Collateral damage: military invasions beget biological invasions

Alberto Santini[1*], Giorgio Maresi[2], David M Richardson[3,4], and Andrew M Liebhold[5,6]

Biological invasions are frequently and closely associated with armed conflict. As a key element of human history, war involves the invasion of (often distant) enemy territories, during which time species can be translocated, intentionally or unintentionally. Large-scale conflicts such as World War I and II, in which thousands of soldiers and supplies (including foodstuffs) were transported within and between continents, resulted in the spread of non-native taxa. However, smaller scale military actions may also involve rapid movements of troops between geographical areas, potentially facilitating the accidental introduction of species into previously unoccupied areas. Furthermore, invasive pests have occasionally been used by armies as weapons to weaken and disrupt opposing forces or nations. The introduction of invasive species during war could be considered relatively minor collateral damage, but many biological invasions in conflict zones have long-lasting effects. Regulation of military practices to minimize or prevent biological invasions through existing international conventions has so far been unsuccessful, necessitating the development of additional measures.

Front Ecol Environ 2023; 21(10): 469–478, doi:10.1002/fee.2640

Armed conflict has played a major role in world history and has impacted social evolution, economic history, and the cultural development of humankind globally (Black 2009). In its traditional meaning, a "civilized war" (Keegan 1993) is a conflict involving insurgent groups, sovereign states, or coalitions for the forcible resolution of domestic or international disputes more or less directly motivated by real or perceived conflicts of ideological and economic interests. War often involves invasion of enemy territories. Invasion in the context of human warfare is a large-scale military operation in which soldiers of a country, or a consortium of allied countries, use violent force to enter a territory controlled by others, with the goal of conquering, liberating, or re-establishing control or possession of that territory. Many military invasions have played key roles in human genetic and social evolution because they have resulted in the introduction of novel cultural components (such as religion, language, and technology) and a mixing of human gene pools.

In a nutshell:

- Armed conflicts are a key element of world history and often involve invasion of territory by military forces
- The flow of supplies to invading armies is a crucial component of their success; together with supplies and the armed force itself, organisms native to the hostile nation may be introduced to the attacked region
- A number of non-native plants, animals, and pathogens (of both humans and plants) have been introduced to previously unoccupied areas, both intentionally and unintentionally, by invading armies
- Species introduced via military conflicts can have long-term impacts on the ecosystems and economies of seized territories and are often difficult to control

Crosby (1986) recognized that biological invasions are often associated with human invasions, specifically noting that European colonization of distant lands was historically associated with introductions (both intentional and accidental) of many different species of flora and fauna. At the core of colonialism is military force, which facilitates one country's dominance over foreign lands and the people therein. Much like colonialism in general, military activity is intimately associated with the phenomenon of biological invasion. The biological invasion literature is replete with military terms (eg "invasion", "bridgehead") and researchers in the field of invasion science have at times been reproached for exploiting such verbiage to evoke fear among the public (Janovsky and Larson 2019). Although the terms "biological invasion" and "military invasion" refer to very different things, they are occasionally causally connected.

Globalization – the worldwide movement of humans and goods – is recognized as the primary driver behind biological invasions (Hulme 2021), defined here as the introduction and establishment of non-native organisms outside their native ranges. In this review, we describe the role of war, and especially that of military invasions, in promoting biological invasions. A variety of specific invasion pathways have facilitated both the

[1]*National Research Council–Institute for Sustainable Plant Protection (CNR-IPSP), Sesto Fiorentino, Italy* [*]*(alberto.santini@cnr.it);* [2]*Centre for Technology Transfer, Fondazione Edmund Mach, San Michele all'Adige, Italy;* [3]*Centre for Invasion Biology, Department of Botany & Zoology, Stellenbosch University, Stellenbosch, South Africa;* [4]*Department of Invasion Ecology, Institute of Botany, The Czech Academy of Sciences, Průhonice, Czech Republic;* [5]*US Forest Service Northern Research Station, Morgantown, WV;* [6]*Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Suchdol, Czech Republic*

intentional and unintentional dispersal of species outside their native ranges (Essl *et al*. 2015). Military activities may modify these existing pathways, create new routes that potentially facilitate movement of invasive taxa, generate disturbances that increase habitat invasibility, and affect factors mediating the performance of species and their progression along the introduction–naturalization–invasion continuum. We present examples of military campaigns that have resulted in introductions of species, particularly plants, phytopathogens, and insects. In addition, we discuss the deliberate introduction of non-native species as weapons of military or social disruption.

