are often considered to underlie the decreasing maturation of soils with increasing latitude, although this has rarely been subject to specific study. In Victoria Land, Cannone et al. (2008) and Bockheim (2008) concluded that microclimate, active layer depth, and several chemical parameters played a more prominent role in soil formation. Nevertheless, other authors imply the existence of a large-scale continental gradient from the interior toward the coastal regions. Claridge and Campbell (1985) describe three major soil zones, based on typical climatic conditions and moisture availability, which almost inevitably include a geographical/latitudinal component: the McMurdo Dry Valleys and ice- and snow-free areas of the Transantarctic Mountains, coastal continental Antarctica, and the maritime Antarctic. Fogg (1998) analogously divided Antarctic soils into (1) tundra soils, occurring mainly in the sub-Antarctic and maritime Antarctic islands, (2) polar desert soils, occurring in coastal regions of Antarctica, and (3) cold desert soils, occurring in the rest of the continent. These zones roughly coincide with those proposed by Bockheim and Ugolini (1990).

### Nutrients

Nutrient gradients manifest over the terrestrial landscape in a number of ways. Legacy sources (see *Climate since the Last Glacial Maximum*) and proximity to the ocean or vertebrate colonies can exert significant influences. Marine and vertebrate fertilization is most apparent in the sub-Antarctic and maritime Antarctic, while at higher latitudes and with progression inland their impact on soil development becomes increasingly localized (Beyer et al. 2000, Smith 2008). Salinity gradients operating over scales of kilometers in inland regions may originate from different sources, including the leaching of soluble anions, down-slope redistribution, and/or wind-driven uphill redistribution (Nkem et al. 2006, Poage et al. 2008).

Habitats close to the shore can receive salt and nutrient inputs through sea spray and locally through biotic vectors such as penguins, seals, and nesting birds which, in turn, will support further soil and vegetation development through organic matter input (Erskine et al. 1998, Bokhorst et al. 2007*a*, Meira et al. 2008, Smith 2008, Smith and Froneman 2008, Chong et al. 2009). Analogous enrichment also occurs tens and up to several hundred kilometers “inland,” associated with bird colonies on nunataks (Ryan and Watkins 1989) or the influence of burrowing petrels in the sub-Antarctic (Smith and Froneman 2008). At much smaller scales, the importance of fertilization is demonstrated by the development of specific lichen or microbial communities around isolated bird perches (Øvstedal and Smith 2001), mummified seal carcasses (Nelson et al. 2008), and on the sites of ancient penguin colonies (Wasley et al. 2012).

TABLE 3. Nutrient concentrations (all measured in  $\mu\text{g/L}$ ) in Antarctic lakes and cryoconites.

Lake	PO <sub>4</sub> -P	NO <sub>3</sub> -N	NH <sub>4</sub> -N	Source
Beaver Lake (epishelf, Bunger Hills)	<1.0–19.0	3.2–161	16.1–187.0	Laybourn-Parry et al. (2006)
Crooked Lake, Vestfold Hills†	<1.0–13.1	<1.0–72.8	1.0–68.7	Bayliss et al. (1997)
Lake Druzhyby, Vestfold Hills†	<8.0	<1.0–84	<1.0–8.4	Laybourn-Parry and Bayliss (1996)
Ace Lake, Vestfold Hills†				
Mixolimnion	<1.0–69	<1.0–15	<1.0–180	Bell and Laybourn-Parry (1999)
Monimolimnion	10–335	<1.0–410	10–412	
Lake Williams, Vestfold Hills	8.0–488	36–140	35–141	Laybourn-Parry et al. (2002)
Highway Lake, Vestfold Hills	5.0–35.0	4.5–10.8	37–103	Laybourn-Parry et al. (2002)
Arctic cryoconites	<1.0–4.77	3.6–6.8	<1.0–19.3	S�awstr�om et al. (2002)

† Data derived over an annual cycle.

Albatross nests on sub-Antarctic islands may likewise form localized nutrient sources, though their effects may be complicated by the changes in temperature effected by incubating birds (Joly et al. 1987, Sinclair and Chown 2006, Smith and Froneman 2008). Changes in biological community composition and activity in response to the creation of such nutrient sources can be very rapid (Smith 2008, Tiao et al. 2012). Analogous point sources of nutrients are seen in the deep marine benthos centered around features such as whale carcasses, where impacts may be seen over both very short (intra-seasonal) and much longer (multidecadal) timescales (Smith and Baco 2003, Higgs et al. 2010).

The marine–terrestrial boundary provides a particularly steep salinity gradient. Alkemade and Van Rijswijk (1993) report “terrestrial” nematodes in seaweed deposited along the coast of King George Island (South Shetland Islands), showing that the higher the salinity, the lower the numbers of nematodes, but also that the C/N ratio of the substratum had a negative correlation with the abundance of nematodes. The location of the strandline (distance to the water’s edge) determined the quality of the substratum, including both the salinity and the C/N ratio. Such strandline gradients may be particularly significant for sub-Antarctic supralittoral terrestrial biota, where this is an important nutrient source supporting a high biomass of decomposers (e.g., Tr ehen et al. 1986, Crafford and Scholtz 1987, Hidalgo et al. 2013). By contrast, standing crop studies (Gremmen et al. 1995) and measurements of the rate of net photosynthesis and CO<sub>2</sub> assimilation of the coastal lichen *Turgidoscolum complicatum* (Smith and Gremmen 2001) provide no evidence of a response to salinity gradient. Huiskes and Moerdijk-Poortvliet (2000) also conclude that salt present in the thallus of this lichen increases water retention, resulting in a longer photosynthetically active period.

In the maritime and continental Antarctic coastal zones there is zonation of the epilithic lichen vegetation (Broady 1989, Gremmen et al. 1994, Kanda and Inoue 1994). Certain terrestrial arthropods are also limited to areas close to the coast, often being found only in supralittoral locations, and other species of mite and springtail are only known from the intertidal zone

(Mercer et al. 2000, Marshall and Convey 2004, Waller et al. 2006).

In extremely arid sites, the ephemeral presence of liquid water can change soil chemical properties by bringing into solution salts accumulated over time from the atmosphere (Claridge and Campbell 1977, Marchant and Denton 1996). Here, soil salinity is more important than moisture in determining community structure (Freckman and Virginia 1997, Courtright et al. 2001, Barrett et al. 2004). Leaching due to increased liquid water availability can dilute salts to within tolerable limits for the metabolism of nematodes, thereby increasing their potential to colonize previously unsuitable habitats (Nkem et al. 2005), and can also influence mosses (Bargagli et al. 1999). However, the relationship between water availability and the positive effects of solubilizing salt encrustations may not be direct; in sites where salts are sequestered in biologically inactive form, a short-time availability of small amounts of water may locally dissolve salts without leaching, therefore making the environment even more unsuitable due to high osmotic potential (Nkem et al. 2005).

Studies of the responses of individual species of terrestrial invertebrates and plants to different levels of salinity are growing, dealing both with mechanistic physiology (e.g., Pammenter and Smith 1983, Chown and Van Drimmelen 1992, Elnitsky et al. 2009, Hidalgo et al. 2013) and responses in abundance and distribution (e.g., Virginia and Wall 1999, Smith et al. 2001, Poage et al. 2008, Lee et al. 2009, le Roux et al. 2013, Raymond et al. 2013, Treasure and Chown 2013). Overall, soil salinity appears to be an important factor governing the local distribution of at least some cryptogams and invertebrates. Its importance relative to other environmental factors will determine its influence on larger scale distributions; if low, a patchy community distribution may result (e.g., Seppelt et al. 1988), and where it varies in synergy with other environmental factors, biological patterns will parallel the salinity gradient (Smith and French 1988, Powers et al. 1998).

Water bodies are classified across a continuum from ultra-oligotrophic (unproductive) to eutrophic (productive). Most lakes in Antarctica lie at the oligotrophic end of the spectrum, but within that range there are marked gradients. Antarctica has a diverse range of lakes from

TABLE 4. Estimates of annual production for higher plants, lichens, and mosses at several locations in Antarctica.

Species	Location	Annual production†	Comments and source
<b>Angiosperms</b>			
<i>Deschampsia antarctica</i>	Signy Island (60° 43' S)	1700 g·m <sup>-2</sup> ·yr <sup>-1</sup>	estimate from model based on microclimate and NP data gravimetric (Edwards 1972, Edwards and Smith 1988)
		390 g·m <sup>-2</sup> ·yr <sup>-1</sup>	
<b>Lichens</b>			
<i>Cladonia rangiferina</i> , <i>Usnea antarctica</i> , <i>U.</i> <i>aurantiaco-atra</i>	Signy Island	80–200 mg/g dm	gravimetric (Hooker 1980)
<i>U. antarctica</i>	King George Island (62° 09' S)	<300 mg CO <sub>2</sub> /g dm	model and year-round microclimate studies (Schroeter et al. 1995)
<i>U. aurantia-co-atra</i>	Signy Island Livingston (62° 40' S)	250 g·m <sup>-2</sup> ·yr <sup>-1</sup> 85 mg CO <sub>2</sub> /g dm	(Smith 1984, Schroeter 1997)
<i>U. sphacelata</i>	Casey (66° 17' S)	14 mg/g dm	estimated from model and assumed season length (Kappen et al. 1991)
Cryptoendolithic lichens	Dry Valleys (77° 35' S)	3 g·m <sup>-2</sup> ·yr <sup>-1</sup>	estimated from NP data and microclimate (Kappen 1993)
<b>Mosses</b>			
<i>Chorisodontium</i>	Signy Island	315–660 g·m <sup>-2</sup> ·yr <sup>-1</sup>	harvest plus prediction (Longton 1970, Collins 1973, 1977)
<i>Polytrichum</i> spp. <i>Calliergidium</i> + <i>Sanionia</i> spp.	Signy Island	223–893 g·m <sup>-2</sup> ·yr <sup>-1</sup>	(Davis 1983)
<i>Bryum pseudotriquetrum</i>	Syowa (69° 00' S)	–16 to +4 g·m <sup>-2</sup> ·yr <sup>-1</sup>	modeling from microclimate (Ino 1983)
<i>B. argenteum</i>	Ross Island (77° 50' S)	100 g·m <sup>-2</sup> ·yr <sup>-1</sup>	modeling from microclimate + NP responses (Longton 1974)

† The Annual production column includes the units presented in the original study. Dry mass is dm.

small, shallow to large, deep freshwater lakes, epishelf lakes, and saline and meromictic lakes that span brackish to hypersaline (Lyons et al. 2006, Vincent and Laybourn-Parry 2008). In many cases they receive limited allochthonous inputs of nutrients or carbon from their catchments, which often have poorly developed vegetation. Lakes adjacent to vertebrate concentrations receive considerable inputs of nitrogen, phosphorus, and carbon, which radically enhance their productivity (Butler 1999, Quayle and Convey 2006).

