Ship traffic connects Antarctica's fragile coasts to worldwide ecosystems

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Antarctica, an isolated and long considered pristine wilderness, is becoming increasingly exposed to the negative effects of ship-borne human activity, and especially the introduction of invasive species. Here, we provide a comprehensive quantitative analysis of ship movements into Antarctic waters and a spatially explicit assessment of introduction risk for nonnative marine species in all Antarctic waters. We show that vessels traverse Antarctica's isolating natural barriers, connecting it directly via an extensive network of ship activity to all global regions, especially South Atlantic and European ports. Ship visits are more than seven times higher to the Antarctic Peninsula (especially east of Anvers Island) and the South Shetland Islands than elsewhere around Antarctica, together accounting for 88% of visits to Southern Ocean ecoregions. Contrary to expectations, we show that while the five recognized "Antarctic Gateway cities" are important last ports of call, especially for research and tourism vessels, an additional 53 ports had vessels directly departing to Antarctica from 2014 to 2018. We identify ports outside Antarctica where biosecurity interventions could be most effectively implemented and the most vulnerable Antarctic locations where monitoring programs for high-risk invaders should be established.

anthropogenic impacts | marine conservation | biofouling | traffic networks

Nonnative species drive ecological changes that impact biodiversity and ecosystem services in almost all marine environments and are one of the most pressing global conservation concerns (1–5). While no established populations of nonnative marine species are confirmed in the waters around Antarctica, some species have been observed free living, with the potential to establish populations (6–15), especially as the effects of climate change become more pronounced (16–18). Antarctica has the most isolated marine environments on Earth, as it is the only continent that has no continental shelf link to another continent (19). Furthermore, for 15 to 30 million years, the Southern Ocean and coastal Antarctica have been isolated by ocean currents that have given rise to extreme environmental conditions and limited natural dispersal from ecosystems outside the Southern Ocean (19–22). As a result, Antarctic ecosystems show high levels of endemism and unique combinations of taxonomic groups (19) that may leave them particularly vulnerable to the impacts of nonnative species. The introduction of mytilid mussels or brachyuran decapod crustaceans, for example, would introduce a new type of habitat (mussel beds) or a new form of predation to Antarctic ecosystems (22, 23). The need to "recognize and mitigate human influences," including invasive species, has been identified as one of the six most pressing issues for Antarctic research and management (24–26) and a priority for ecological research globally (22, 27, 28). Antarctica represents the last global opportunity to protect an extensive marine area from the harmful effects of nonnative species.

There is growing awareness that ship activity spreads invasive nonnative species, especially through transport in ballast water and hull fouling (1, 29), including into warming areas of the Arctic (30, 31). Effective mitigation of ship-borne transport of nonnative biota requires quantified and detailed information on ship movements so that appropriate policies, monitoring and biosecurity measures can be implemented. This is especially pressing in Antarctica because no single country or organization controls ship activity, and, with no permanent inhabitants and few visitors compared to temperate or tropical regions, nonnative species may stay undetected without targeted monitoring programs. Moreover, while human disturbance footprints are frequently considered in terrestrial terms (32), they can have major, if less understood, impacts on marine environments (33, 34). In the ocean, a key driver of disturbance is ship traffic, which, in addition to nonnative species introductions, is associated with physical change to the benthos, operational and accidental discharges of pollutants, wildlife collisions, noise pollution, discharge of garbage and debris such as plastics and abandoned fishing equipment, propeller wash, and vessel wake (35).

Identifying the likely sources and introduction locations for nonnative species around Antarctica is essential for developing suitable prevention and mitigation measures. Hull fouling, the focus of this study, is the most likely anthropogenic vector for Antarctica (14, 36, 37). While ballast water discharge can be a major vector of introductions in marine systems (1, 38), the nature of Antarctic logistics means that ballast water is typically taken up in the Southern Ocean and released when vessels reach ports outside Antarctica (37). In addition, regulations

Significance

Ship movements related to fishing, tourism, research, and supply expose the Antarctic continent to human impacts. Until now, only rough estimates or industry-specific information have been available to inform evidence-based policy to mitigate the introduction of nonnative marine species. Antarctica's Southern Ocean supports a unique biota and represents the only global marine region without any known biological invasions. However, climate change is removing physiological barriers to potential invasive nonnative species and increasing ship activities are raising propagule pressure. The successful conservation of iconic Antarctic species and environments relies on addressing both climate change and direct, localized human impact. We have identified high-risk areas for introduced species and provide essential data that will underpin better evidence-based management in the region.

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outlined in the Polar Code (39) and International Maritime Organisation Ballast Water Convention (40) require treating ballast water and midwater exchange to minimize the risk of transfer of organisms. No such regulations exist yet for hull fouling of Antarctic-going vessels, even though such biofouling may be responsible for as many or more global marine introductions in other regions (38, 41–43).

Some species may arrive by rafting on seaweeds (6, 44), upon marine debris (45), or as epibionts of megafauna (46). However, unlike in other regions of the world where rafting can transport vast numbers of organisms across marine regions (47), rafting vectors in the Southern Ocean occur in much lower frequencies than elsewhere (48) because of localized circulations of ocean currents only transporting organisms within the region. This can result in rafting debris taking months to years to travel from sub-Antarctic islands to continental Antarctica (44). Furthermore, floating vectors are frequently blocked by and become encased in the vast envelope of sea ice that surrounds the continent, decreasing survival even of cold-adapted benthic species and, thus, limiting the propagule pressure reaching Antarctic coastlines, especially in areas with high levels of sea ice. In contrast to rafting, ships can make the journey to the Antarctic continent in a matter of days, losing relatively little of their biofouling communities, especially if they circumvent rather than breaking through ice (49, 50). Understanding the patterns of ship activity into and out of Antarctica is key for developing management interventions to minimize the introduction of nonnative marine species and identifying where to focus conservation efforts.