Military provisioning

The flow of supplies to an invading army is a crucial component of its success, as forces require replenished weapons and provisions. In ancient times, invading armies often relied on plundering invaded regions for food, water, and other essentials. However, because such resources were not always abundant (eg due to seasonal availability of crops), the role of an organized supply chain (even during antiquity) was critical for the sustenance of larger and coordinated armies. Descriptions of medieval European armies typically depict the positioning of strategic resources, such as crates of arrows for English bowmen, immediately behind the main forces (Wadge 2012). Also found in these provisioning columns were herds of cattle, sheep, and horses trailing behind the army, as reservoirs of "standing meat" (Wadge 2012). In modern wars, the logistic capabilities that guarantee a continuous flow of supplies are even more crucial for an army's ability to conduct operations over extended time frames and in remote, sparsely inhabited regions.

Ample historical examples illustrate the critical importance of logistic chains in provisioning during major military campaigns. For instance, Napoleon's unsuccessful invasion of Russia in 1812 was attributed to the French army's constrained provisioning capabilities. In contrast, England's Duke of Wellington demonstrated exemplary logistic skills during the winning campaign of the Peninsular War (1808–1814). During World War II (WWII), both the invasion of the Soviet Union by Axis powers (1941–1944) and their North African operations (1941–1943) were greatly hindered by long and unreliable food and fuel supply chains. Conversely, the successful invasions of Italy (1943–1945) and France (1944–1945) by Allied Forces can be attributed in part to the enormous and continuous flow of supplies; in early 1945, 37,000 tons of supplies per day were provided to US armies on the Western Front via a continuous logistic chain (Ruppenthal 1995; Lopez *et al*. 2018). The importance of provisioning combat units is such that the US Defense Logistics Agency alone employs thousands of civilians, and the US Army supports an institution (the US Army Sustainment University) dedicated to training soldiers in the practice of logistics.

Much like civilian supply chains, the movement of military units and materiel (military materials and equipment) provides pathways for the introduction of non-native species. Examples of such invasions are replete throughout the history of war (WebTable 1). Many of the organisms introduced via military provisioning have become damaging invasive species, contributing to the ecological impacts of warfare on invaded countries.

Transport of foodstuffs as an invasion pathway

International trade in grains, fruits, vegetables, and meat is a prominent invasion pathway (Hulme *et al*. 2008), and the same is true for military movements of foodstuffs. Heightened risk of unintentional species introductions with military provisions, especially foodstuffs, is attributable to both the high volume (and associated high propagule pressure) of materiel transported and by the rapidity of transport, which allows many organisms to survive despite suboptimal transit conditions. The need for rapid shipment of foodstuffs during military operations also means that there is little time for implementing sanitary and/or decontamination practices, and the risk of inadvertently relocating species, such as plant pests, has historically not been taken into consideration (Panel 1; Figure 1).

Transport of equipment as an invasion pathway

Many types of organisms may be conveyed to new areas as hitchhikers on weaponry and in combat transports (motor vehicles, aircraft, or ships), or even by adhering to the uniforms of military personnel (Figure 2). McNeely (2006) reported the accidental spread of numerous plant species via attachment to military equipment and vehicles (eg seeds stuck to the wheels of airplanes). Many species of grasses with hooked seeds are easily dispersed by adhering to clothing. For instance, several plants collectively referred to as *flora castrense* (from Latin "*flora*" = plants and "*castra*" = military camps) flourished after World War I (WWI) near depots and camps (Panel 2; Figure 3). Similarly, many insects, plant pathogens, saprotrophic fungi, and even vertebrates (notably the brown tree snake [*Boiga irregularis*]) have been accidentally transported as hitchhikers in military shipments (WebTable 1).

