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Research Article

Range expansion within the northern USA by the accidentally introduced *Carabus granulatus* Linnaeus, 1758 (Coleoptera: Carabidae)

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Abstract

The Palearctic ground beetle *Carabus granulatus* Linneaus, 1758 has been accidentally introduced to North America on multiple occasions. We review previous reports of its North American colonization history, and document range expansion into northern California, Montana, New York state, Vermont, and Maine. We also review its several reported interceptions. The species is eurytopic, occupying marginal heathland and open wet forest habitats in the Old World, and is not particularly associated with human habitation. New World populations retain these habitat preferences, with established introductions often occurring along coastlines or waterways. Spread by the flightless *C. granulatus* in North America is compared to two other carabid species introduced to North America: 1, the exceedingly synanthropic, also flightless, *Carabus nemoralis* Müller; and 2, the flight-capable, extremely eurytopic *Nebria brevicollis* (F.). Geographic expansion in all three species is positively associated with breadth of habitat preference, dispersal ability, and degree of synanthropic association. For all three species, transport via human activities is an important factor promoting range expansion. Based on the Palearctic distribution of *C. granulatus*, its North American range can be expected to expand trans-continentally, coalescing populations originating from the independent colonizations, while also expanding southward where habitats meet the ecological criteria necessary for the species' persistence.

Key words: adventive introduction, invasive species, flightlessness, geographic distribution, ground beetle

Introduction

The Holarctic biogeographic region is characterized by numerous species exhibiting natural, circumpolar geographic ranges, and by higher taxa with aggregate north temperate distributions (Darlington 1957). Overlain on this pattern is the anthropogenic phenomenon of species shared between the Palearctic and Nearctic due to their transport by humans (Lindroth 1957; Niemelä and Mattson 1996). The global distribution of Carabidae (Coleoptera) amply exhibits historical patterns of human movement, with Lindroth (1954, 1957) documenting 46 of 91 species shared between Europe

and North America having achieved that distribution through the aid of anthropogenic transport. More recently, Bousquet (2012) documented 64 carabid beetle species introduced to North America from Europe, this fraction comprising 2.6% of the 2439 carabid species known to be present in North America at that time. All but two of these were accidentally introduced through human activities.

Historically this westward means of entry of carabids to North America involved transport in terrestrial ballast of otherwise lightly loaded sailing ships travelling to Maritime Canada from Great Britain and Ireland yearly at the start of the fishing season. These ships would deposit their ballast on shore, and then, once loaded with the season's catch, sail to the Iberian Peninsula in order to sell their cargo. The ships then returned north to their home ports lightly loaded at the end of the sailing season (Lindroth 1957). Later, alien species transported via human commerce often exhibited distributions in northeast Canada and New England, USA, complemented by a separate set of populations in the northwestern USA plus British Columbia, Canada, introduced via shipping along the Pacific coast. Such divided distributional ranges were termed immature by Lindroth (1957), and proposed by him as a criterion for recognizing alien European taxa in the New World. Subsequent geographic spread along the Pacific Coast of North America may have been facilitated by the movement of plant nursery stock and associated soil, as hypothesized for the soil-dwelling carabid beetle, *Trechus obtusus* Erichson (Kavanaugh and Erwin 1985).

Carabus granulatus Linnaeus, 1758 was one of those Palearctic species introduced to North America that initially exhibited this bipartite, immature distribution (Lindroth 1957). The species was initially introduced to Maritime Canada at St. John, New Brunswick in 1890 (Harrington 1892, corrected by Brown 1940). This introduction comprised beetles assignable to *Carabus granulatus hibernicus* Lindroth, 1956, a subspecies described for populations from Ireland and western England diagnosable by greenish body coloration and well-developed, granulate elytral microsculpture between the glaucous elytral ridges (Lindroth 1974). *Carabus g. hibernicus* (Lindroth 1957; Bousquet and Larochelle 1993) subsequently spread to Nova Scotia by 1910 (Brown 1940), Newfoundland by 1981 (Larson and Langor 1982), St. Pierre et Miquelon by 1983 (Roux 1984), and Prince Edward Island by 1987 (Majka et al. 2006). A second independent Canadian introduction to Montreal, Quebec in 1948 (see Supplementary material Appendix 1) comprised beetles representing the typical form of *C. granulatus* recorded from eastern England and central Europe (Lindroth 1974; Turin et al. 2003). This form exhibits a more bronzed body coloration and glossy elevated elytral ridges (Lindroth 1961, 1985). Within the United States, the typical form of *C. granulatus* was first recorded at Seattle, WA in 1924 (Hatch 1933), and then at Natick, MA in 1931 (Brown 1940). Two years after its introduction to Seattle, the typical form of *C. granulatus* was