The absence of established nonnative marine species in Antarctica is a boon for conservation, but it restricts the methods available to predict species flow into the region. For example, methods used for global or regional risk assessments of nonnative marine introductions via ballast water and hull fouling (51–54) are not possible for Antarctica, for which data are insufficient on propagule pressure, species introductions, or species spread to validate models. Nevertheless, the potential source of nonnative biofouling species, where they might be introduced to, and the introduction risk from different activities (e.g., research, tourism, and fishing) are all functions of the traffic network of ship operations. Previous studies have shown that global maritime networks are robust and efficient, with few well-connected ports or clusters that also reflect geography and dominant trade patterns (54–59). Our results are a comprehensive quantification of ship traffic associated with Antarctica and a spatially explicit assessment of introduction risk for nonnative marine species in all Antarctic waters.

To quantify the global range and intensity of Antarctic ship-based traffic, we created a ship traffic network using commercial maritime intelligence data provided by Lloyd's Maritime Intelligence and Orbcomm (LLI). Because Antarctica has no recognized ports it has been overlooked in previous maritime network studies (58). We therefore developed a method to combine verified port call data from terrestrial AIS (Automatic Identification System), as used in previous maritime network studies (54, 60), with raw satellite AIS observations of all ship activity south of −60°. The satellite AIS data were used to create Antarctic port equivalents based on known Antarctic locations. Ship observations in Antarctic locations were combined with ships' worldwide port calls from 2014 to 2018, inclusive. Networks were generated for ports and ecoregions [ecologically similar marine areas as identified in the Marine Ecoregions of the World (61)] for all ships and for each activity type (fishing, tourism, research, supply, other). Here, we reveal the extent of the global ship network connected to Antarctica and identify key ports and global ecoregions that are strongly connected to Antarctica, representing likely source regions for nonnative species. We test assumptions that activity is higher

in certain Antarctic locations and that "Antarctic Gateway cities," cultural and logistic hubs for Antarctic activity, are the primary conduits through which ships travel to the Southern Ocean (14, 62).

Results and Discussion

Global Connections. Antarctica is globally connected. Each of the 1,581 ports outside the Southern Ocean in our network [15% of worldwide ports observed by LLI (52)] is a potential source location for nonnative species, suggesting that nonnative species could arrive from almost anywhere on the globe (Fig. 1). The 1,581 non-Antarctic ports in our study represent 86% of nodes in a previous network examining global biofouling from 2012 onwards (52), demonstrating that the Antarctic network overlaps heavily with the global shipping network. The present network, however, was more strongly clustered and overall less dense (*SI Appendix,* Table S5) than the previous network (52). The overlap of our Antarctic ship network with the global shipping network may reflect general increases in global shipping (59), as earlier global maritime networks contained almost half the nodes of our Antarctic network, were more clustered, and showed shorter average paths connecting nodes (54, 56). The overlap between our Antarctic network and previous global maritime networks shows that ships connect coastal Antarctica to the rest of the world and that Antarctica is not as isolated as previously thought.

From our analysis of the most visited regions outside Antarctica, we expect species from northern Europe, southern South America, and the northwest Pacific to comprise the largest proportions of biofouling organisms on Antarctic-going vessels. The composition of the biological communities on a ship's hull is a product of where it has been and how long it spent there; the number of individuals on a ship's hull (propagule pressure) increases with the time spent in ports, and the number of different species (colonization pressure) increases with the number of regions visited (63). In our network, when outside the Southern Ocean, ships spent the most time cumulatively in ecoregions in the Northern European Seas province, followed by the Magellanic province of southern South America and the Warm Temperate Northwest Pacific (*SI Appendix,* Fig. S1). Indeed, biofouling communities on the few Antarctic-going vessels that have been surveyed comprise taxa found in the temperate regions outside Antarctica where those ships are primarily active (14, 36, 37, 49, 50, 64, 65).

Substantial physiological tolerances are required for biofouling organisms to survive the voyages from temperate Northern Hemisphere to temperate Southern Hemisphere or indeed from there to Antarctic ecoregions. Many species, however, have already colonized regions in both hemispheres (42, 66), including species that are abundant in Northern Europe and the Arctic, considered high risk for Antarctica, and found biofouling Antarctic-going vessels (14, 36, 37, 49, 50, 64, 65). Whether they could also establish in Antarctica, either directly or via bridgeheads (27, 52) in the Southern Hemisphere, is uncertain. However, many high-risk species including mytilid mussels, tunicates, bryozoans, and decapod and amphipod crustaceans (14, 67) have widespread distributions from southern temperate regions into the high Arctic (68) and may well be capable of surviving in Antarctica either now or under near-future scenarios (7, 69). Indeed, three species of mytilid mussels, a tunicate, and two decapod crustaceans have all been included in a list of terrestrial and marine species of high concern for Antarctica because of their potential to tolerate Antarctic conditions and have negative impacts on Antarctic ecosystems and biodiversity (67).