Containers and packing materials associated with military equipment may also facilitate species dispersal. A good example is provided by wood, which played a prominent role in the packaging and transport of weapons (Figures 2 and 4). Wooden pallets were invented in 1925, but it was during WWII that their use became a cornerstone of modern logistics operations (LeBlanc 2002). Wood has diverse applications in military settings, ranging from ammunition boxes to building materials, furniture, poles, and so forth. It was estimated that in WWII about 0.12 m^3 of wood were required each month to keep an overseas soldier supplied, and about ten times that quantity was needed to ship that same soldier's initial equipment from the US (Novick *et al*. 1949). Wood packaging is a well-known vector for non-native tree pathogens and pests (Haack *et al*. 2014). These examples provide

Panel 1. The Colorado potato beetle

The Colorado potato beetle (*Leptinotarsa decemlineata*) feeds on endemic plants of the family Solanaceae in its native Mexican range. The beetle species spread across the US during the second half of the 1800s, at a rate of 100 km per year. During World War I, the beetle was apparently accidentally introduced to Europe in a shipment of food to Bordeaux, France, the main port for provisioning of American forces during the conflict (Casagrande 1987). In the early phase of World War II (WWII), the French army – having previously observed the impact of this pest – secretly developed methods to mass-rear the Colorado potato beetle at the Poudrerie Nationale laboratories in Le Bouchet for use as a weapon (Garrett 1996). When German occupation forces discovered the laboratories, this concept became the basis for a German biological warfare program. During WWII, German scientists investigated similar propagation of at least 15 species of insects based on their ability to inflict major damage to crops with subsequent economic impacts in enemy countries (ie Great Britain; Geissler 1999).