recorded from Vancouver, British Columbia, Canada. By 2006, the species' distribution in British Columbia had expanded to include Graham Island in the Haida Gwaii (Queen Charlotte Islands) (Kavanaugh 2010).

The native range of *C. granulatus* extends across the Palearctic, from Europe excluding the Iberian Peninsula, eastward through Russia, the Caucasus, Kazakhstan, the forest steppe and taiga of Central and Western Siberia, Mongolia, the Russian Far East, and across Japan (Turin et al. 2003; Deuve 2004). Its distribution in Europe and Russia lies between 40°N and 70°N, with more easterly recorded localities in Siberia and Japan south of 60°N (GBIF 2022). It is a eurytopic species occurring in moist to wet forest habitats, wet grasslands and riparian corridors, as well as moist arable lands (Thiele 1977; Turin 2000; Turin et al. 2003). In a comparative analysis of all carabid beetles recorded from The Netherlands, *C. granulatus* was most prevalent in peat bog and wet moorland habitats, though also relatively common in moist to wet forests (Turin et al. 2022). Thiele (1977) summarized its occurrence in forest types across central Europe, and found *C. granulatus* was present at over 75% of the sites characterized as *Fraxinus-Ulmus* lowland water-meadow forest, versus less than 25% of more mesic sites dominated by *Quercus* and *Carpinus*. Among the carabid fauna of Argyll, Scotland, *C. granulatus* was restricted to wet habitats along the margins of water bodies at low elevations, and was not present in moorland or montane habitats at higher elevations (Greenslade 1968). Most individuals are brachypterous, i.e. they lack fully-developed metathoracic flight wings and associated flight muscles, though fully-winged individuals rarely occur throughout Central Europe (Turin et al. 2003). Winged flight has been recorded in central and southern European populations (Lindroth 1992), though not in North America. Adult *C. granulatus* are large—16–24 mm body length (Lindroth 1956)—agile runners able to climb dense vegetation and tree trunks and run on downed logs. During spring and summer the beetles may be found resting under loose bark during the day, and during winter they have been found aggregating in large numbers under loose bark of rotten logs, or under thick cushions of moss (Scherney 1961; Lindroth 1992; Turin 2000; Bousquet *pers. comm.*, JKL *unpubl. data*). In one clearcut and three adjacent forest tracts near Greifswald, Germany, Broen (1964) trapped 96 individuals in the clearcut area versus only 3 in the various forested sites, consistent with: 1, the species' ability to reproduce in the clearcut areas; and 2, their preference for the warmer, drier subcortical overwintering sites available there (Thiele 1977).

Range expansion by *C. granulatus* in North America has been documented since the first 1890 New Brunswick record (Brown 1940). Several reports document its spread across Canada (Majka et al. 2006; Kavanaugh 2010; Bell et al. 2014; Fleming and Beresford 2017; but see Appendix 1). Additionally, *C. granulatus* has also been reported from several northern United States: Idaho (2005; Hatten et al. 2009), Minnesota (2005; Gandhi et al. 2011),

Connecticut (2007; W. L. Krinsky *pers. comm.*, see Appendix 1), and Oregon (2012; LaBonte 2022). We add an additional five states to its known US distribution and discuss potential factors associated with this range expansion.

The pattern of range expansion in North America, with multiple independent introductions, demonstrates the importance of human-mediated transport for spread of *C. granulatus*. Fleming and Beresford (2017) analyzed historical spread of the species in eastern North America and found that the species had spread continuously via neighborhood diffusion with a radial spread rate of ca. 10 km/yr. The appearance of disjunct populations in western North America suggests that over larger spatial scales spread has been facilitated by long-range jump dispersal facilitated by accidental human transport (Shigesada et al. 1995). In this paper, we assemble recent records of the distribution of *C. granulatus* in North America to document its current range and the recent range expansion that has taken place along distributional fronts among the various populations. We also report various interceptions of *C. granulatus* that did not result in its establishment, with the circumstances of those discoveries helping to elucidate possible means of its introduction to North America.