In aquatic habitats lacking such inputs, concentrations of NO<sub>3</sub>-N, NH<sub>4</sub>-N, and PO<sub>4</sub>-P, as well as dissolved organic carbon (DOC) exhibit wide gradients (Laybourn-Parry et al. 2002). At one extreme, in the largest epishelf lake in Antarctica (Beaver Lake, MacRobertson Land) PO<sub>4</sub>-P falls below the limit of detection in summer. In the highly transparent waters of this ultra-oligotrophic lake the euphotic zone, where primary production is possible, extends to around 100 m depth, where the highest rates of photosynthesis occur. DOC concentrations are also very low and sometimes undetectable. Since DOC is the substrate for bacterial production, both PO<sub>4</sub>-P and DOC are likely to limit bacterial productivity at times in summer (Laybourn-Parry et al. 2006). Large freshwater lakes in the Vestfold Hills are also ultra-oligotrophic (Table 3), with consistently low levels of both primary and bacterial production (Bayliss et al. 1997, Henshaw and Laybourn-Parry 2002). Studies covering annual cycles show that nutrient levels increase in winter when primary production is reduced, with phases of limitation during

summer (Laybourn-Parry and Bayliss 1996, Bayliss et al. 1997). In contrast, saline lakes are relatively eutrophic. For example hypersaline (50–60‰) Lake Williams in the Vestfold Hills has concentrations of PO<sub>4</sub>-P more than 10 times greater than brackish Highway Lake (4‰) (Table 3), with these differences being reflected in chlorophyll *a* and DOC concentrations during the austral summer (Laybourn-Parry et al. 2002).

Meromictic lakes show strong, permanent, physical and chemical gradients. In Ace Lake (Vestfold Hills) an upper water layer that is ice-covered for most of the year has a temperature that varies depending on the presence of ice cover. Water temperature increases over the boundary layer or chemocline into the lower anoxic monimolimnion. Salinity also increases twofold over the chemocline (Bell and Laybourn-Parry 1999). The monimolimnion is dominated by a community of methanogen and sulphur-reducing bacteria. This part of the water column has very high levels of nitrogen and phosphorus compared to the mixolimnion (Table 3). An extreme example of such short-distance but intense chemical gradients is provided by epishelf lakes. These are usually permanently ice covered, and have an upper, freshwater layer overlying a lower marine layer that is in direct contact with the neighboring sea. There is a sharp halocline between the two layers which host, respectively, independent freshwater or marine communities otherwise entirely normal for their location.

Glaciers represent an aquatic ecosystem within the ice biome (Anesio and Laybourn-Parry 2011). Their surfaces carry mini-lakes with straight-sided walls (cryo-

TABLE 5. Estimates of growth rates for lichens and mosses from various locations in Antarctica.

Species	Location	Growth rate (mm/yr) unless otherwise stated)	Source
<b>Lichens</b>			
Crustose spp.	King George Island (on whale bones)	0.51 (40 mm in 78 yr)	Kappen (1993)
<i>Caloplaca sublobulata</i>	Livingston Island	0.86	Sancho and Pintado (2004)
<i>Acarospora macrocyclos</i>	Signy Island/Livingston Island	1–3/0.72	Lindsay (1973), Sancho and Pintado (2004)
<i>Xanthoria elegans</i>	Signy Island	0.2–0.5	Lindsay (1973)
<i>Rhizocarpon geographicum</i>	Signy Island/Livingston Island	0.34/0.5	Lindsay (1973), Sancho and Pintado (2004)
<i>Buellia latemarginata</i>	Livingston Island	0.87	Sancho and Pintado (2004)
<i>B. frigida</i>	Cape Hallett	0.07	Sancho et al. (2007)
<i>B. frigida</i>	Asgard Range (Dry Valleys)	0.01	Green et al. (2012)
<b>Mosses</b>			
<i>Polytrichum strictum</i>	Signy Island	2–5	Longton (1970)
<i>Calliergidium austrostramineum</i>	Signy Island	10–32	Collins (1973)
<i>Sanionia uncinata</i>	Signy Island	11–16	Collins (1973)
<i>Bryum inconnexum</i>	Syowa Coast	<1	Matsuda (1968)
<i>Ceratodon purpureus</i>	Windmill Islands	0.2–3.5/2.6–5.6	Clarke et al. (2012)
<i>Schistidium antarctici</i>	Windmill Islands	0.4–1.2/0.1–3.0	Selkirk and Skotnicki (2007)
<i>Bryum pseudotriquetrum</i>	Windmill Islands, Grimmia Gorge, Vestfold Hills, Wilkes Land	0.1–4.6/1.0–2.6 up to 3.2	Selkirk and Skotnicki (2007)
<i>Bryum algens</i>	Mawson	1.2	Seppelt and Ashton (1978)
<i>Henediella heimii</i>	Taylor Valley	<0.2	T. G. Allan Green, unpublished data
<i>Bryoerythrophyllum recurvirostre</i>	Vestfold Hills	0.5–2.4	Clarke et al. (2012)

conites), that can be up to 0.5 m deep and 0.5 m wide although are typically much smaller, and normally have a dark sediment layer overlain by water with a temperature close to freezing. These represent a different endpoint of the nutrient gradient (Table 3). Their microbe-dominated communities exert a major influence on biogeochemical cycling of nutrients on glaciers (Bagshaw et al. 2007, Hodson et al. 2008). In regions where surface snow melts in summer, snow algae communities can also develop (Laybourn-Parry et al. 2011). This is particularly the case on some sub-Antarctic islands and in the northern maritime Antarctic, giving the currently unquantified potential for significant nutrient input into surrounding terrestrial, freshwater, and nearshore marine ecosystems (Stibal et al. 2012).

#### Productivity

A considerable gradient in productivity of plants exists from the sub-Antarctic islands to the Antarctic continent (Table 4) (V. R. Smith 1988, Green et al. 2007). There is little difference between the higher rates for both lichens and mosses, and both groups show a strong decline toward the higher latitudes. The majority of estimates come from the sub-Antarctic and maritime Antarctic regions and are based on earlier studies (e.g., see Davis 1981, V. R. Smith 1988, and references therein). Values for productivity for Antarctic plants have mainly been produced by the application of models

constructed by linking CO<sub>2</sub> exchange and microclimate data sets (e.g., Davis 1983), and only for the higher plants and/or in the sub-Antarctic islands by repeat harvesting. The two largest data sets are those for the cryptoendolithic community in the McMurdo Dry Valleys (Friedmann et al. 1993) and for the lichen *Usnea aurantiaco-atra* on Livingston Island in the South Shetland Islands (Schroeter et al. 2000). In the latter case, productivity gains are predicted throughout the year, with spring and autumn having the higher rates and winter and summer limited by cold and drought, respectively. Considerable interannual variation in production has also been reported (Schroeter et al. 1995). These studies indicate that lichens are rarely active under optimal photosynthesis conditions, often being limited by desiccation at high PAR and high temperatures, and that water availability is the main limitation. However, while it is clear that large-scale productivity gradients must exist, rigorous studies are not yet available across these gradients to permit an integrated approach to their analysis.

Given the lack of comparability in available productivity data, because of the assumptions involved and use of different methodologies, growth rates may provide a useful proxy (Table 5). The majority of estimates are from the northern maritime Antarctic and there are few data overall. There is again a steep productivity gradient from the maritime to the continental Antarctic. For comparable species of mosses, growth rates decline from

10 mm/yr in the northern maritime Antarctic (Sancho and Pintado 2004) to 0.2–4.6 mm/yr in the Windmill Islands (Selkirk and Skotnicki 2007, Clarke et al. 2012) and 0.5–2.6 mm/yr in the Vestfold Hills (Clarke et al. 2012) at the continental margin, to <0.2 mm/yr in the McMurdo Dry Valleys (Brabyn et al. 2005). There is an approximately 100-fold difference in growth rate for crustose lichens of the maritime Antarctic and the McMurdo Dry Valleys (Sancho et al. 2007, Green et al. 2012). Growth rate appears to be strongly linked to precipitation, plateauing above ~700 mm rainfall equivalent. At present, cryptogam growth rates seem to be the best available bioindicator of autotrophic productivity gradients on land in Antarctica, as well as for indicating climate change responses in terrestrial ecosystems.