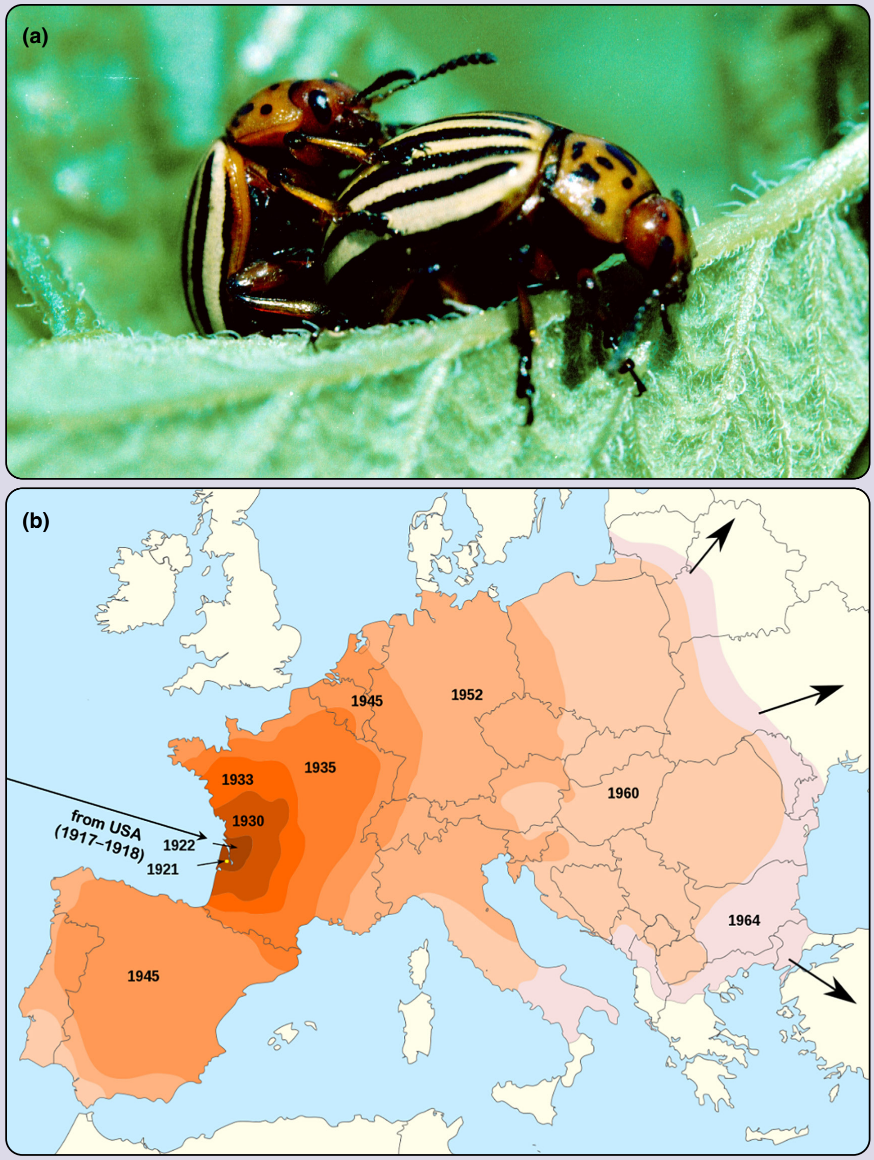

Figure 1. The Colorado potato beetle (*Leptinotarsa decemlineata*): (a) mating pair and (b) historical spread across Europe by year. Image credits: (a) Clemson University/USDA Cooperative Extension Slide Series/forestryimages.org, (b) modified from Spedona (CC BY-SA 4.0).

evidence of the role of wood packaging in military provisioning as a pathway for introduction of non-native species. Many authors (eg Grasso 1951; Cristinzio *et al*. 1973; Gonthier *et al*. 2004) have attributed the establishment of certain plant pathogens in Europe after WWII to the use of ammunition crates made from infected wood. Likewise, the reuse of military materiel by civilians may have facilitated the further spread of such pathogens (Figure 4). Recognizing the risks associated with wood packaging in commerce, the International Plant Protection Convention implemented mandatory phytosanitary treatments under International Standards for Phytosanitary Measures No 15 (Humble 2010; Haack *et al*. 2014; Leung *et al*. 2014). However, the transport of wood in military provisioning has received scant attention and remains largely unregulated. Moreover, the proliferation of maritime shipping containers following WWII greatly increased the efficiency of long-distance movement of weapons but also facilitated the spread of non-native species (Stanaway *et al*. 2001). Military vessels are also known to play a role in the movement of non-native marine organisms; Coles *et al*. (1999) documented increases in the numbers of previously undocumented non-native marine organisms in Pearl Harbor, Hawaii, associated with naval traffic during WWII.