Materials and methods

Our determination of the *C. granulatus* range is based on historical records of occurrence from various sources. Because *C. granulatus* is a large, charismatic beetle with diagnostic features visible in dorsal view, it can be conclusively identified from well-resolved, well-lit photographs, increasingly available through citizen science biodiversity projects: e.g., BugGuide (2022) and iNaturalist (2022), the latter restricted to research grade observations summarized in GBIF (2022). We followed up on these records when deemed essential for documenting its spread via physical examination of specimens. State and university insect collections, especially in northern states where the species had not yet been found, were contacted (see Acknowledgments for collaborators, institutions, and codens). Specimens from new locations were determined using Van Dyke (1945) and Lindroth (1961). In addition, GBIF (2022) was used to locate physical specimens, leading to study of specimens in several institutional collections: California Academy of Sciences, San Francisco (CAS); the Charles A. Triplehorn Entomological Collection of The Ohio State University, Columbus (CTAC), Montana Entomological Collection, Montana State University, Bozeman (MTEC); the Ouellet-Robert Entomological Collection, Université de Montréal (QMOR); and the U.S. National Museum of Natural History, Washington, D.C. (NMNH). Specimens were studied either by taking them on loan from these institutions or by examining diagnostic photographs from collaborating colleagues. Where label data are presented verbatim, lines of text are separated by a single slash, and separate labels by a double slash.

Table 1. First *Carabus granulatus* records for Canadian Provinces (*), French Territory (ǂ), and United States, with citations for previously published records, and institutional repositories (curator or data platform) for newly reported earliest occurrences. Infraspecific taxon represented in the various introductions include *Carabus granulatus* L. (*C. g.*) and *Carabus granulatus hibernicus* Lindroth (*C. g. h.*).

Locality	Year	Reference	Subspecies
St John, New Brunswick*	1890	Brown (1940)	*C. g. h.*
Yarmouth, Nova Scotia*	1910	Brown (1940)	*C. g. h.*
Seattle, Washington	1924	Hatch (1933)	*C. g.*
Vancouver, British Columbia*	1926	Lindroth (1961)	*C. g.*
Natick, Massachusetts	1931	Brown (1940)	*C. g.*
La Prairie, Quebec*	1948	QMOR (C Favret *pers. comm.*)	*C. g.*
Eureka, California	1953	CAS (GBIF 2022)	*C. g.*
Cochrane, Ontario*	1973	UGIC (S Paiero *pers. comm.*)	*C. g.*
Deer Lake, Newfoundland*	1981	Larson and Langor (1982)	*C. g. h.*
St. Pierre, St. Pierre et Miquelonǂ	1983	Roux (1984)	*C. g. h.*
Winnipeg, Manitoba*	1983	UASM (GBIF 2022)	*C. g.*
Prince Edward Island*	1987	Majka et al. (2006)	*C. g. h.*
Edmonton, Alberta*	1989	CNC (Bell et al. 2014)	*C. g.*
Minneapolis, Minnesota	2005	Gandhi et al. (2011)	*C. g.*
Boundary Co., Idaho	2005	Hatten et al. (2009)	*C. g.*
East Hampton, Connecticut	2007	UCONN (WL Krinsky *pers. comm.*)	*C. g.*
Billings, Montana	2007	MTEC (J Rainey *pers. comm.*)	*C. g.*
Regina, Saskatchewan*	2010	Bell et al. (2014)	*C. g.*
Bangor, Maine	2012	BugGuide (2022)	*C. g.*
Coos Bay, Oregon	2012	LaBonte (2022)	*C. g.*
Appleton, New York	2019	iNaturalist (GBIF 2022)	*C. g.*
Lake Runnenede, Windsor, Vermont	2021	iNaturalist (GBIF 2022)	*C. g.*

We retain the distinction between the nominate subspecies *C. granulatus* and the subspecies described for Irish populations by Lindroth (1956)—*C. granulatus hibernicus*—even though Deuve (2004) synonymized the two taxa based on the inability to diagnose all individuals of all populations within this species using the less elevated elytral ridges and more evenly distributed microsculpture proposed by Lindroth as diagnostic characters for his subspecies. We do this because the elytral characteristics present among many individuals occupying the Canadian Maritime provinces provide morphological evidence regarding their point of origin in Ireland and the British Isles.