#### *Disturbance*

Freeze–thaw activity and other periglacial processes are particularly important in Antarctic terrestrial ecosystems (Thomas et al. 2008), with surface layers of soils often too unstable to permit biota to colonize. Periglacial features range in age from those still under active formation to others that are several million years old (Boelhouwers et al. 2003, Hodgson et al. 2012). These features are characterized by a gradient of stability from fine, unstable material to larger stones around the edge. The latter also tend to accumulate snow, providing both water and a substratum for microbial and vegetation community development (Engelen et al. 2008, see also Haussmann et al. 2009).

Extreme events are a form of disturbance, and include, for example, changes in the frequency and duration of climate events, which can have consequences on ecosystem functioning and biodiversity (Smith 2011). The McMurdo Dry Valleys have experienced several recent austral summers with temperatures elevated above the longer-term average. Across the landscape, patches of darkened, wetted ground developed due to changes in hydrology. Two events reactivated non-annual ephemeral streams and generated greater water flow across the land surface. These warming events increased soil moisture, altered soil invertebrate community composition and soil and stream chemistry, as well as increasing lake levels, with many of these effects still apparent the following summer season (Barrett et al. 2008, Nielsen et al. 2012).

Animals are major agents of disturbance to communities and ecosystems globally, typically through predation/grazing, incidental mechanical damage, pollution, or, at a larger scale, by habitat modification. In the Antarctic terrestrial environment disturbance relates largely to the intensity of trampling or manuring impacts associated with marine vertebrate aggregations, around which steep gradients of intensity exist. Where vertebrate populations change in size or location, these result in very rapid changes in the impacted terrestrial ecosystems, whose members are generally unable to

tolerate this type of disturbance (R. I. L. Smith 1988, Bergstrom et al. 2009, Favero-Longo et al. 2011).

#### *Spatial variation at the largest extents*

Broad-scale regional gradients of decreasing terrestrial diversity clearly exist between the sub- and inland continental Antarctic regions (Convey 2013), as might be expected from more general, global, patterns (e.g., Gaston 2000). However, detailed examination of diversity along the Antarctic Peninsula and Scotia arc suggests that this feature is underlain by smaller-scale variation and systematic differences between biogeographical regions rather than latitude per se (Peat et al. 2007, Casanovas et al. 2013). In Victoria Land, there is little evidence for decreasing diversity with increasing latitude, and indeed, one of the most southern sites examined has among the highest diversity levels (Green et al. 2011a). In this region, environmental signals are often underpinned by distribution patterns driven by isolation and subsequent radiation over glacial cycles (Adams et al. 2006, Stevens et al. 2006a). Green et al. (2011b) propose a broad-scale separation of Antarctica into a “microenvironmental” zone at latitudes >72° S, where microclimate is the dominant control of biodiversity, and a “macroenvironmental” zone north of 72° S, where precipitation starts to be influential and latitude-related gradients become stronger. However, survey effort may also explain many of the signals of environmental influence currently proposed. In most areas, survey effort has been low and a strong relationship exists between numbers of records per area and species recorded (Terauds et al. 2012). By contrast, much is known about the diversity of vascular plants, insects, land birds, and seabirds across the Southern Ocean islands, and strong gradients in diversity, associated with available energy (and therefore latitude), are present in native species (Chown et al. 1998).

These broad-scale patterns hide considerable complexity within regions (e.g., Chown et al. 1998, Adams et al. 2006, Stevens et al. 2006a, Peat et al. 2007, Shaw et al. 2010, Green et al. 2011b, Casanovas et al. 2013), particularly relating to the imprint of glacial history and biogeographic isolation (Convey et al. 2008). They also vary with taxa, which may be related directly to dispersal ability (Greve et al. 2005). Evidence for latitudinal gradients in soil and associated biodiversity within Antarctica is equivocal, depending on the organisms and soils considered. A molecular clone library study of soil eukaryote diversity (Lawley et al. 2004), while finding a broad-scale regional difference between maritime Antarctic and inland continental Antarctic soils, failed to identify a gradient across the entire maritime Antarctic. Likewise, data presented by Yergeau et al. (2007) illustrate decreasing microbial diversity across large-scale biogeographic regions, but no gradient in certain habitats within the maritime Antarctic when considered alone, consistent also with a recent study of soil fungal diversity in the latter region

(Dennis et al. 2012). Several recent studies (e.g., Niederberger et al. 2008, Cary et al. 2010, Vyverman et al. 2010) suggest that bacterial diversity in Antarctic soils is considerably greater than previously thought, and hence that lack of survey data compromises identification of any gradients that do exist (Chong et al. 2012).

The biodiversity of Antarctic lakes declines with increasing latitude. As conditions become more extreme, food webs become progressively truncated and dominated by microorganisms. Shallow aquatic ecosystems are dominated by cyanobacterial mats (Quesada et al. 2008, Quesada and Vincent 2012, Vincent and Quesada 2012). Although some cyanobacterial species or genotypes are apparently closely related in microbial mats from different Antarctic regions (Michaud et al. 2012), depending on the measure used their biodiversity is generally distinct (Kleinteich et al. 2012). In the South Shetland Islands (62° S) microbial mats are very diverse, containing numerous eukaryotic algae, fungi, ciliates, rotifers, tardigrades, and nematodes (Velazquez 2011), while, at the continental Dufek Massif (82° S), diversity is the lowest observed in any Antarctic location (Hodgson et al. 2010), with very few cyanobacteria and only three tardigrades and occasional rotifers found. Although community dynamics in microbial mats are yet to be studied in detail, Velazquez (2011) suggests they will be complex. The lakes of the sub-Antarctic islands and the maritime Antarctic contain a significant metazoan community, including benthic and planktonic crustaceans (Pugh et al. 2002), chironomid midges, oligochaetes (Rodriguez and Rico 2008) and, limited to sub-Antarctic South Georgia, dytiscid diving beetles (Arnold and Convey 1998). Six crustaceans are reported from the lakes of Îles Kerguelen (Brehm 1954), and three from the well-studied lakes of the South Orkney and South Shetland Islands. The lakes of the Vestfold Hills, a continental coastal oasis, usually have only one species of planktonic crustacean. Those of the McMurdo Dry Valleys were thought to possess only rotifers (Roberts et al. 2004), although the recent confirmation of a calanoid copepod in Lake House in the Taylor Valley has caused reconsideration of this view (Hansson et al. 2012).

From a mechanistic perspective, large-scale patterns in diversity are ultimately driven by immigration, emigration, speciation, and extinction. Extinction has been assumed to be a key driver of terrestrial and nonmarine aquatic biodiversity patterns in Antarctica through time, with good reason (see e.g., Convey et al. 2009). However, significant refugia are likely to have existed (Fraser et al. 2012). Likewise, speciation has clearly played a role, though it has been less extensively investigated (e.g., Chown 1990, Stevens et al. 2006, Mortimer et al. 2011a). By contrast, colonization, which involves elements of (long-distance) transfer, arrival and survival at an appropriate location, and population expansion, has been much studied. The vast majority of

Antarctic terrestrial, lacustrine, and even some marine benthic communities are effectively islands, separated by sea, ice, or depth (Bergstrom and Chown 1999). In Antarctica, gradients of isolation differ in spatial scale as well as historical extent, and have determined different patterns and degrees of segregation between populations of both marine and terrestrial organisms. Terrestrial communities on the sub-Antarctic islands include elements that show the influence of wind dispersal following the prevailing westerly winds (Muñoz et al. 2004, Bergstrom et al. 2006). Within the continent itself, patterns are most distinct, with little overlap between Peninsula/Scotia arc invertebrate faunas and those of Patagonia/South America. There is increasing molecular and classical biogeographic evidence for ancient radiations and vicariance (e.g., Allegrucci et al. 2006, 2012, Maslen and Convey 2006, Chown and Convey 2007), and/or expansion from refugial centers within the region itself, and survival through (at least) multiple Pleistocene glacial cycles (Stevens et al. 2006, McGaughan et al. 2010, Mortimer et al. 2011a). Even apparently highly dispersible groups such as some Antarctic soil microbiota carry a strong signal of long-term geographical isolation, suggesting that local radiation on evolutionary timescales has outweighed the influence of incoming dispersers (De Wever et al. 2009, Vyverman et al. 2010, Chong et al. 2012, Peeters et al. 2012).

#### *Human impacts*

Human activities have significant impacts on the Antarctic environment on at least three scales: (1) anthropogenic climate change and long-traveled atmospheric contamination, (2) regional activities from scientific operations, marine industries, and ecotourism, and (3) local activities due to station operations and direct human contact (Bargagli 2005, Barnes and Conlan 2007, Tin et al. 2009, Lynch et al. 2010, Aronson et al. 2011, Chown et al. 2012b).

As the planet warms the distributional limits of many more temperate species are likely to shift toward the poles, and in an Antarctic and Southern Ocean context, Patagonia in particular will become a major bottleneck for both marine and terrestrial species movements. Climate change along the Antarctic Peninsula has resulted in temperature amelioration and effectively moved temperature isotherms southwards (Vaughan 2006). Recent evidence shows that warming is widespread across West Antarctica (Bromwich et al. 2013). This change is predicted to lead to expansion of indigenous species ranges, both in terms of local population expansion and by extending distributions further south. Although there is clear evidence for the former (Fowbert and Smith 1994, le Roux and McGeoch 2008b, Parnikoza et al. 2009), instances of the latter have yet to be described (Convey 2011).