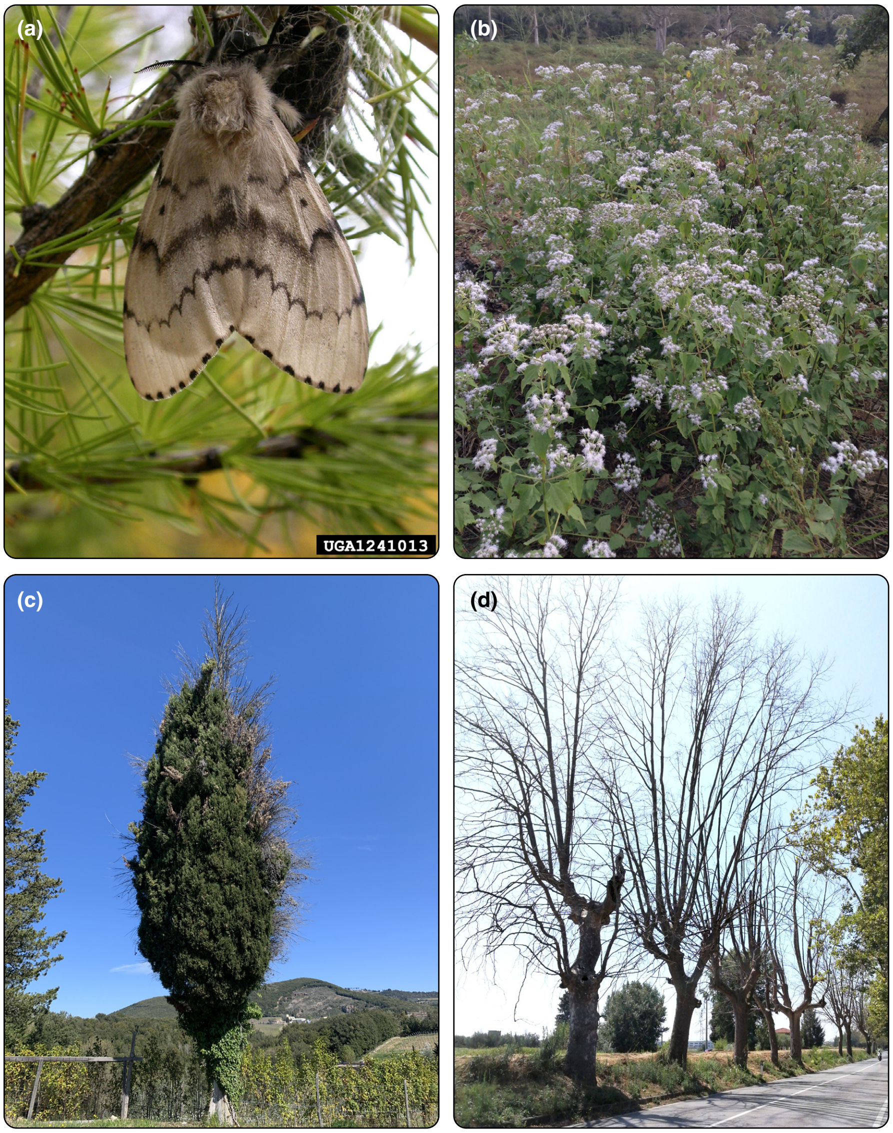

Figure 2. Examples of invasions facilitated by military activity. (a) Asian spongy moth (*Lymantria dispar asiatica*) in North America. (b) Devil weed (*Chromolaena odorata*), an invasive plant in western Angola. (c) Cypress canker caused by the fungus *Seiridium cardinale* on Mediterranean cypress (*Cupressus sempervirens*) in Tuscany, Italy. (d) Canker stain disease caused by the fungus *Ceratocystis platani* on London plane (*Platanus acerifolia*) in Italy. Image credits: (a) J Ghent/Bugwood.org, (b) DM Richardson, (c) A Santini, (d) F Pecori/CNR-IPSP.

Increased invasibility

Many invasive plants are excellent colonizers of bare or disturbed soil. Military activities often create such conditions, thereby favoring the establishment of invasive plants, as evidenced by the Western and Alpine fronts during WWI. In some cases, the aftermath of military actions, such as bombing, can lead to the creation of new microhabitats that benefit invasive plants; for instance, butterfly bush (*Buddleja davidii*) became established in England after WWII due to colonization of bomb craters around London (Sumner 2019).

Creation of fields and construction of roads, depots, airports, and other infrastructure often involve the removal of vegetation and movement of soil, rendering such areas susceptible to invasion by early successional plant species. Vehicles or materiel (possibly contaminated with propagules) tend to concentrate in such locations, increasing the likelihood of spread (Panel 2).

Invasions can also be triggered indirectly by efforts to restore areas damaged by military activities. Many cases of species invasions were initiated by the reliance on non-native plants in postwar revegetation efforts (WebTable 1; McNeely 2005; Ewel *et al*. 1999), when inadequate planning, lack of native plant stock, and the need for rapid restoration of vegetation cover encouraged the planting and spread of non-native invasive flora.

Intentional introductions as provisions

Prior to the advent of modern transport technologies, provisioning of overseas military forces was much more difficult. During the colonial era, providing troops with fresh vegetables, fruit, and meat necessitated the overseas shipment of many species of plants and animals. In particular, European navies frequently introduced ungulates to islands in the Pacific and Indian oceans as sources of food either for colonists or for sailors should they become stranded (Lowney *et al*. 2005). Often harboring numerous endemic plant and animal species, islands are exceptionally vulnerable to invasions, and many of these introduced ungulates have severely impacted island communities. In the 17th and 18th centuries, navies also introduced many plants to remote islands as future food sources, which frequently became invasive (Binggeli 2001). Intentionally or accidentally introduced to islands around the world by both commercial and military maritime activities, mice and rats have also had massive impacts on island ecosystems, especially on native bird populations (Drake and Hunt 2009).