Results

Geographic Spread

The first occurrences of *C. granulatus* in each newly recorded state are presented below along with data on distribution, collector, specimen repository, and manner of specimen documentation (Table 1, Figure 1).

California: Humboldt Co., Eureka, 40.8026; −124.1632, 10 August 1953, Paul H. Arnaud, Jr. (CAS; specimen examined by JKL, located using GBIF 2022; https://www.gbif.org/occurrence/1845419772).

Montana: Yellowstone Co., Billings, Norm's Island (city park on Yellowstone R.), 45.739871; −108.539961, 15–16 June 2007, Hopp collector (MTEC, 6 specimens); specimens examined by Jordan Rainey (*pers. comm.*) with photographs provided to authors.

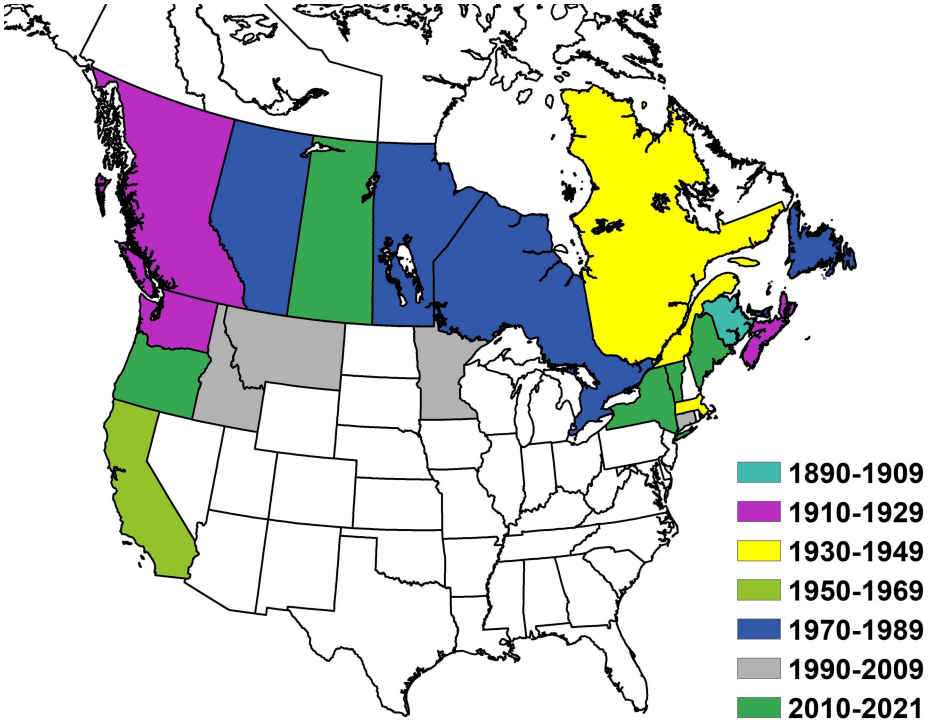

Figure 1. Sequential colonization by *Carabus granulatus* of the various Canadian Provinces and United States (see Table 1).

Maine: Penobscot Co., Bangor, 44.845944; −68.741269 27 July 2012, B. Woo collector (single specimen found under a light at night (BugGuide 2022; https://bugguide.net/node/view/681278, B. Woo personal collection, loaned to and examined by JKL).

Vermont: Windsor Co., Lake Runnenede, 43.486138; −72.388691, 30 March 2021 (GBIF 2022; iNaturalist 2022, https://www.inaturalist.org/observations/72475246). Photograph presents diagnostic features distinguishing specimen from all other *Carabus* spp. in Vermont (Bell 2015; Lindroth 1961). Fleming et al. (2022) record *C. granulatus* from neighboring New Hampshire, that state comprising the eastern shore of the Connecticut River very near Lake Runnenede (Table 1, Figure 2). Fleming (*pers. comm.*) could not provide specimen data for that record, nor are there other observations or specimens of *C. granulatus* from New Hampshire (Bell 2015; G.B.I.F. 2022; D.S. Chandler *pers. comm.*).