While many more local impacts are effectively point sources of disturbance, they can be considered in terms

of gradients of impact intensity. As human effects on ecosystems are focused on ice-free regions, which are more frequent at lower latitudes along with higher densities of human activities, a gradient of these effects is intuitively reasonable, though depending upon accessibility rather than latitude per se (Chown et al. 2012a, Convey et al. 2012b). Even low levels of human activity are, for instance, sufficient to generate a steep gradient of soil compaction and impact on contained invertebrate communities over distances of centimeters to meters (Tejedo et al. 2009). On land and in freshwaters, as well as in the nearshore marine environment, pollution is an important source of disturbance. Although pollution levels in Antarctica are typically several orders of magnitude lower than elsewhere, in places there have been marked local impacts (Bargagli 2005, Kennicutt et al. 2010, Aronson et al. 2011). There is also evidence of strong local gradients in organism response to pollution, and it is expected that the signal of Antarctic pollution to date will take extended periods to dissipate (Hughes and Nobbs 2004, Jaraula et al. 2009).

Recent records of non-Antarctic species indicate the development of a new, human-assisted, means of overcoming the previous isolation of the continent. The increasing extent of human contact with Antarctica, and between different regions within Antarctica, means that the potential supply of nonindigenous species is increasing (Frenot et al. 2005, Whinam et al. 2005, Hull and Bergstrom 2006, Lee and Chown 2009, Chown et al. 2012a). Within this, there is a gradient of “risk,” with the most visited parts of Antarctica, and those with the least extreme environmental conditions, and those warming most rapidly, being most vulnerable to both human-assisted and natural processes of colonization (with the former thought to far outweigh the latter [Frenot et al. 2005, Chown et al. 2012a]). The sign of the relationship between native and nonindigenous species richness can also vary depending on the communities and the underlying human impact and environmental gradients considered, as described on South Island, New Zealand (Tomasetto et al. 2012). These factors underlie both the historical prevalence of introduction events to the sub-Antarctic islands (Frenot et al. 2005, Convey and Lebouvier 2009), and the increasing concerns over the risks to and means of protection of the northern maritime Antarctic in particular and the continent in general (Hughes and Convey 2010, 2012).

#### SPATIAL VARIATION IN MARINE SYSTEMS

The Southern Ocean exhibits significant environmental variability, and therefore gradients, from the short-term fluctuations associated with weather, through the seasonal cycle, to variation on sub-decadal and much longer timescales. Of these, the striking difference between summer and winter at high latitudes has led to the seasonal cycle receiving most attention. For many marine organisms the annual cycles of sea ice and phytoplankton are the key environmental drivers of life

history (Clarke 1988). Sea ice around Antarctica is seasonally variable, reaching maximum extent around September–October. Its formation and growth are affected by temperature (water and air), sunlight, and hydrodynamic conditions. Sea ice is an important habitat, providing substrata, refuges and/or food for taxa as diverse as bacteria, microalgae, amphipods, krill, and cryopelagic fauna including fishes, as well as having a fundamentally important linkage (as a major nursery ground for pelagic species including krill) to the entire Southern Ocean food web (Thomas et al. 2008). Strong gradients are also present over small spatial scales within sea ice, in particular relating to osmotic stress and temperature (both linked with brine concentration), and to light.

#### *Solar radiation and photoperiod*

Within the Southern Ocean there is a small but significant latitudinal gradient in the timing of the availability of PAR in spring, with the season being longer and starting earlier in the sub-Antarctic islands than in habitats close to the continent. The fraction of incident PAR that reaches the water column is also greatly affected by the presence of sea ice (Winkler et al. 2000, Pannowitz et al. 2003b). Paradoxically, the local dynamics of ice can result in the phytoplankton bloom at higher latitudes starting earlier than at lower latitudes (Clarke et al. 2008).

#### *Temperature*

Ocean currents and tidal cycles disrupt the correlation between thermal environment and latitude over much of the world's coastline (e.g., Helmuth et al. 2002). In the Southern Ocean, for instance, the Weddell Sea gyre transports cooled southern water to Signy Island (60° S), giving it a similar thermal profile to that of Adelaide Island at 68° S (Barnes et al. 2006a). However, shallow water (<50 m depth) on the western Antarctic Peninsula has an approximately consistent thermal gradient with latitude that extends from the Ross Sea (76° S) to sub-Antarctic South Georgia (54° S). This gradient is characterized by constant low temperatures with only a 4.4°C range in maximum 10–20 m depth seawater temperature (−0.4° to 4°C). The annual variability is also low in global terms, but increases from 1.6°C at 76° S to approximately 5°C at 54° S.

Below the shallows, at typical shelf depths, variability in sea temperature is much lower and can be broadly categorized into three regimes. The majority of the continental shelf is overlain by cold water. In the case of the wide Ross and Weddell Sea shelves this is destined to become Antarctic Bottom Water. In contrast to this, the western Antarctic Peninsula and southern Bellingshausen Sea shelves are flooded by warmer (~1°C) Circumpolar Deep Water (CDW) (Clarke et al. 2009), which is warmer than the water both below and, for most of the year, above. Finally the Amundsen Sea shelf may represent an intermediate state where warm tongues of

TABLE 6. Summary of the major ice disturbance mechanisms impacting benthic ecosystems in the Antarctic.

Ice type	Disturbance		Impacted Antarctic latitudes†
	Direct impacts	Indirect impacts	
Sea ice	scour	dampens wave action, alters light regime, dispersal	low to high
Ice foot	scour	reduces light, oxygen and water flow to substratum (esp. sediments)	mid- to high
Anchor ice	encasement of seafloor organisms and sediments, removal	dispersal	high
Icebergs	scour	dispersal, colonization (drop stones)	mid- to high

Notes: These disturbances are described more fully in Dayton et al. (1970), Clarke (1996), Barnes (1999), Gutt (2001), and Barnes and Conlan (2007).

† High latitudes are  $\geq 70^\circ$  S, mid latitudes are  $60^\circ$ – $70^\circ$  S, low latitudes are  $50^\circ$ – $60^\circ$  S.

CDW water penetrate, but vary in volume and duration on a variety of time scales (Thoma et al. 2008).

#### *Sea ice duration and extent*

Ice dominates the ecology of Antarctic marine and intertidal environments. In the Southern Ocean an area the size of the continent itself freezes and thaws each year. This creates gradients in light, salinity, and wind mixing over spatial ranges of millimeters to thousands of kilometers and timescales of seconds to months, and has much significance for biodiversity and ecosystem functioning in the Southern Ocean (e.g., Knox 1994, Massom and Stammerjohn 2010). Interactions among sea ice extent, krill, and ecosystem functioning are especially important in terms of functioning and changes to Southern Ocean food webs (e.g., Atkinson et al. 2004, Rogers et al. 2012a), and are the subject of much work as evidence grows of changing sea ice patterns in the region (e.g., Bintanja et al. 2013). Given this interest and the growing numbers of reviews and studies, we focus here rather on benthic systems.

Ice-mediated habitat stability is more prevalent at higher latitudes where sea ice persists for longer each year, or for multiple years, than at lower latitudes (Lohrer et al. 2012). The protection it gives from wind and wave disturbance is exemplified by the contrast between the eastern and western sides of McMurdo Sound ( $78^\circ$  S), which are only 100 km apart. The latter has semipermanent (multi-year) sea ice (and is oligotrophic), while the former has annual sea ice (and is eutrophic) (Dayton and Oliver 1977), and their benthic community compositions are very different (Stockton 1984, Berkman 1990, Berkman et al. 2004, Schiaparelli and Linse 2006).

For the benthos, fast ice is especially significant. It forms in winter, and much of it breaks up and melts during summer, although it may persist as multiyear ice, particularly at high-latitude coastal localities. Distinguishing between fast ice and another component, icebergs, is important. Fast ice stabilizes the water column and minimizes disturbance (e.g., by restricting iceberg movement), whereas icebergs cause disturbance, and are probably the major agent of mortality to

benthos (Barnes and Conlan 2007). Ice formation varies between locations and seasons under the influence of physical (e.g., wind) and hydrodynamic conditions and large-scale climate factors such as the El Niño Southern Oscillation, ENSO, and the Southern Annular Mode, SAM (Arrigo and Van Dijken 2004). Polynyas (areas of seawater that remain unfrozen despite being surrounded by pack ice) also occur at various latitudes and can persist year round, sometimes extending over 100 km (Arrigo and Van Dijken 2003). The considerable interannual variability and local spatial variation in patterns of sea ice formation mean that the timing of formation or breakout can vary widely (Falconer and Pyne 2004). Exceptional phenomena such as major icebergs can have large effects on regional circulation patterns, including preventing ice breakout (Arrigo et al. 2002, Arrigo and Van Dijken 2003, Robinson and Williams 2012) and influencing a variety of fauna from penguins (e.g., Kooyman et al. 2007, Lescroël et al. 2009) to benthos (Thrush and Cummings 2011).

The Ross Sea region provides an excellent example of the biodiversity effects of sea ice, especially since it is one of the few remaining ocean systems relatively undisturbed by humans (Faranda et al. 2000, Cressey 2012). Latitude is one of several variables explaining between-location differences in shallow water macrofaunal and/or epifaunal community composition between three McMurdo Sound locations (Cummings et al. 2006), where it is considered a likely surrogate for ice conditions. Differences in the trophic structure of these benthic food webs are consistent with variation in sea ice, and consequently, food supply (Norkko et al. 2007). Similarly, Antarctic scallop (*Adamussium colbecki*) populations exhibit maximum biomass at shallower depths, and timing of reproduction is earlier at southern McMurdo Sound sites compared with Terra Nova Bay (Chiantore et al. 2001), a pattern attributed to variation in ice cover persistence and predator distribution. A sevenfold increase in primary production from  $72^\circ$ – $73^\circ$  S to  $75^\circ$  S is likewise likely related to a southward shortening of photoperiod and longer persistence of pack ice (Saggiomo et al. 2000). In deeper coastal waters (100–500 m) from northwestern Ross Sea shelf ( $71^\circ$ – $74^\circ$

S), neither latitude nor depth are good predictors of macrofaunal community composition (Cummings et al. 2010). In fact, there is little evidence of simple patterns in Ross Sea benthic assemblage composition with such factors, and distributions are generally better explained by sediment type, hydrodynamic conditions, and iceberg disturbance (Cummings et al. 2010).