Gateways to Antarctica. During 2014 to 2018, 58 ports in 23 countries were departure points for direct journeys to coastal
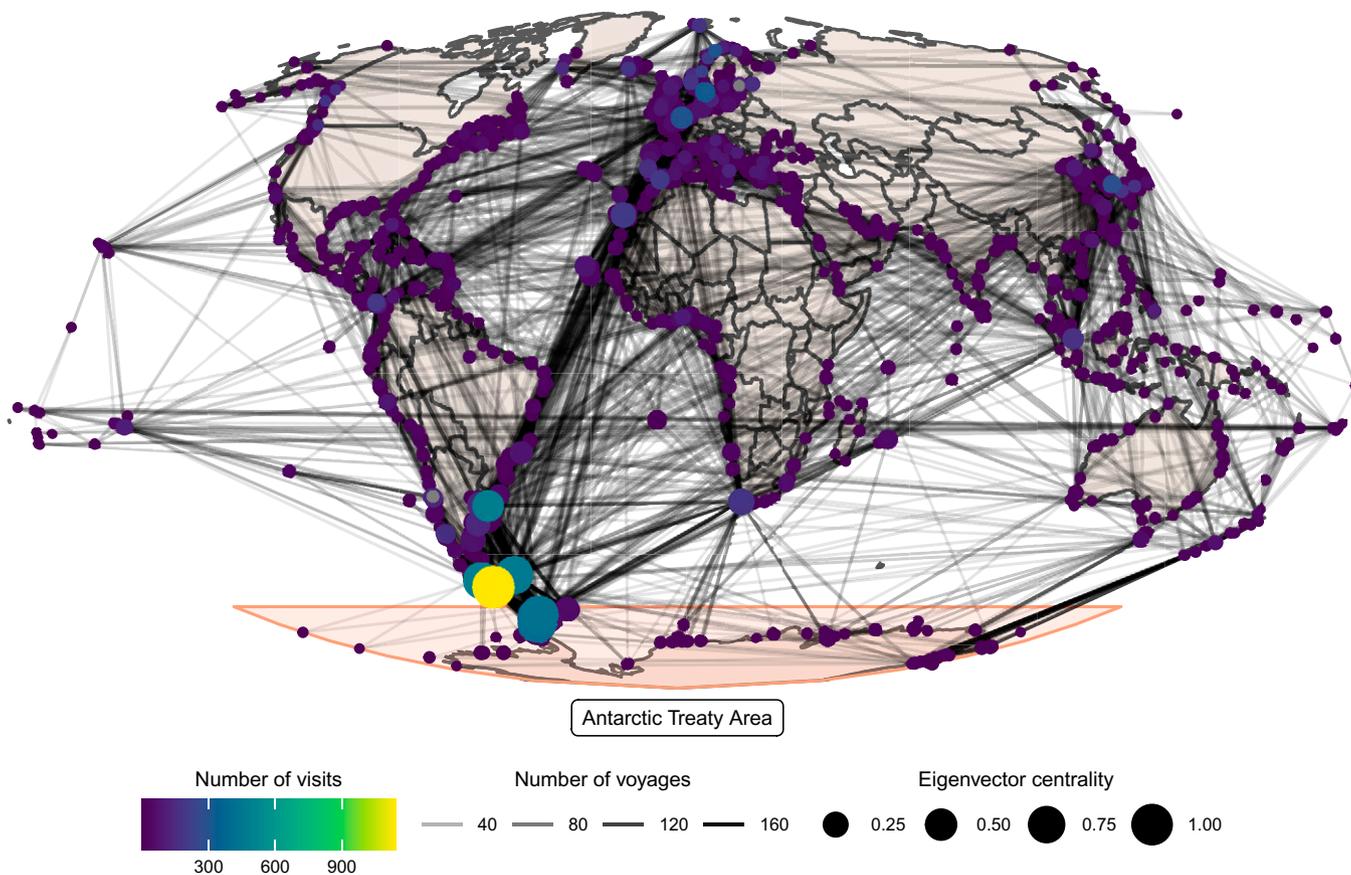
Fig. 1. Global port-to-port traffic network of all ships that visited Antarctica from 2014 to 2018. Ships connect Antarctica to every region across the globe, with important hubs in South America and particularly strong connections throughout the Atlantic to Europe. Lines represent voyages between locations, and darker lines indicating more journeys, but lines do not reflect the path traveled. For example, voyages across the Pacific are represented by lines crossing over continents and the Atlantic Ocean. Circle color indicates the number of visits to each port. Circle size represents eigenvector centrality: the relative importance of ports within the network based on their connectivity to other highly ranked ports.

Antarctic locations (Fig. 2), 33 of which (from 16 countries) had more than one ship departure. This is 10 times more ports than the number of formally recognized "Antarctic Gateway" cities and includes previously unrecognized potential source locations of nonnative species in East Asia, North Africa, and Europe. Five "Antarctic Gateway" cities are formally recognized cultural and logistical hubs for Antarctic activity (both by sea and air) and are assumed to be the primary last ports of call for most voyages into the Southern Ocean (62). These ports have been identified previously as key locations for implementing vessel inspections for safety and biosecurity (70). The importance of Ushuaia (Argentina), Punta Arenas (Chile), Hobart (Australia), Christchurch (New Zealand), and Cape Town (South Africa) for Antarctic activity was formally recognized by the Statement of Intent Between the Southern Rim Gateway Cities to Antarctica 2009.

Despite the wide range of departure ports identified here, the majority of voyages to Antarctica come from a small number of ports. Recognized Gateway cities were last ports of call for 63% of voyages to Antarctica during 2014 to 2018, primarily comprising departures from Ushuaia (47%) and Punta Arenas (11%) (*SI Appendix*, Table S1). Stanley, in the Falkland Islands/Islas Malvinas, is sometimes considered a Gateway city for tourism (62) and was the departure port for 14% of voyages into Antarctica, second only to Ushuaia. The top 10 departure ports (91% of departures) were in seven countries: Argentina, Chile, Falkland Islands/Islas Malvinas, Australia, New Zealand, South Africa, and Uruguay. These nations are all consultative Parties

of the Antarctic Treaty and together comprised 97% of departures. With sufficient support and international cooperation, these nations could perform critical biosecurity and environmental inspections in their ports, in line with Antarctic regulations (70). Channels of cooperation already exist through the Antarctic Treaty System that may address this. For example, the Environment Protocol specifically prohibits the introduction of nonnative species without a permit. The Protocol is implemented by the Committee for Environmental Protection, which has produced guidelines for ballast water exchange (71) and a manual on nonnative species (25) and could be the platform through which decisions are made on the nature and implementation of any biofouling guidelines (72, 73). We recommend that for biosecurity and environmental considerations, the recognition of Gateway cities or responsible port states to be expanded to include at least these seven nations and their ports.