New York: Niagara Co., Appleton, 43.325381; −78.671947, 12 August 2019 (iNaturalist 2022; https://www.inaturalist.org/observations/30743295). Photograph presents diagnostic features distinguishing specimen from all other *Carabus* spp. in North America (Van Dyke 1945).

Interceptions

Carabus granulatus has also been intercepted in various commodity shipments without evidence of subsequent establishment.

North Carolina: New Hanover Co., Wilmington (verbatim label data: Wilmingt. N.C. / W.F. Wenzel // C.V. Riley collection // *C. granulatus* from

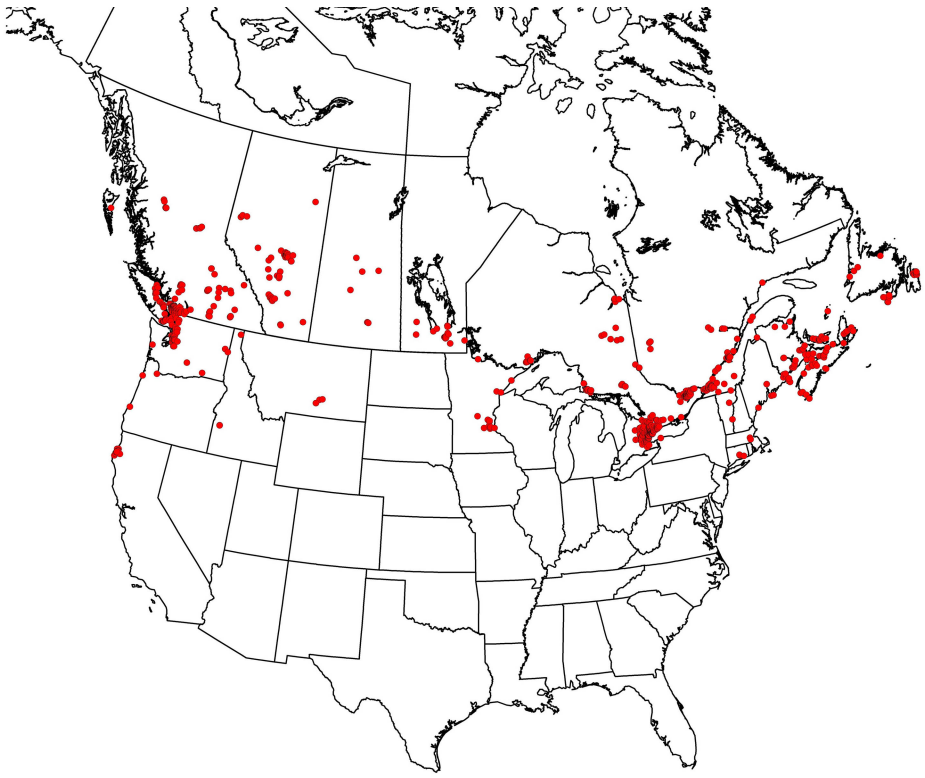

Figure 2. North American distribution of *Carabus granulatus* currently provided by GBIF (2022) incorporating confirmed research grade observations of iNaturalist (2022), complemented by novel records reported herein.

Europe!!!); NMNH, 1 specimen (I. Sokokov *pers. comm.*). Because the specimen was labeled as part of the C.V. Riley collection, it must have been collected and subsequently determined prior to the 1885 incorporation of Riley's personal collection into the NMNH (Wheeler et al. 2010), making this the earliest documented occurrence of *C. granulatus* in North America.

Kansas: Imported into Kansas during 1914–1915 in "nursery stock… from various points in Holland, Belgium, France and Austria (Hunter 1916)". Documentation by specimen not possible due to absence of such from the University of Kansas (Z. Falin *pers. comm.*) and the NMNH (I. Sokolov *pers. comm.*).