#### *Ice scour disturbance*

Ice scour is a key element of marine disturbance in Antarctica (Table 6 [see also Gutt 2001, Gutt and Starmans 2001, Brown et al. 2004, Thrush et al. 2006]). Scouring by sea ice and the ice foot occurs in the intertidal and very shallow subtidal zones (Barnes 1999, Smale et al. 2008a). The form of ice disturbance varies spatially with bathymetry and approximate latitude. Icebergs impact the seafloor from the shallow subtidal to 500–600 m depth, though scours occur at depths down to ~1000 m. Anchor ice disturbance is largely a shallow water (<33 m) phenomenon, resulting in zonation of benthic communities depending on the extent and frequency of its occurrence (Dayton et al. 1970, Battershill 1989, Dayton 1989). However, there are few direct studies of the effects of anchor ice on Antarctic benthos. Anchor ice occurrence varies spatially, being noted in the Ross Sea and Haswell Islands (East Antarctica), but not common in the Antarctic Peninsula region or the South Orkney Islands (Gutt 2001, Barnes and Conlan 2007). Depth thus provides a refuge from scouring, as the intensity declines with increasing depth (Gutt and Starmans 2001, Smale et al. 2007). Below ~30 m, anchor ice is rare, and biological factors, such as competition and predation, predominantly determine faunal distributions (Dayton et al. 1969, 1974).

Considering the slow growth and long development times typical of Antarctic marine ectotherms, the influence of disturbance may be especially important (Barnes 1999, Gutt 2001, Knust et al. 2003, Barnes and Conlan 2007). Survival rates for benthos in iceberg-impacted areas are very low, but differ across taxa (Peck et al. 1999, Lee et al. 2001, Smale et al. 2008a). The degree of ice disturbance on shallow-water encrusting communities increases with latitude from South Georgia to Adelaide Island (54°–68° S [Barnes and Arnold 1999]). In less disturbed areas, marine benthic communities show greater structural complexity, and the rate of species turnover with distance is decreased or mainly under biological control (Dayton et al. 1974, see also Thrush et al. 2010). Winter-fast ice formation reduces the movement of, and consequently damage by, larger icebergs (Barnes 1999). Geomorphological features and other site-specific constraints also create patchiness, even at smaller horizontal scales (~500 m) (Smale 2008). The physical size of scouring agents opens up a size-related gradient of opportunity, whereby habitat selection may promote survival (e.g., Peck et al. 1997). Similarly, cryptic communities exist among rocks and boulders in the intertidal zone (Waller et al. 2006, Waller

2008). Such shelter may also result in a gradient of decreasing grazing pressure on less exposed surfaces (Bowden 2005, Bowden et al. 2006). Some predictability for habitat stability is therefore possible at temporal and spatial scales, as it varies according to seasonal sea ice formation/clearance in areas at different latitudes.

Biological responses to the gradients of ice disturbance with depth exist. Shells of the limpet *Nacella concinna* are three times thicker in the intertidal zone than at 25 m depth, part of a continuous trend in shell thickness with depth existing within a genetically homogeneous population (Hoffman et al. 2010). Likewise, Harper et al. (2012) show a clear relationship between levels of ice scour, shell damage, and shell thickness at a range of sites around Antarctica in the infaunal bivalve *Laternula elliptica*, again within genetically homogeneous populations.

Iceberg disturbance is an important driver of beta and gamma diversity of benthic shelf ecosystems, as it generates communities at different stages of recovery from scour (Gutt et al. 1996, Gutt 2000, 2001, Gutt and Piepenburg 2003). This underlies the apparent higher regional diversity in mollusc assemblages at 71°–72° S compared to southernmost latitudes, which may reflect increased habitat heterogeneity due to scouring (Schiaparelli et al. 2006), although the increased influence of ice foot formation at higher latitudes cannot be discounted. Future collapse of ice shelves together with increased retreat and calving of glaciers means the influence of ice scour is likely to increase over the next century, but will ultimately rapidly decrease as glaciers pass their grounding lines (see Smale and Barnes 2008). For example, in the area local to Rothera Research Station (Adelaide Island), remote sensing data suggest that the decrease in the duration of winter-fast ice over the last 25 years has been 10 times greater than that of the overall vicinity, leading to a rise in iceberg scouring in the shallows and to significant increases in mortality (Smale et al. 2008b, Barnes and Souster 2011).

#### *Glacial influence*

Glacial factors produce a heterogeneous environmental matrix of gradients leading to strong spatial and temporal variation in biodiversity in both the marine plankton and benthos around Antarctica. Phytoplankton blooms often reach biomass levels of >500 mg chl *a*/m<sup>2</sup> in nearshore sites (within 5 km of the shore), but are usually 2–5 times lower than this in offshore waters >20 km from land (Ducklow et al. 2006, Clarke et al. 2008, Peck et al. 2010a). Meltwater runoff causes marked reductions in surface salinities at nearshore sites that can lower salinity in the top 2 m by up to 3 PSU at distances >4 km from the nearest large glacier (Clarke et al. 2008), and effects on salinity can be observed out to the continental shelf margin and at depths to 100 m (Meredith et al. 2013). Glacial freshening may also influence the species composition of the phytoplankton

assemblage (Moline et al. 2000; but see also Garibotti et al. 2005), which may have implications for climate change-driven alterations of community composition and foodweb dynamics.

During summer periods a southward flowing current forms along the Antarctic Peninsula (the Antarctic Peninsula Coastal Current, APCC). Runoff from land and precipitation over the ocean are thought to be the primary sources for the APCC, and the major glacial freshwater inputs are constrained to this water mass (Moffat et al. 2008), which effectively isolates more offshore sites from these inputs. Marine waters also exhibit strong near-surface salinity gradients during sea ice formation and melt. Over 80% of glaciers on the Antarctic Peninsula are in retreat (Cook et al. 2005), and the meltwater outflow can add a local buoyancy flux to the coastal zone, contributing to shallow mixed layers observed inshore along the western Antarctic Peninsula (Dierssen et al. 2002).

Glaciers influence the seabed substratum, resulting in strong gradients in sediment characteristics both along and across the axis of depositional flow (Drewry 1986, Hambrey and Alean 2004). Sediment types change spatially and temporally across a wide range of spatial scales. Strong gradients in sediment type exist with distance from glaciers, glacier size and type, and also with bottom topography entraining sedimentation processes (Dowdeswell et al. 2006). Biodiversity patterns in areas not subject to iceberg scouring have been shown to be primarily controlled by substratum type (Beaman and Harris 2005).

#### *CaCO<sub>3</sub> and compensation depth*

Levels of calcium carbonate (CaCO<sub>3</sub>) solubility in the ocean vary in time and in space. Typically solubility increases with depth, such that below a certain level, the saturation horizon, CaCO<sub>3</sub> dissolves. Geographically, because solubility decreases with temperature, the sub-Antarctic and much of the Southern Ocean have the lowest sea surface saturation levels on Earth. The depth of the saturation horizon is also shallowest in these regions, and in some places the carbonate compensation depth may be only a few hundred meters (e.g., Li et al. 2000). Animals living below the saturation horizon tend to have thinner skeletons, but the nature of the relationship between skeleton thickness and CaCO<sub>3</sub> solubility is complex. The skeletons of molluscs, echinoids, and brachiopods are generally thinner at high latitude, except where ecological factors such as ice disturbance might explain the need for a thick shell (Watson et al. 2012). Skeleton thickness may also be driven by defense against predation, which is thought to decrease with depth and toward the poles (e.g., Harper and Peck 2003, Aronson et al. 2007, Harper et al. 2012).

The depth of the saturation horizon is critical for the synthesis and maintenance of CaCO<sub>3</sub> skeletons by many organisms (Watson 2009, Cummings et al. 2011, Watson et al. 2012), although few studies have addressed their

flexibility over either realistic or evolutionary timescales to respond to changes (see Orr et al. 2005). Importantly, CaCO<sub>3</sub> solubility levels fluctuate on many timescales, notably in the Southern Ocean (and elsewhere) on seasonal and decadal scales due to changes in the carbon cycle. Over longer periods of thousands to millions of years, ocean pH has varied, but not at the rate expected now with rapid CO<sub>2</sub> release (Hönisch et al. 2012). The implications of this are particularly important for the Southern Ocean due to its naturally lower levels of saturation, and it is considered that this will be among the first areas to become under-saturated. Indeed, a recent study provides evidence of widespread shell dissolution in Southern Ocean pteropods (Bednaršek et al. 2012).