Highest-Risk Areas in Antarctica. The risk of introducing nonnative marine species to a given location via biofouling increases with the number of ship visits (74) and duration of stay (52). Based on these measures, the most likely introduction sites for nonnative marine species to Antarctica are on the South Shetland Islands (SSI) and Antarctic Peninsula, which together received 7.3 times more ship visits than the remaining Southern Ocean ecoregions combined (Fig. 3). The top 20 "highest-risk" locations were primarily in two clusters: the SSI and southeast of Anvers Island on the Antarctic Peninsula (Fig. 3 and Table 1). These areas are frequent landing sites for International

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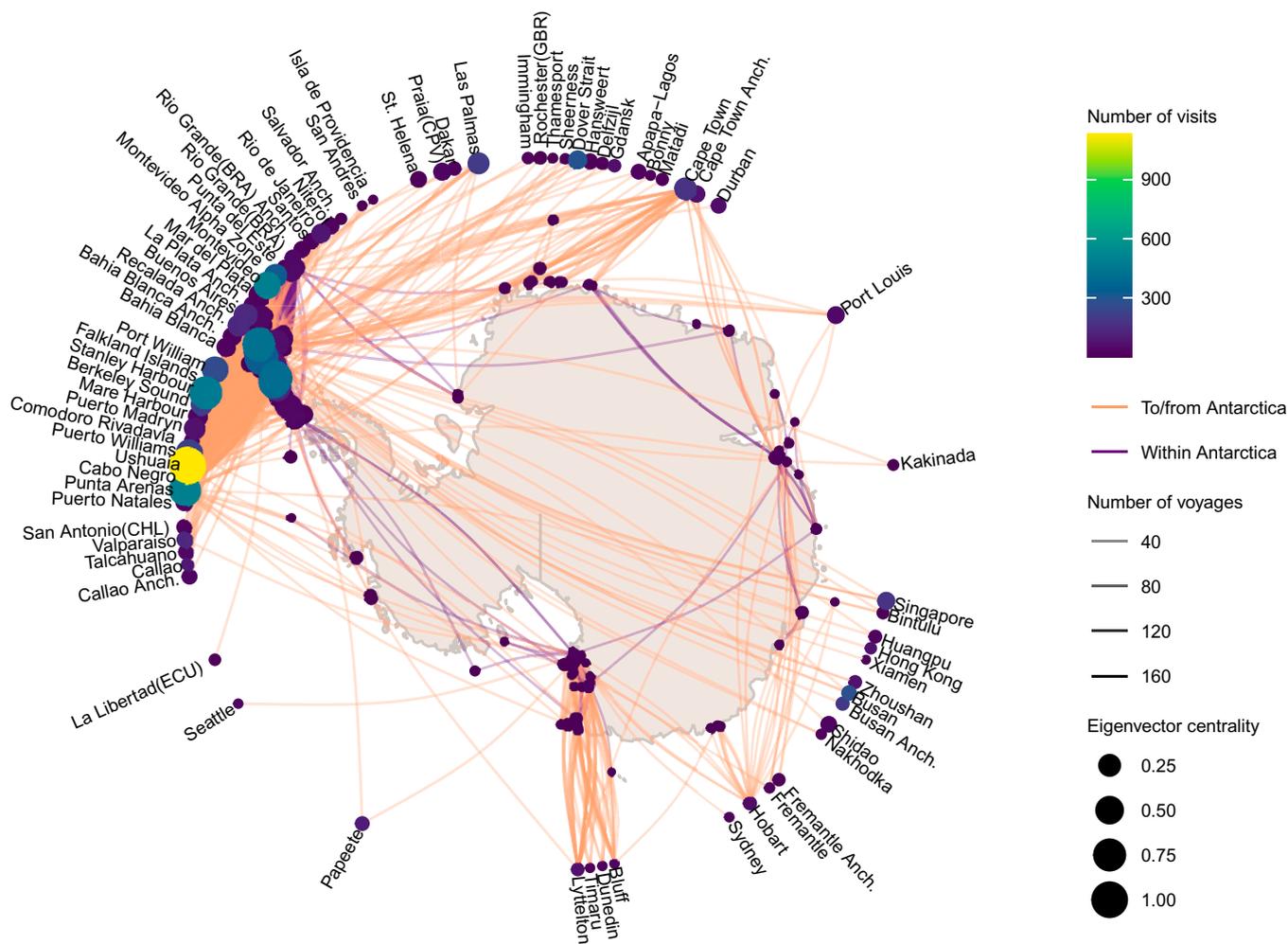
Fig. 2. The port-to-port traffic network of all ships that visited Antarctica from 2014 to 2018 shows 75 ports had direct links to Antarctica, including 58 last ports of call for Antarctic voyages. The most frequently used gateways (90% of port departures) are in South America and the South Atlantic, and 90% of traffic visits the Antarctic Peninsula and SSI. Lines show connections between locations but do not show the path traveled. Line opacity reflects the number of voyages between ports, with darker lines representing more voyages. Circle color indicates the number of visits to each port, and circle size represents eigenvector centrality, the relative importance of ports within the network based on their connectivity to other highly ranked ports.

Association of Antarctica Tour Operators (IAATO) member vessels (75, 76) and are visited regularly by research and supply vessels servicing the 46 research stations and facilities located along the Antarctic Peninsula and SSI, which comprise 42% of all Antarctic facilities (77). Our results provide quantitative support from recent ship activity to focus increased protection on the Antarctic Peninsula and SSI (78).

Certain vessel types, including research vessels, fishing vessels, and yachts, may have a higher probability of introduction via biofouling than most cargo and passenger vessels because they have longer periods of average duration of stay (52). We found that research vessels stopped for, on average (± SD), 1.61 ± 2.52 d, longer than tourism (17.2 ± 14.43 h) but shorter than fishing (2.44 ± 4.45 d) and supply vessels (2.61 ± 4.5 d). We also found that while tourism accounted for 67% of visits to all Antarctic locations (followed by research, 21%; fishing, 7%; supply, 5%; and other, <1%), research vessels were the only activity type with connections to all areas of the continent (*SI Appendix*, Fig. S2). Some locations were visited almost exclusively by a single activity type and others by all kinds of vessels. For example, in the top 20 sites (Fig. 3), Dovizio Rock (ranked first) received a wide range of vessel types including fishing

(32% of visits), tourism (32%), research (9%), and supply (25%). However, >99% of visits to Kerr Point (ranked 10th) were from tourist vessels. Maxwell Bay, the second site overall, was the most visited site by research vessels, yet they only accounted for 35% of visits. In contrast, at Cheshire Island (ranked 11th), which is located off the British Antarctic Survey's Rothera Research Station, research vessels comprised 88% of all visits. Meanwhile, 52% of visits to Mario Zucchelli Station (ranked 19th) were from supply vessels. Therefore, while comprising only 26% of visits to Antarctica, research and supply vessels may pose a relatively high introduction risk to certain locations. Since different vessel types, because of their activity within the Antarctic region, are managed by different organizations, protection from nonnative species may require tailored solutions for different Antarctic locations and cooperation between management organizations.