Texas: Bexar Co., Kelly Field (verbatim label data: Kelly Field / Nov. 1917 Tex. // C W Stockwell / Collector // *Carabus* /*granulatus* Linneaus / det. G. H. Edelbrock 1987 ; NMNH, 1 specimen (I. Sokolov *pers. comm.*). This occurrence was cited by Erwin (2007: 112). Kelly Field was a major training center for the U.S. Army Air Corps (U.S. National Park Service 2017), of which C. W. Stockwell was a member during World War I (Journal of Economic Entomology 1919). Materiel and personnel were repeatedly shipped to and from France (U.S. Army Aviation Section Signal Corps (1918) Kelly Field Eagle 1(1): 2 pp (25 April 1918)).

Ontario: Lindroth (1961: 37) reported it "in a shipment from Holland (CNC)."

Northwest Territories: Lindroth (1961, 37) also wrote of an interception: "Quite accidental was the find at Norman Wells, N.W. Terr. 'among frozen strawberries from B.C. (CNC).'" Fleming et al. (2022) listed Northwest Territories as part of the present-day range of *C. granulatus*. However, because its discovery in a shipment of frozen fruit has never been followed by any record from nature, we view this record as an interception only, not evidence of establishment or geographic spread. Fleming et al. (2022) also list Nunavut as part of the range of *C. granulatus*, although they (Fleming *pers. comm.*) acknowledge that mention is in error.

Discussion

The currently documented distribution of *C. granulatus* in North America (Figure 2) extends across the middle of the continent north of 43°N latitude, with populations extended southward to about 40°N along both the Atlantic and Pacific coasts. This information provides a good example of how citizen-science data can be used as a resource to characterize ranges of adventive species (Crall et al. 2010; Chandler et al. 2017).

Generalist natural enemies become established most easily compared to natural enemies with narrower host ranges (Weber et al. 2021). *Carabus granulatus* is polyphagous in its native European range, with larvae and adults feeding primarily on snails, but also on insects and annelid worms occurring within its preferred habitats (Lindroth 1992). Spread by *C. granulatus* has been relatively slow compared with other carabid species such as *Nebria brevicollis* (LaBonte 2022) and *Carabus nemoralis* (Lindroth 1957). Turin et al. (2022) demonstrated that *N. brevicollis* is among the most eurytopic species of Dutch carabid beetles, and so its greater rate of spread may be based in part on its very broad habitat preference and concomitant avenues for range expansion. It is also a flight-capable species (Turin 2000), though adults develop flight muscles only when the larvae experience favorable conditions during development (Nelemans 1987) suggesting that the possibility of range expansion through adult flight is most likely when a population experiences an abundance of food resources. In Oregon, USA, it was initially detected in November 2007, and by 2008 it was present at 13 sites across 5 counties of northwestern Oregon (Kavanaugh and LaBonte 2008). Two years later 2010 its distribution ranged 150 km north to south, and 90 km east to west, including a site in Washington state north of the Columbia River (LaBonte 2011). In this initial surge, *N. brevicollis* colonized a wide range of habitats; from industrial sites to pristine old-growth forest, to rocky mountain summits, these sites ranging from sea level to 1250 m elevation.

Carabus nemoralis is also a generalist species—among the most eurytopic European carabid beetles (Lindroth 1992)—occupying a wide variety of forest types on various soils, plus areas highly impacted by human activity such as urban parks, gardens, forest edges and agricultural fields (Turin et al. 2003). Such broad ecological preferences and persistence in human-

modified habitats are mirrored by the North American populations (Rivard 1974; Fan et al. 1993; Werner and Raffa 2003; Bouchard et al. 2005; Hajek et al. 2007). Lindroth (1957, fig. 7) reported an immature bicoastal distribution for *C. nemoralis* consisting of an eastern set of populations that had extended westward to Chicago, IL by 1926 (Park 1929) and to Milwaukee, WI by 1934 (Lindroth 1955), and a western distribution that extended from Seattle, WA in 1909 (Hatch 1933), to San Francisco, CA in 1919 (Essig 1931), and eastward to Salmon Arm in interior British Columbia by 1933 (Leech 1935). Within 60 years this species colonized a broad swath of North America, closing the distributional gap between east and west while colonizing Minnesota, Manitoba, Saskatchewan, Alberta, Montana, Wyoming, and Idaho (Byrne 1988; Bousquet and Larochelle 1993). Recent records from GBIF (2022) document its occurrence as of 1996 in Colorado (https://www.gbif.org/occurrence/2432191461), at Sitka, southern Alaska in 2007 (https://www.gbif.org/occurrence/2427871433) and Anchorage, Alaska in 2020 (https://www.gbif.org/occurrence/3062716301). *Carabus nemoralis* adults are all flightless, strongly suggesting that human activities facilitated the closing of this 2500 km gap accomplished at a rate estimated here to average ~ 20 km/year, assuming similar eastward and westward expansions from the two previously isolated sets of populations. Leech (1935: 121) posited such means of dispersal across British Columbia, stating "It is probable that freight cars, especially of the open cattle-car type, were the means of the beetles spreading so far inland; Salmon Arm is on the main line of the Canadian Pacific Railway".