#### *Macro- and micronutrients*

Throughout the Southern Ocean macronutrients (N, P, and Si) are usually available in concentrations well above limiting thresholds, except in localized zones in mid- to late summer when high rates of primary production can reduce them to near depletion (Ducklow 2007). In addition to the phytoplankton zonation mentioned above, there are large-scale regions of elevated phytoplankton biomass extending in broadly circumpolar arcs downwind to the east of Patagonia and Australia and downstream of the Scotia arc (Korb et al. 2008). These patterns reflect partial release of phytoplankton populations from micronutrient (trace metal) limitation, specifically by iron (Martin et al. 1994, Boyd et al. 2000, Ducklow et al. 2003). Atmospheric dust deposition is the ultimate source of new iron to the oceans over glacial–interglacial timescales (Jickells et al. 2005). The principal iron supply over timescales of phytoplankton growth and physiological responses is not in dust aerosols, as originally assumed (Wagener et al. 2008), but through dissolved iron being mobilized into the water during contact with sediments and the shelf break (Hopkinson et al. 2007). Intense mixing enriches offshore waters as surface currents flow past irregular topography when water masses interact (Hewes et al. 2008). These inferences are supported by detailed process studies of “natural” iron fertilization conducted near mid-ocean plateaus. Waters over the Kerguelen Plateau are enriched in iron and clearly productive. The fertilization efficiency (an index of carbon export divided by iron input) in this area was up to an order of magnitude greater than in artificial fertilization studies (Blain et al. 2007). A further, but entirely unquantified, source of iron and nutrient fertilization may be through water run-off from land (including under ice), and glacial surface melt containing biologically fixed nutrients, into adjacent coastal waters. If so, this source is likely to become increasingly influential in regions such as the Antarctic Peninsula as its climate warms and consequential glacial and snow melt and runoff increase both in quantity and geographical extent.

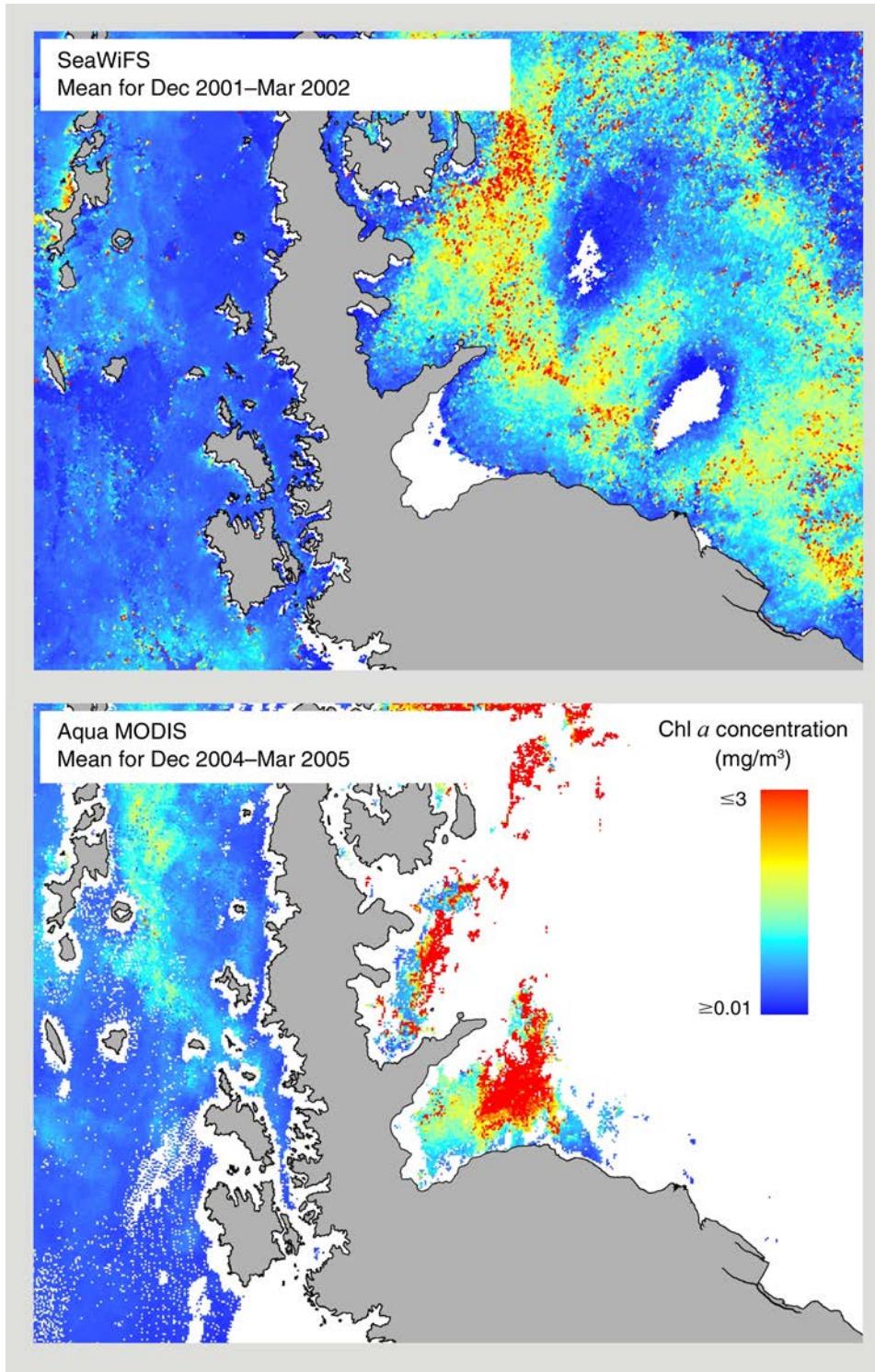


FIG. 4. Satellite images of the Larsen B Ice Shelf showing the ice-covered area in December–March 2001/2002 before its collapse (top), and chlorophyll from the dense phytoplankton bloom that was subsequently present there in December–March 2004/2005 (bottom) (from Peck et al. 2010a).

### Production and growth

Pelagic primary production is dominated by unicellular phytoplankton. Antarctic phytoplankton also include specialized ice algae that colonize the interstitial brine channels of sea ice, where they face intense salinity and temperature gradients (Thomas et al. 2008). In the Southern Ocean, the spatial distribution of phytoplankton biomass and rates of primary production are relatively homogeneous within rough concentric bands, reflecting primarily meridional water mass boundaries around the continent (Treguer and Jacques 1992, Thomas et al. 2008). High standing stocks are found in the marginal ice zones near the continent, there are moderate levels over the shelf and in frontal boundaries, and lower levels farther offshore (Fig. 4).

Light is the principal factor determining rates of photosynthesis and distribution of primary production. Light availability in the water column depends primarily on mixed layer depth (MLD) and (as in freshwater systems) turbidity. Deep mixing circulates phytoplankton cells below the physiological compensation depth where respiration exceeds photosynthesis. Thus rates of photosynthesis are inversely related to the MLD. MLD is also strongly influenced by the extent and duration of sea ice cover and the timing of retreat (Smith and Nelson 1985, Mitchell et al. 1991). When ice retreats early in the season, winds are still strong, mixing is more intense, and primary production tends to be lower, and vice versa when ice retreats later and winds are lower (Vernet et al. 2008). To the west of the Antarctic Peninsula, sea ice advance and retreat are later and earlier, respectively, offshore than nearshore (Stammerjohn et al. 2008a, b), setting up a corresponding gradient in the average summer primary production rate (Fig. 5 and Vernet et al. 2008).

Changing production patterns are apparent off the Antarctic Peninsula, and highlight the complexity of factors contributing to gradients. The nearshore contrast between current high rates of primary production in the south and lower production rates in the north was not as evident in an earlier (1995–2006) period when production tended to be higher in the north than the recent mean condition (Montes-Hugo et al. 2009). Surface chlorophyll concentrations in the northern part of the western Antarctic Peninsula have declined by almost 90% in response to decreasing sea ice duration. In contrast, in the south they have increased by 60%. These effects are modulated by differential north–south changes in winds and cloudiness. In the north, sea ice has declined from moderate to low annual duration, lessening the influence of ice melt on water column stability. In the south, ocean areas formerly covered have opened up and become illuminated, and now support greater production (see Peck et al. 2010a for an analogous consequence of the loss of floating ice shelves on local production).

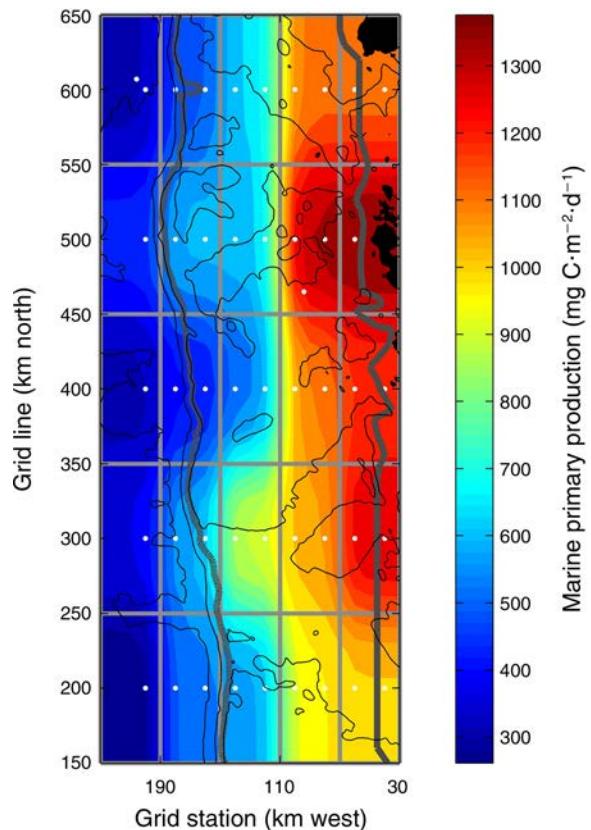


FIG. 5. Mean climatological distribution of marine primary production rates west of the Antarctic Peninsula, 1993–2012. Grid references are kilometers to the west and north of an arbitrary origin at 69.0° S, 73.5° W. The thick gray line on the left represents the continental shelf break (1000 m depth contour); thick gray line on the right delineates the boundary between the coastal zone and continental shelf. The Peninsula is shown in black on the upper right side of the graph (data available online: <http://oceaninformatics.ucsd.edu/datazoo/data/pallter/datasets>).