The likelihood of an introduced species establishing a population is not only a factor of propagule pressure (in this study ship activity is used as a proxy) but also the interaction between environmental conditions and physiological traits of the nonnative species (14). Since Antarctic-going vessels spend most of their time in temperate waters (*SI Appendix*, Fig. S1), we expect
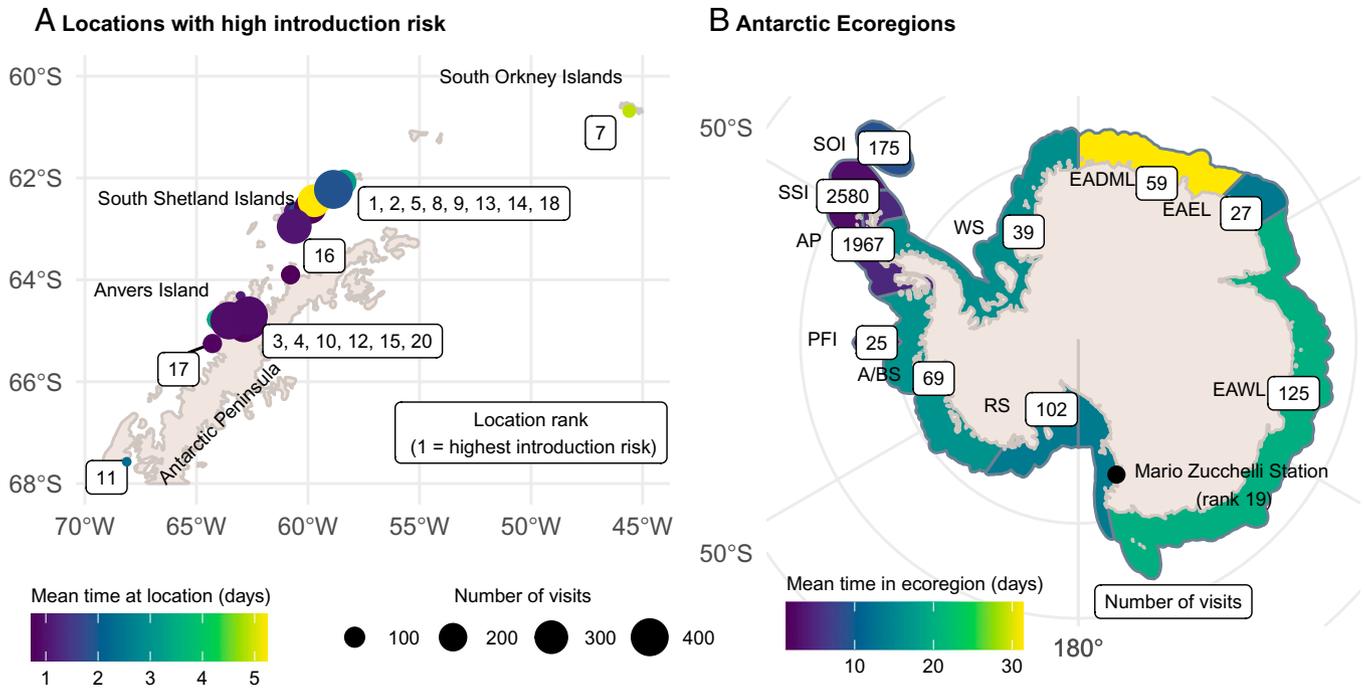
Fig. 3. Ship activity in the top 20 Antarctic locations at risk for introduction of nonnative marine species and the Antarctic marine ecoregions. (*A*) 19 of the top 20 Antarctic locations at risk for nonnative marine species introductions (the other location, Mario Zucchelli Station, ranked 19, is in the Ross Sea, and its location is shown in *B*). Locations shown are on the SSI, the Antarctic Peninsula, and the South Orkney Islands. Circle color represents mean time stopped, and size represents the number of visits. The number label refers to rank in Table 1: 1 Dovizio Rock, 2 Maxwell Bay, 3 Kristie Cove, 4 Gloria, Punta, 5 Deception Island, 6 British Point, 7 Berry Head, 8 South Bay, 9 Potter Cove, 10 Kerr Point, 11 Cheshire Island, 12 Theta Islands, 13 Walker Bay, 14 Point Thomas, 15 Coughtrey Peninsula, 16 Bombay Island, 17 Argentine Islands, 18 Girardi, Islote, 19 Mario Zucchelli Station, 20 Andvord Bay. (*B*) Antarctic ecoregions; ecoregion color represents the mean time stopped by ships. The number of ship visits is shown in the number label on each ecoregion. A/BS, Amundsen/Bellingshausen Sea; AP, Antarctic Peninsula; EADML, East Antarctic Dronning Maud Land; EAEL, East Antarctic Enderby Land; EAWL, East Antarctic Wilkes Land; PFI, Peter the First Island; RS, Ross Sea; SOI, South Orkney Islands; WD, Weddell Sea.

that most biofouling will be species with predominantly temperate or cool temperate distributions that are ill-suited to current Antarctic conditions. Further, the absence of nonnative species around Antarctica has been at least partially attributed to the cold temperatures acting as a physiological barrier (14, 23, 79–82). Yet, most of the top 20 at-risk sites (Table 1) are in the warmest (83) and fastest-warming (16, 17) coastal areas of continental and maritime Antarctica and therefore represent the locations most likely to be the first to become habitable by nonnative species in the future.