Intentional introductions as weapons

History is replete with reports of species intentionally introduced by adversaries to inflict damage on their enemies (Lockwood 2012). In many cases, these introductions were conducted for defensive purposes, with some of the species involved subsequently becoming invasive (McNeely 2001). For example, the Japanese army planted *Leucaena leucocephala*, a fast-growing shrub native to Central America, to

Panel 2. *Flora castrense* in World War I

To support an army of 200,000 men and 30,000 quadrupeds during World War I, 240 tons of fodder were needed daily (Leoni 2015). Maintaining the numbers of livestock (including mules and horses) required by the warring factions often required more hay and pasture than was available locally. Moreover, while in previous wars movement allowed for a change of pasture, trench warfare forced animals to remain within a confined space, to which fodder was delivered. In addition, soldiers slept on hay or on mattresses of grasses, resulting in dispersal of seeds attached to uniforms (Vernier 2014). On the Alpine Front, between Italy and Austria, the presence of allochthonous plants from other parts of the Alps, the Apennines, or the Dinaric area was reported after the war. The presence of these plants often closely aligned with the locations of army encampments, barracks, depots, and logistical hubs, and the plants were often observed in proximity to the cableways used to supply hay to pack animals in defensive lines at high elevations. These plant species seldom became truly invasive and many vanished after just a few years; however, populations of others can still be observed around former depot and cableway sites, and as such can be considered a record of the war (Prosser 2015).

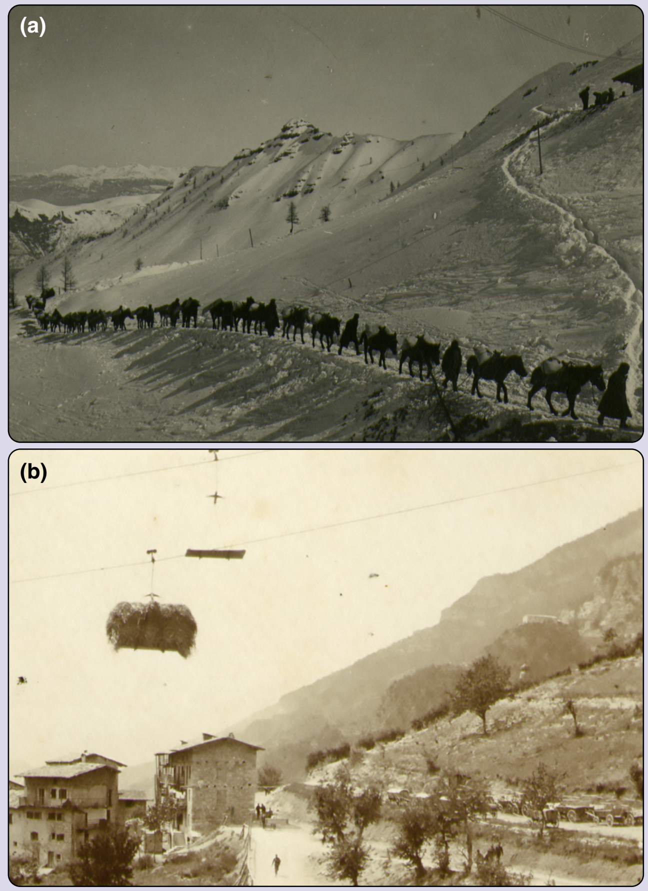

Figure 3. Provisioning along the Alpine Front during World War I. (a) Baggage from Austria being transported into Italy across Mount Pasubio. (b) Forage for mules carried to high elevations via a military cableway (Val Terragnolo). Such transport often resulted in the dispersal of plant propagules. Image credits (a–b): Museo storico Italiano della guerra, Rovereto, Italy.

hide artillery placements on the Ogasawara Islands in the northwestern Pacific (Binggeli 2001).

Since antiquity, a common strategy to weaken enemy forces has been deprivation of enemy food supplies by purposefully damaging or burning crops and forests (Suffert *et al*. 2009). Intentional introduction of invasive plant pests or pathogens with the intent to destroy food sources and spur economic losses occurred in several European countries between 1920 and 1940, a type of warfare that has been termed "agroterrorism" (Foxwell 2001; Stack *et al*. 2006). Agroterrorist acts have also been employed as a means of undermining political stability or the status quo in countries where agriculture is economically predominant (Fletcher *et al*. 2006; Suffert *et al*. 2008; Caldas and Perz 2013). This type of action may reduce food supplies, create food shortages, and decrease exports, in turn triggering financial crises and sparking social unrest and political instability. For this reason, agroterrorism is increasingly considered to be a potential driver of ecological and economic change at the global level (Pimentel *et al*. 2000; Chalk 2004; Caldas and Perz 2013). The concept of such warfare was hypothesized by Haldane (1937), who speculated on the use of military aircraft to distribute pests across potato (*Solanum tuberosum*) fields in enemy territory. During WWII, France and Germany in the European theater and the US and Japan in the Asian theater investigated programs to inflict damage to principal food crops in those continents – potato and rice (*Oryza sativa*), respectively – through the introduction of plant pests as pathogenic agents (Madden and Wheelis 2003; Suffert *et al*. 2009).