### Biodiversity gradients within Antarctica

In the Northern Hemisphere there is strong evidence in several taxa (Roy et al. 1998, Clarke and Lidgard 2000) for a nonlinear decline in continental shelf epifaunal diversity from 20°–30° N to the Arctic. In contrast, the Southern Ocean shows far less intense gradients in marine diversity (Gray 2001). Indeed, several taxa (e.g., polychaetes and pycnogonids) are represented at higher than global average levels in Antarctica (Clarke and Johnston 2003, Barnes and Peck 2008). The South Orkney Islands have an overall species richness as high as temperate and some tropical archipelagos (Barnes et al. 2009a). However, while the extremely high richness of many marine taxa in the Indo-West Pacific (IWP) area seems to be caused by the presence of large numbers of rare and small-sized species in the shallows (Bouchet et al. 2002), rare species are far less well represented in the few polar assemblages studied to date (Clarke 2009). The high IWP marine

biodiversity appears to be related to changes in global sea level driven by ice sheet mass changes and ultimately by variability in Earth's solar orbit (Clarke and Crame 1989). Changes in the thermohaline circulation, driven by glacial/interglacial cycles, may have also facilitated the radiation of Southern Ocean fauna into world-wide deep-sea environments, as has recently been demonstrated for deep-water octopuses (Strugnell et al. 2008), and are likely to have played a major role in shaping the diversity of deep-water taxa at a global scale.

Life is typically abundant in the Southern Ocean, but measuring its diversity is difficult because of high community patchiness and a complex hierarchy of scales of spatial variation (Gray 2001, Teixido et al. 2002, Thrush et al. 2010). As elsewhere, such measurement is affected above all by the scale of the investigation (Willis and Whittaker 2002), which can override the influences of age, isolation, and history of any given area. Current estimates of marine biodiversity in most areas of the Southern Ocean probably reflect sampling effort (Clarke et al. 2007), as noted previously for the Antarctic terrestrial environment. This varies from small well-sampled locations such as King George Island, to the Amundsen Sea, which spans almost 40° of longitude, but where no fauna had been collected prior to 2008 (Kaiser et al. 2009).

The vast majority of sampling and knowledge of diversity relates to the continental shelf (Arntz et al. 1994, Clarke and Johnston 2003, Griffiths et al. 2011b). This environment appears to contain few barriers to dispersal around the continent, and thus little evidence of consistent patterns distinct at species or higher taxonomic levels (Griffiths et al. 2009). A range of distribution patterns are, however, apparent in different taxa, depending on both life history and evolutionary history (e.g., Linse et al. 2006, Barnes and Griffiths 2008, Griffiths et al. 2009, Hemery et al. 2012, Strugnell et al. 2012). Some groups, such as pycnogonids, show a global hotspot of diversity within the Southern Ocean, and when examined at a regional scale, have distinct local hotspots such as the South Shetland Islands (Griffiths et al. 2011a). Others, such as gastropod molluscs, show an overall global pattern of reduced diversity at higher latitudes (Linse et al. 2006), but with no evidence of a latitudinal gradient around continental Antarctica (Clarke et al. 2007). Many Antarctic taxa have their northern geographic range limits close to the Polar Front in regions such as South Georgia and Îles Kerguelen, which also host many temperate species at their southern limits (Barnes et al. 2009b, Convey et al. 2012a).

The number of bryozoan species found on island shelves around Antarctica is generally in direct proportion to the distance to the nearest continental shelf (Barnes 2008). There is a clear gradient, especially around the Scotia arc, in distance from supply sources, although analyses of current dynamics and genetics are required to identify these sources (see Linse et al. 2007).

Population genetic and phylogeographic methods are providing new insights into sources of recruits and gene flow around Antarctica (e.g., Hunter and Halanych 2008), and timescales of isolation (Convey et al. 2009). Large-scale oceanographic and atmospheric features can also over-ride physical proximity; for instance, the strong clockwise flow of the Antarctic Circumpolar Current, and west wind drift, have resulted in a signal of decreasing faunal similarity to South America with progression eastwards (Griffiths et al. 2009), meaning that areas such as the Bellingshausen Sea, while being close geographically to South America, have the lowest faunal similarities.

Antarctica is arguably the most isolated large area on the planet, but within the Southern Ocean and continent, sites grade from high connectivity to extreme isolation as well as from great age to very recent origin (e.g., Poulin et al. 2002, Pothoff et al. 2005, Griffiths et al. 2009). Many marine animals have planktonic larvae, and therefore it has been considered that the Antarctic shelf fauna was predominantly circumpolar, while also highly isolated from lower-latitude shelf areas, leading to very high endemism (see Arntz et al. 1997).

Even in instances where Antarctic taxa have previously been thought to show clear affinity with South American relatives (e.g., Dell 1972, Arntz et al. 1994, Dayton et al. 1994) the timescales of evolutionary divergence are often unknown. Molecular studies are increasingly identifying instances of cryptic speciation (Bernardi and Goswami 1997, Held 2003, Held and Wägele 2005, Raupach and Wägele 2006, Hunter and Halanych 2008, Pawlowski et al. 2008), so "species" with ranges spanning, for instance, the Drake Passage or wide (eurybathic) depth ranges must be regarded with caution. Combining molecular techniques, fossil record data and biogeographical evidence gives a powerful tool for estimation of divergence isolation of Antarctic taxa (Strugnell and Linse 2007), revealing a mosaic of different clade-specific patterns and timescales of isolation (reviewed by Convey et al. 2009, 2012a, Allcock and Strugnell 2012, Fraser et al. 2012).

The Scotia arc's submerged ridges and exposed archipelagos are potential "stepping stones" for migration, giving an area where distributional gradients of species could be more marked (Fell et al. 1969). Indeed, within the marine biota of this area, there is a greater affinity with the Magellanic area in its northern branch (Arntz and Brey 2003, Barnes 2005). However, phylogeographic analyses suggest that species disperse from the western Antarctic Peninsula to the Scotia arc (e.g., Linse et al. 2007) rather than from South America (i.e., that the arc provides stepping stones largely from Antarctic rather than Patagonian sources).

The existence of complex genetic structure among and within Antarctic marine species seems to be the result of adaptations that are typical in their life cycles (e.g., the use and duration of pelagic vs. protected larval stages, low mobility of adults), which can sharply limit the

spatial scale of gene flow. This is also modulated by typically very extended life cycles, presumably slowing the overall rate of evolution. Clear examples are given by the broadcast spawning limpet *Nacella concinna*, that has much greater gene flow along the Antarctic Peninsula and Scotia arc, and hence less within-population genetic structure, than the brooding gastropod *Margarella antarctica* (Hoffman et al. 2011a, b). Over the longer term, genetic drift is, therefore, the prevailing evolutionary process (Held and Leese 2007). For example, *Adamussium colbecki*, which has a long, planktotrophic larval phase, shows demonstrable genetic isolation in populations both at relatively large (~450 km) and more local spatial scales (within ~50 km), although the latter differences are of an order of magnitude lower (Guidetti et al. 2006). The genetic and biogeographic structure of this and other species may therefore reflect a complex pattern of isolation events and range expansions occurring at different spatial and temporal scales (further examples in Held and Wägele 2005, Linse et al. 2006, 2007, Barnes and Hillenbrand 2010). However, other species lacking a pelagic larval stage and therefore expected to show high degrees of isolation have instead been found to be capable of substantial dispersal, thereby maintaining genetic homogeneity (Hunter and Halanych 2008). Clearly, considerable caution is required in identification and interpretation of gradients of isolation and gene flow.

#### INTEGRATION

##### *Environmental drivers*

General environmental conditions typical of Antarctic and sub-Antarctic terrestrial environments are reasonably well described (e.g., Walton 1984, Selkirk et al. 1990, Kennedy 1993, le Roux and McGeoch 2008c), although there remains a critical lack of long-term data obtained at biologically relevant microclimatic scales, or a strong linkage between that and meteorological macroclimate (Convey 2011). One example is provided by the integration of melt using degree-days above freezing to explain ecosystem properties influenced by glacial melt stream flows (Howard-Williams et al. 2010). Similarly, the Antarctic marine environment is generally well characterized (e.g., Clarke et al. 2008, Martinson et al. 2008), although in reality data are only available from a few sites, and long-term and year-round data sets are rare. Major environmental drivers in terrestrial ecosystems are photoperiod (defined by latitude), the period temperatures are above 0°C (biological activity threshold), the period of snow/ice cover and the duration of presence of free water. In limnetic ecosystems there are important influences from salinity, nutrient availability, oxygenation, and ice cover and extent. In marine ecosystems ice dynamics (encompassing disturbance, light, and productivity regimes) are considered the major environmental driver. In all environments, stochastic and extreme events are impor-

tant, particularly in the context of local extinction and colonization or recolonization.

##### *Environmental variability*

How and where organisms live are both limited and shaped by the environment around them (Gaston and Spicer 2004). Environmental variability is a major element of this, but it is relatively little studied. Stevens (1989) proposed that environmental variability explained the gross patterns of distribution across the planet, and Grime (1973) was possibly the first to suggest that diversity is highest at intermediate levels of environmental disturbance. Antarctic terrestrial and freshwater systems experience among the most variable temperature ranges on Earth, while neighboring marine systems may vary by only fractions of a degree annually (Peck et al. 2006). Resource availability on land and in aquatic environments is highly seasonal for primary consumers, but less so for scavengers and carnivores in the sea (Obermuller et al. 2010).