Like *C. nemoralis*, North American *C. granulatus* individuals are flightless (Larochelle and Larivière 2003) suggesting that spread within North America has been largely dependent on human transport. The adults reside under bark or at tree bases, sometimes in large aggregations (Scherney 1961; Lindroth 1961; Turin et al. 2003). This coupled with its ability to colonize clear-cut areas adjacent to forested sites (Broen 1964) puts the species squarely within the logging environment, and therefore potentially available for transport in logs. In addition, it is a species most frequently found in wetlands and moist forests (Greenslade 1968; Turin et al. 2022), suggesting its establishment and subsequent spread is dependent on availability of such habitats, often connected to shipping ports by riparian corridors.

Previously, four separate introductions of *C. granulatus* had been proposed: three on the northeast coast and one on the northwest coast, based on records from New Brunswick (1890), Washington (1924), Massachusetts (1931), and Quebec (1948) (Table 1). The New Brunswick colonization event involved individuals with the *C. g. hibernicus* subspecies morphology (Lindroth 1956), allowing discrimination of this event from the Massachusetts-centered introduction that was initiated by individuals of the typical *C. granulatus* form. As the first record from Maine is a specimen with the typical *C. granulatus* morphology characteristic of the Massachusetts

population, we conclude that the species has spread northward from the Boston area to, at least, Bangor, ME. Elsewhere in the east, the two recorded localities for *C. granulatus* in Vermont span the distributions within Quebec and Massachusetts. The Connecticut River serves as a riparian connector between the southern Vermont locality at Lake Runnenede, and the earliest Connecticut record from Middlesex Co. (see Appendix 1). The first New York record lies along the south shore of Lake Ontario approximately 30 km east of the nearest known locality in Ontario (CTAC, label data: Ridgeway, Ontario / H.W. Wenzel Collection, GBIF 2022: https://www.gbif.org/occurrence/872980778) supporting movement by the species along the riparian corridor bordering the Niagara River and Lake Ontario.

We report significant southern geographic expansion by *C. granulatus* based on the 1953 specimen from Eureka in northwest California (Table 1). As individuals constituting the Pacific Northwest Washington/British Columbia populations and the original 1953 California specimen both represent the typical *C. granulatus* morphology, we cannot determine whether the source of the California colonization event was from populations further north, or from another site altogether that supports the typical *C. granulatus* form, although relative geographic proximity would suggest the former. Such a jump may have involved coastal commercial transport , as Eureka lies on Humboldt Bay, one of the few seaports between Seattle, Portland, OR, and San Francisco, CA. Interceptions of *C. granulatus* in Kansas (Hunter 1916) and Northwest Territory (Lindroth 1961) both involved transported plant materials. Geographic expansion southward from the Seattle area to Portland, OR, and San Francisco, CA was also documented for the European introduction, *Trechus obtusus* Erichson (Kavanaugh and Erwin 1985, figs. 2–3), with shipment of nursery stock suggested as the means of transport. Alternatively, the predilection of *C. granulatus* beetles for the subcortical microhabitat (Lindroth 1961) suggests the possibility of transport with logs.