In our top 20 Antarctic sites, four have conservatively estimated sea surface temperatures over 0 °C for approximately 3 months (25%) or more of the year (Girardi Islote, Theta Islands, Dovizio Rock, Kerr Point). Three sites (Deception Island, Theta Islands, Bombay Island) were ice-free for approximately eight months or more per year, providing substantial time for growth and reproduction for species that can survive but not reproduce in ice-covered waters. Deception Island, ranked fifth, had 277.0 ± 25.1 ice-free days per year and estimated sea surface temperature over 0 °C for 10.9 ± 3.2% of the time during the study period. Further, Deception Island has geothermal activity that creates warm temperature anomalies (0 to 6 °C in winter) in coastal environments (84), which may facilitate the survival of nonnative species from temperate regions. We expect the sites that rank higher on factors relating to both propagule pressure (ship-related factors) and environmental conditions (warmer temperatures and less sea ice), for example, Dovizio Rock, Maxwell Bay, and Deception Island, would likely be the first sites for nonnative species to establish.

No nonnative marine species have been demonstrated to have established in Antarctica; however, 10 species have been recorded that were likely transported via ships (7, 14). Six of

these 10 species were found in the SSI. Juvenile nonnative mussels, *Mytilus cf. platensis*, were found at Maxwell Bay (also known as Bahia Fildes) (7), the most visited site in Antarctica in this study. Further, live nonnative kelp (*Macrocystis pyrifera* and *Durvillaea antarctica*) and epibiontic species, including the invasive bryozoan *Membranipora membranacea*, were reported for the first time in Antarctic waters in 2020 at Deception Island and Livingston Island (SSI, location of South Bay, Walker Bay, and Girardi Islote) (6). Although they likely arrived via kelp rafting rather than on a ship-mediated transport (6), their survival in these locations indicates that environmental conditions may already be suitable for some temperate invasive nonnative species to survive in the most heavily visited Antarctic locations. It appears we may be on the cusp of the establishment of nonnative marine species in Antarctica. We recommend establishing coordinated monitoring programs at the highest-risk sites (Table 1) to facilitate early detection and rapid response to managing nonnative species.

Calls to protect the Antarctic Peninsula from human impacts are stronger than ever (78) and rely on accurate evaluations of where human activity is most intensive. We have shown that ships connect coastal Antarctic ecosystems to all regions of the world, but especially coastlines in southern South America, Northern Europe, and the western Pacific Ocean. With many ships alternating activities between Arctic and Antarctic summers, there may be potential for transporting cold-adapted species. We have identified that 88% of visits to Antarctic ecoregions are to the Antarctic Peninsula and SSI and that ships travel to Antarctica from a wide range of departure ports in all continents. We see a clear requirement for wide-scale data collection on species being transported by ships, especially from vessels working in the Arctic or cold temperate regions and

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Table 1. Top 20 sites at risk for nonnative species introductions, based on the total number of visits, number of ships, and median time stopped from 2014 to 2018 inclusive, and four sites from East Antarctica for comparison

Rank	Place (ecoregion)	No. of visits	No. of ships	Median time stopped (h)	Visit trend	Estimated percentage of annual sea surface temperature above 0 °C (mean ± SD)	Estimated annual ice-free days (mean ± SD)
1	Dovizio Rock (SSI)	284	79	35.3	=	24.5 ± 2.4	194.0 ± 21.0
2	Maxwell Bay (SSI)	424	64	22.2	+	19.1 ± 2.6	135.0 ± 17.7
3	Kristie Cove (AP)	105	23	50.6	=	19.7 ± 5.6	69.0 ± 21.5
4	Gloria Punta (AP)	392	47	15.5	+	19.0 ± 7.0	12.0 ± 4.9
5	Deception Island (SSI)	326	58	14.3	=	10.9 ± 3.2	277.0 ± 25.1
6	British Point (SSI)	150	16	21.4	−	5.2 ± 2.1	37.8 ± 10.4
7	Berry Head (SOI)	48	14	35.9	=	6.8 ± 4.1	140.8 ± 56.1
8	South Bay (SSI)	72	23	20.8	+	19.8 ± 4.3	148.0 ± 20.9
9	Potter Cove (SSI)	68	20	21.0	+	15.3 ± 2.6	147.0 ± 13.8
10	Kerr Point (AP)	402	43	12.2	=	22.8 ± 2.7	29.2 ± 8.4
11	Cheshire Island (AP)	41	12	32.8	=	18.6 ± 5.7	207.8 ± 53.2
12	Theta Islands (AP)	41	24	19.6	=	31.5 ± 4.0	246.3 ± 15.36
13	Walker Bay (SSI)	64	30	14.6	+	16.0 ± 3.7	176.1 ± 20.0
14	Point Thomas (SSI)	125	22	12.8	−	15.9 ± 2.6	59.6 ± 3.4
15	Coughtrey Peninsula (AP)	287	38	10.0	+	8.4 ± 2.3	6.2 ± 4.3
16	Bombay Island (AP)	82	26	12.	+	18.8 ± 3.9	234.6 ± 8.7
17	Argentine Islands (AP)	82	25	12.4	−	15.9 ± 2.5	145.6 ± 20.7
18	Girardi, Islote (SSI)	269	44	9.7	+	30.3 ± 2.2	226.0 ± 23.0
19	Mario Zucchelli Station (RS)	23	11	23.5	−	8.6 ± 3.7	74.6 ± 12.3
20	Andvord Bay (AP)	312	39	9.2	=	21.2 ± 3.1	13.6 ± 3.5
East Antarctic locations for comparison							
32	Arrival Heights	23	8	20.3	−	0.1 ± 0.3	26.5 ± 20.5
60	Anchorage Island	10	2	165.4	=	13.60 ± 2.1	22.6 ± 5.4
90	Cuvier Island	7	2	86.7	=	4.0 ± 2.6	3.6 ± 5.9
230	Atka Bank	3	2	3.6	=	0.04 ± 0.08	47.0 ± 11.3

Additional factors are related to the possible introduction and survival of nonnative species from outside the Southern Ocean. AP, Antarctic Peninsula; RS, Ross Sea; SOI, South Orkney Islands. Visit trend is increasing (+), decreasing (−), or steady (=), based on the cumulative mean number of visits from 2014 to 2018 (*SI Appendix*, Fig. S3). Mean winter temperature for the top 20 locations shown range from −1.727 °C to −1.379 °C and for East Antarctic locations −1.890 °C to −1.784 °C, data from NOAA World Ocean Atlas (113). The mean ice-free days and estimated percentage of days above 0 °C for each location is for 2014 to 2018.

then Antarctica for significant parts of the year. We now call for Antarctic researchers and managers from all sectors and nations to work together to set up monitoring programs in the most at-risk sites, to support nations with Antarctic departure ports to ensure biosecurity protocols and environmental protection measures are employed, and to take the information presented here to inform decisions that choose a brighter future for Antarctic biodiversity (85).