The effects of these differences in environmental variability in Antarctica are clear in life histories, the evolution of specific adaptations, and both the functioning rates and biological capacities of the organisms living there. On land the biota show great flexibility, functioning over wide ranges of temperature. Some also exhibit metabolic rates higher at any given temperature than lower-latitude counterparts, thought to be a consequence of the unpredictability of the environment and the temporal restriction of resources (Peck et al. 2006). In contrast marine species show no such rate elevation (Clarke and Johnston 1999), and other biological characteristics of growth, development, and activity are also slowed compared to temperate species (Peck 2002). Discussion of these adaptations is usually based around low-temperature or resource limitation, but strong variability in resource availability combined with temperature stability may be important. Marine species are also very sensitive to elevated temperatures, including some that have the least flexibility known (Pörtner et al. 2007, Peck et al. 2009). Further consequences are seen in the evolution of antifreeze in terrestrial species and marine fish, the loss of haemoglobin in several icefish species, and the loss of the heat shock response in marine species. Freshwater species, like those on land, exhibit large physiological flexibility (Peck 2004). This again suggests that the great temperature variability in these environments is key in driving evolution toward biological flexibility and larger physiological capacities.

##### *Evolutionary rates*

The rate of evolution might be expected to be slower in polar taxa, both directly because of the low temperature (Martin and Palumbi 1993, Gillooly et al. 2005), and also because of longer generation times. There are few estimates available using either fossil-based or molecular techniques for Antarctic biota.

Crame and Clarke (1997) provide the only fossil-based estimate, finding no differences in the diversification rates of 20 molluscan taxa from tropical, temperate, and polar waters. Held (2001) detected no reduction in molecular substitution rates in Antarctic marine crustaceans. Other molecular studies have determined the shape of radiations in key taxa such as teleost fish (reviewed by Clarke and Johnston 1996), euphausiids (Bargelloni et al. 2000), and octopuses (Strugnell et al. 2008, 2012), and rates have been proposed by alignment with key climatic or tectonic events such as the opening of Drake Passage. In notothenioid fishes, an exceptionally increased rate of molecular evolution has been determined for two subunits of the ATPase complex encoded in the mitochondrial genome (Papetti et al. 2007). These two genes show increased rates of amino acid substitutions at functional sites (directional selection) compared to other teleosts and to other mitochondrial encoded genes. This sharply increased rate of evolution may be correlated with the high oxygen content of the cold Antarctic waters, and/or be the consequence of the loss of the mitochondrial *nad6* gene in notothenioid fishes. Stevens and Hogg (2006) reported apparently considerably faster rates of substitution in the same gene sequence isolated from springtails than from prostigmatid mites that regionally co-occur in Victoria Land. Other than these studies, we lack data to judge whether the environmental and ecological gradients present in Antarctica and the Southern Ocean have promoted or slowed evolutionary rates.

One comparative means of estimating evolutionary rates in morphological and molecular components is to assess levels of genetic divergence and variability among morphologically uniform, but geographically isolated, populations. An example is given by the springtail *Friesea grisea*, the only species of this group currently reported from both continental and maritime Antarctica (Greenslade 1995). Torricelli et al. (2010) found unexpectedly high levels of genetic divergence in the mitochondrial genome of *F. grisea*, consistent with the presence of cryptic species. These data suggest that morphological and molecular rates of evolution may be decoupled, the former being restricted by the preservation of adaptation to extreme environmental conditions, the latter being stimulated by geographic isolation and, possibly, increased mutational rates.

#### *Endemism*

Considerable levels of endemism characterize Antarctic biota at both continental/Southern Ocean and intraregional scales, although these are variable across taxa (Greve et al. 2005, Pugh and Convey 2008, Griffiths et al. 2009). Species-level endemism is particularly high in terrestrial arthropods (springtails, mites), and is possibly 100% in nematodes. These findings support an ancient origin for many Antarctic taxa and in situ evolution over multi-million year timescales (Convey et

al. 2008, Vyverman et al. 2010). Evolution over such an extended timescale implicitly includes survival of and adaptation to the increasing environmental and ecophysiological challenges, and supports the research focus on ecophysiological, biochemical, and, increasingly, genomic, studies of organisms from these environments, as “end member” representatives of the suite of gradients and adaptations available on the planet (Peck et al. 2006).

#### *Distribution patterns and diversity*

Antarctica provides gradients in biological diversity and ecosystem complexity, ranging from some of the simplest ecosystems known on land to some strikingly diverse and high-biomass systems in the sea. The simplest faunal communities apparently contain producers, consumers, and predators/omnivores, although specific autecological studies are often lacking (Hogg et al. 2006). Therefore, they intrinsically contain biological and functional interactions, all of which may respond to environmental variability and change. Furthermore, many functional groups are missing from some of these ecosystems. This provides an excellent opportunity for fundamental ecological research on the controls and assembly rules for ecosystem structure, including tests of the predicted relative performance of environmental niche models and mechanistic ones (Kearney and Porter 2009, Gutt et al. 2012). It also implies vulnerability to the introduction of biota contributing some of the “missing” functions.

On a regional scale, the distribution of terrestrial biota is strongly influenced by three major factors: historical contingency, geographical barriers to movement and dispersal, and local availability of suitable environmental conditions (water, temperature, protection, resources). Molecular phylogeographic approaches are greatly advancing our understanding of relationships among populations (Rogers 2007) and their history (e.g., Fraser et al. 2009, 2012, Janosik et al. 2011, Mortimer et al. 2011a, b). At the continental scale, the role of any simple spatial gradient (or environmental factor that this is proxy for) in structuring patterns of diversity is variable and depends on the taxa involved. At the local level, particularly on the continent, the availability of water often obscures the contribution of other biotic and abiotic factors, including temperature (Block 1996, Sinclair 2002). By contrast, across the Southern Ocean islands, conventional energy-related diversity gradients are readily discernible for both terrestrial and marine groups (Chown et al. 1998, Davies et al. 2010, Terauds et al. 2011).

Marine communities, by contrast, do not generally face limited availability of suitable environmental conditions or substrata. The importance of historical contingency is again clear in the levels of genetic structure and differentiation becoming apparent in studies of many (but by no means all) taxa. The fact that these patterns of differentiation rarely as yet appear

to coincide across different taxa (except, at the highest level, demonstrating the importance of the Antarctic Polar Front as an isolating mechanism) suggest that a search for any single overriding mechanism determining large-scale patterns of marine diversity in Antarctica may be unproductive. However, at smaller spatial scales, both biological (e.g., primary productivity) and physical (e.g., ice cover, ice scour, salinity) mechanisms are clearly important determinants of diversity at habitat and community level.

#### CONCLUDING REMARKS

The Antarctic exhibits substantial spatial heterogeneity, superimposed on strong environmental gradients. Many features of this spatial structure show striking parallels to those elsewhere, including the influence of barriers to dispersal on assemblage composition, and of spatial heterogeneity of water availability on small-scale variation in diversity and abundance of terrestrial biota, and the role of disturbance in governing assemblage diversity in the shallow sea. The particular interest of the Antarctic biota comes from a juxtaposition of these factors with those that are specific to Antarctica.

Antarctica is the most isolated large landmass on the globe, has the most extreme seasonality of photoperiod and temperature, and it is at the end of important gradients in key variables such as incident radiation, UV intensity, and mean environmental temperature. It is this combination of isolation, strong gradients, and marked spatial heterogeneity that makes ecological research in Antarctica so important. It provides a natural laboratory for distinguishing the individual effects of temperature and productivity on biological diversity, allows examination of the dynamics of the simplest ecosystems on the planet, and provides the opportunity to probe responses to environmental change in some of the most thermally sensitive organisms known.

Ecological research in Antarctica has revealed a clear indication of the importance of historical legacy. The species that form current assemblages are largely those that have survived glacial cycles, together with a smaller number that have managed to overcome the dispersal and establishment barriers. There are also important legacies in terms of environmental factors such as nutrient availability and ice/snow cover on land, and the location of refugia in both terrestrial and marine realms.

Unexpected and subtle trade-offs are now being recognized that may influence how the system will respond to continued environmental change. A striking diversity is being recognized in many invertebrate groups in the sea, as well as an ever-increasing incidence of cryptic diversity in what were previously regarded as widely distributed species. The extent to which this cryptic diversity is greater than, equal to, or less than elsewhere is currently unknown, but it does point, along with other lines of evidence from molecular studies, to

temperature being no significant barrier to diversification.

There is an urgent need, both intellectual and practical, to understand how ecological systems will respond to continuing environmental change. Ecological work in Antarctica has a significant role to play in furthering this understanding. In some parts of the continent, regional climatic change is among the fastest anywhere (Turner et al. 2009, 2013, Bromwich et al. 2013), and the wide latitudinal range covered by Antarctica allows separation of broad-scale environmental influences from those driven by small-scale heterogeneity. The relative isolation of the system coupled with the marked sensitivity of many of the component species, and a combination of simple and moderately diverse ecological systems, provide an unrivalled laboratory in which to probe among the most pressing problems facing mankind today. The work summarized in this review shows that the important groundwork has been done. We now have an excellent grasp of which features of Antarctic ecology reflect widespread general factors, and which reflect those specific to Antarctica. Future work will require a judicious mix of focused studies to tease out processes, with broad-scale studies along or across spatial gradients of key environmental factors.

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