Presently, the localized distribution of *C. granulatus* surrounding its 1953 Eureka, CA introduction extends 43 km from Ferndale northward to McKinleyville (GBIF 2022). Using mark-recapture methods in potato fields, Scherney (1960) found that adult *Carabus* beetles of *C. auratus* L., *C. cancellatus* Illiger, and *C. granulatus* could maximally disperse about 120 m over 10 days. Given the recorded seasonal activity period of European *C. granulatus*—200 days from April to mid-October (Scherney 1961), incorporating a 37–52 day larval and pupal developmental period of the newly emerging summer generation (Sturani 1962)—dispersal by adults could maximally account for ~ 1800 m of geographic spread over continuously favorable terrain per season; a rate that could credibly account for the ~ 25 km radial expansion of the species' distribution centered on Eureka. Conversely, the species was recorded in 2012 at Coos Bay, Oregon (LaBonte 2022), 300 km

from Eureka. In this instance, terrestrial perambulation at < 2 km/yr cannot account for movement of this species into Oregon over the intervening 69 years, 1953 to 2012. The < 2 km/yr rate of terrestrial movement estimated from potato field experiments is also far less than the 10 km/yr rate of radial geographic spread calculated for *C. granulatus* across eastern North America (Fleming and Beresford 2017), pointing again to the overwhelming importance of human transport for range expansion of this adventive species.

Since 2012, *C. granulatus* has been documented from northern Oregon, at Beaverton (iNaturalist 2022; https://www.inaturalist.org/observations/116306640) and Tillamook Co. (LaBonte 2022). These localities are closer to known coastal localities in Washington State—e.g., Hoquiam (iNaturalist 2022; https://www.inaturalist.org/observations/120592903)—than to southern Oregon, but as with the other Pacific coastal localities occupied by this species, logging and other shipping activities are close at hand, supporting the likelihood of human transport.

Carabus granulatus has also spread eastward from Washington and British Columbia, most recently being recorded from northern Idaho by 2005, central Montana by 2007, and Saskatchewan by 2010 (Figure 1). The newly reported Montana record is from along the Yellowstone River, yet another riparian setting. As mentioned by Bell et al. (2014), whether the Saskatchewan populations have been derived from the west or from the east via Manitoba, is currently unknown. Ultimately, a more definitive reconstruction of *C. granulatus* spread in North America will require comprehensive genetic comparisons among populations.

The successful coastal colonizations of *C. granulatus* are complemented by five known interceptions at localities from which there is no evidence of establishment. Three of these—Wilmington, NC before 1885, Kansas in 1913–1914, and Texas in 1917—lie well south of the current 40°N latitudinal limit of this species, whereas the interception at Norman Wells, Northern Territory lies well north of the present-day distribution. That the individuals intercepted appeared to have been few in number and confined to commodities may explain the lack of successful colonization. The North American history of the Palearctic *Nebria brevicollis* includes similar early misadventures, with single adults collected in southern Quebec in 1930 and on Miquelon Island in 1937, fully 70 years before the successful, explosive colonization of Oregon's Willamette Valley (Kavanaugh and LaBonte 2008). For *C. granulatus*, it cannot be assumed that all of the sites where it failed to establish are necessarily unsuitable, given the many well-established populations occupying North America, and the species history of colonizing coastal ports. *Carabus granulatus* will test the suitability of novel venues as it moves in synchrony with human commerce along routes intersecting multiple corridors of suitable habitat. Based on the broad latitudinal range of its distribution in Europe and Asia (Turin et al. 2003; Deuve 2004; GBIF 2022), we predict that substantial geographic expansion by *C. granulatus*

will occur in areas of suitable habitat across North America; i.e. wooded water margins, wet forests, and heathlands. The distribution of such suitable habitats will be influenced by climatic factors, with progressive movement of *C. granulatus* populations documentable by citizen science websites such as BugGuide (2022), and iNaturalist (2022) archived by GBIF (2022).

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Ethics and permits

All biological specimens mentioned in this manuscript are either deposited within institutional collections, or are documented on publicly available websites, ensuring legal collection from nature.

Author contributions

AEH, JKL, research conceptualization; AEH, AML, JKL, sample design and methodology; JKL, AEH, BW, AML, investigation and data collection; JKL, AML, AEH, data analysis and interpretation; AML, funding provision; JKL, AEH, roles/writing – original draft; JKL, AEH, AML, BW writing – review and editing.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. Corrected information regarding the first occurrences of *C. granulatus* within Quebec, Ontario, and Connecticut (Table 1).

This material is available as part of online article from:
http://www.reabic.net/journals/bir/2023/Supplements/BIR_2023_Liebherr_etal_SupplementaryMaterial.pdf