Materials and Methods

Data Acquisition and QC.

Ship movements. Ship voyage data for Antarctic-going vessels were purchased from LLI, one of the most reliable sources of maritime intelligence and ship movement information. The database includes ships with IMO numbers but excludes many noncommercial and sailing vessels. As there are no recognized ports in Antarctica, previous global studies using port call data to assess introduction risk from global shipping have not included data for Antarctica (51, 52, 54). To address this gap, satellite AIS data for all ships that entered the area south of −60° latitude ("Southern Ocean sightings") were obtained from 2014 to 2018, inclusive. For those ships that entered the area south of −60°, we obtained worldwide port call data ("movements") for the same period. Two sets of satellite AIS data (and movement data from some additional ships) were supplied and extracted by Informa using slightly different methods (all satellite AIS location fixes and summarized satellite AIS location fixes) but were checked using the same quality control procedure. The data required considerable

quality control to filter out ships with false positive satellite AIS reads (*SI Appendix*, Table S2) for observations and ships at each stage. This was a six-stage process with the following criteria (stages 1 to 3 were conducted together manually in Microsoft Excel, and stages 4 to 6 were conducted in R (86–93)]:

1. If all the ship's Southern Ocean sightings were on land, the ship was removed from subsequent analyses.
2. If the ship's port calls clearly conflicted with its Southern Ocean sightings, it was removed.
3. If the ship was a wholly unsuitable vessel, it was removed. If there was any doubt, the ship was not removed. Small tugs and inland barges were considered unsuitable. They typically also had other factors that made them likely false positives, e.g., few, disconnected Southern Ocean sightings and unlikely (and some impossible) port calls.
4. All duplicated readings (from both Southern Ocean sightings and port call movements) were removed along with any missing a date/time fix or satellite sightings that overlapped with land.
5. A speed filter (94) was applied that removed all points that would require a ship to travel faster than 60 km/h (maximum theoretical speed plus 10% for the fastest vessel in these data, based on selection of 15% of vessels, from all vessel and activity types).
6. After each stage of filtering, all ships that no longer had any AIS sightings in the Southern Ocean were removed.

Port and ship details. Metadata on ships and the ports they visited were provided by LLI. All ports with missing information had country, region, and

coordinate information added manually. Seven locations that appeared in port calls only as very large regions did not have missing information added because it was not possible to verify a suitable replacement port. The locations and number of observations for each are as follows: "China," six observations; "Greenland," eight observations; "Indonesia," six observations; "Newfoundland," two observations; "Queensland," one observation; "Venezuela," 10 observations; and "Vietnam," four observations. Most replacement coordinates were taken from MarineTraffic.com (95) by searching for the port name. When that was not available, a suitable anchorage or lighthouse location was chosen. One Antarctic location was verified using the Scientific Committee on Antarctic Reserach (SCAR) Gazetteer of Antarctic Place Names (96).

During stages 1 to 3 of quality control, each ship was assigned an "activity type" of tourism, fishing, research/national operations, supply, or other. Ships were allocated based on their presence on the IAATO member vessels list (tourism) (97), Council of Managers of National Antarctic Programs (COMNAP) list of vessels (research/national operations or supply) (98), or Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) list of licensed fishing vessels (fishing) (99). Ships that were not found on any of those lists were allocated to "supply" or "other," depending on the vessel type. "Other" includes vessels used by nongovernmental and activist organizations and private yachts. Each ship was given an ice classification of low, medium, high, or NA (for cases where the information was not available).

Marine ecoregions. Ship observations and ports were assigned to their relevant ecoregions, provinces, and realms based on the Marine Ecoregions of the World (61, 88).

Network Creation.

Ports in Antarctica. Since there are no recognized ports in Antarctica, the satellite data for the Southern Ocean were used to identify Antarctic locations, which act as port equivalents because they are regularly visited and ships spend significant time there at rest. Potential coastal locations around Antarctica were identified using the Scientific Committee on Antarctic Research (SCAR) Gazetteer of Antarctic Place Names (96), with a preference for UK names when multiple names existed. Because the accuracy of satellite AIS observations is variable and many of the features described in the gazetteer are fairly large, buffer zones of 5-km radius were created; any ship observation within the buffer zone was considered to be visiting that site (equivalent to a port call) (87, 88, 90–93, 100–102). The buffer zone of 5 km was chosen because it reflected the distance between most distinct stopping points in crowded areas, such as the SSI, and was a suitable size for most of the features described.

In many cases, the 5-km buffer zones of nearby locations overlapped, creating clusters of locations. Some ship observations were located within the buffer zones of multiple locations. To ensure ship observations were recorded only in one buffer zone, locations were iteratively removed by the following:

1. Taking the visited circles with 1-km buffer, identifying clusters of overlapping circles.
2. For clusters with fewer than 10 overlapping locations, the top location per cluster based on number of unique ships (and number of observations) within the circle was selected.
3. For clusters with more than 10 overlapping locations, all were kept.
4. Steps 1 to 3 were repeated for 2-km buffers, first removing all locations that had been removed with 1-km buffers, and again for the 5 km, first removing all locations that had been removed in the 1-km and 2-km stages.
5. For the extremely busy areas such as around the Antarctic Peninsula, the final and most suitable nonoverlapping sites were manually selected to best represent the ship observations and known landing sites.
6. Ship observations were assigned to the Antarctic location they overlapped (88). If they did not overlap with any designated Antarctic location, they were considered "offshore."

In this manner, 126 Antarctic locations were identified and added to the list of 1,848 worldwide ports. We found that 19% of Southern Ocean observations were registered within 5 km of the Antarctic coastline. Approximately 6% of Southern Ocean observations are considered visiting the 126 Antarctic locations; this is 30% of observations within 5 km of the shore. Of the 255 ships that passed the quality control procedure, 157 (62%) were observed within 5 km of the coastline; 113 of these (44%) ships in total (72% of the ships observed within 5km of the coastline) visited an identified Antarctic location. Therefore, 113 ships were included in the port-to-port network analyses.

Port networks. Networks are composed of nodes (or vertices) and edges, which are the links between nodes. The Southern Ocean sightings and port call data were combined to form an edge list of voyages between ports, from

which a directional network, weighted by the number of voyages for each edge, was created (88, 103–107). The node list was created by combining the list of ports provided by LLI with the selected Antarctic locations described above. The network was weighted by the number of visits to each port. Total time and median time spent in each port and connecting ports were calculated and included as node or edge attributes, as applicable. Equivalent networks were created for each ship activity type: fishing, tourism, research, supply, and other.

Ecoregion networks. Weighted, directional networks with ecoregions, rather than ports, as nodes were created for all ships and for each activity type. The network was weighted by the number of visits in each ecoregion. The Marine Ecoregions of the World (61) in the Southern Ocean captured 81% of the satellite AIS Southern Ocean observations from LLI (after quality control processing). Of the 255 ships, 217 (85%) were observed within ecoregions and included in ecoregion-to-ecoregion network analyses. Total time and median time spent in each ecoregion and connecting ecoregions were calculated and included as node or edge attributes, as applicable. Time spent for ecoregions outside the Southern Ocean was calculated from the arrival date and time at a given port to the departure date and time of the last port within the same ecoregion if the next port visited was in a different ecoregion. For ecoregions within the Southern Ocean, time spent was calculated from the first to last observation (of a given ship) within a given ecoregion.

Figures were created in R (86) using the packages "tidyverse" (87), "sf" (88), "tidygraph" (103), "ggraph" (107), "nngeo" (108), "raster" (109),"rnaturalearth" (106),"igraph" (101), "ggrepel" (110), and "cowplot" (89).

Identifying highest-risk areas. A list of the "top 20" locations with the potentially highest risk of nonnative species introductions was created and included in Table 1. We consider that the risk of any nonnative species being introduced to Antarctica is linked to propagule and colonization pressure and is distinct from the risk of species establishing in a new location, which is related to environmental factors and individual species tolerances. As data on introduction or establishment rates are not available for Antarctic marine ecosystems, methods relying on quantified propagule pressure and known establishment events to create probabilities of invasion (51, 52, 60, 111) were considered unreliable methods for this context. Hence, we have adopted an approach to estimate approximate introduction risk for different locations using features of ship traffic as proxies. These locations were identified by ranking all Antarctic locations by the following criteria: number of visits, number of ships, and median time stopped (higher values in each resulting in a higher ranking). The mean of the three ranks was calculated for each location and used to create the final ranking, from which the top 20 sites were selected. In this case, we consider number of voyages to be a proxy for propagule pressure (number of individuals). We consider number of ships to be a proxy for colonization pressure (number of species), since the unique voyage history of each vessel will likely result in different species inhabiting different vessels. Median time stopped is included to acknowledge that more time in a given location increases the potential for organisms to be transferred from a ship's hull to the environment. Four sites from East Antarctica were also included in Table 1 for comparison.

To provide contextual information on key environmental conditions in each of the top 20 locations, we estimated the number of days above 0 °C and the number of ice-free days. Since Antarctic-going vessels collectively spent more time outside of polar regions, species found on these vessels are more likely to be temperate species and the ability to withstand cold temperatures and the effects of ice are likely to be critical factors relating to the potential establishment of nonnative species in Antarctic waters. The number of days above 0 °C was selected because water temperatures in the nearest cold temperate environment of southern South America rarely drop below 0 °C and, when they do, are below 0 °C for very short periods (7). In addition, the impact of cold temperatures on physiological processes, especially reproduction, in marine invertebrates (112) is such that the cumulative time at low temperatures may determine whether or not a given species is able to complete its reproductive cycle. Likewise, for species that rely on ice-free coastal areas for reproduction, the number of ice-free days is a key factor that could determine successful establishment. We acknowledge that these thresholds are likely to be species-specific, or even population-specific, and warrant further research for species and populations already within invasion pathways to Antarctica.

Mean winter surface temperatures from 2005 to 2017 for selected Antarctic locations were obtained from the National Oceanic and Atmospheric Administration's World Ocean Atlas 2018 (113). Estimates of annual sea surface temperature above 0 °C were generated using NASA Oceancolor Aqua Modis satellite data (114) for 8-d periods each calendar year 2014 to 2018 in 4-km grids. The number of 8-d periods for which each grid was greater than 0 °C was calculated, then extracted for all grids that overlapped select

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Antarctic locations within a 5-km buffer and the mean calculated for each calendar year in 2014 to 2018 inclusive. Since not all grids had data for each 8-d period because of sea ice and cloud cover, the number of periods with data were also extracted for each location. Annual estimates of sea surface temperature over 0 °C were calculated by taking the percentage of 8-d periods over 0 °C out of the total possible 46 periods per year. It was assumed that 8-d periods with no data would frequently represent sea-ice cover, which indicates a sea surface temperature below 0 °C. As such, our values underestimate of the proportion of time when sea surface temperatures are above 0 °C, especially for locations that are ice-free for most of the year.

The number of ice-free days for the top 20 most at-risk locations were calculated from the Advanced Microwave Scanning Radiometer 2 (AMSR-2) Sea-ice concentration data (115) for each calendar year 2014 to 2018, based on pixels that are 6.25km square and an ice-free threshold of 15%, a typical threshold used to delineate sea-ice edges. The number of ice-free days was extracted for all raster pixels that overlapped the points within a 5-km buffer and the mean of those pixels taken for each location each year. Atka Bank (each year), Cuvier Island (2014 and 2017), and Arrival Heights (2018) did not have data pixels within a 5-km buffer, so a 10-km buffer was used instead. The mean number of ice-free days and the SD was then calculated for the 5-y study period.

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