Following WWII, the Cold War emerged as geopolitical tension between the two emerging dominant military powers: the Soviet Union and the US. During the initial period of the Cold War (1947–1979), both nations consolidated their influence over several countries, which essentially divided much of

Figure 4. Wooden boxes used for munitions shipments. (a) Workers at a depot in Newbury, England, unloading boxes of 18 lb (8.16 kg) shells being broken down for inspection and restacking on 20 May 1917 during World War I. (b) A wooden box used to transport ammunition during World War II (WWII). (c) A WWII-era wooden box of military origin recycled for use as a flour cupboard. (d) Ammunition boxes repurposed as a chicken cage. Image credits: (a) ©IWM Q 110256, (b–d) G Maresi/Museo della Linea Gotica.

the world into two blocs. These blocs competed for influence in many parts of the world, giving rise to conventional wars, civil wars, coups d'état, guerrilla warfare, terrorism, and other violent actions. Throughout this period there were reciprocal accusations of agroterrorism between the two blocs (WebTable 1; Madden and Wheelis 2003; Suffert *et al*. 2009). During the Iran–Iraq conflict of 1980–1988, Iraq was repeatedly accused of targeting Iranian civilians via biological warfare on wheat (*Triticum* spp) crops through the use of the fungus *Aspergillus* (Whitby 2002).

Biological warfare using plant pests was also either conducted or considered as a potential strategy by the US to counter overseas production of recreational drugs. In 1988, the US Congress funded research on plant pathogens as part of an anti-drug campaign (Rogers *et al*. 1999). Likewise, in the 1990s and 2000s, the UN Drug Control Program supported the use of specific plant pathogens – mainly the fungus *Fusarium oxysporum* – in Central Asia (Afghanistan) and South America (Colombia) for controlling opium poppy (*Papaver somniferum*) and coca (*Erythroxylum* spp) production, respectively (Suffert *et al*. 2008, 2009; Gullino 2021).

There are a few well-known cases of human disease introductions that facilitated the invasion of territories and the destruction of local populations. The European conquest of the Americas can be considered perhaps the most extensive instance of biological warfare in history. Beginning with Christopher Columbus' second voyage to the New World in 1493, Europeans brought many novel disease agents, including the organisms responsible for smallpox, measles, plague, influenza, salmonella, scarlet fever, and chickenpox, to the hitherto unexposed Indigenous peoples of the Americas. Introduced into Mexico in 1520, smallpox caused the death of nearly half the Aztec population, including the emperor, which facilitated the conquest by Spanish troops led by Hernando Cortés (Diamond 1998). Similarly, Francisco Pizarro's conquest of present-day Peru was facilitated by a smallpox epidemic that occurred several years before his arrival. In 1763, Jeffery Amherst, a general of the British Army in North America, approved the use of germ warfare to sap resistance among Indigenous peoples of the continent through the distribution of smallpox-infected blankets to members of the Delaware people, resulting in high rates of infection and decimation of their population (Anderson 2000).

Conclusions

We have reported several examples of non-native species introductions by military operations (WebTable 1). Not all such examples are supported by scientific data, however; in some cases, they are anecdotal, speculative, or based on limited observations. Indeed, some reports, especially of intentional introductions, may be products of political disinformation campaigns or government propaganda. Obtaining verifiable evidence is often difficult if not impossible due to the amount of time that has passed since the events transpired. Even information obtained from molecular analyses is not always conclusive in distinguishing whether a species was introduced in the context of a war or on another occasion. Nevertheless, the military operations of WWI and WWII, which involved the transport of people, supplies (including foodstuffs), and machines within and between continents, clearly represent globalization events on an unprecedented scale. It is therefore not surprising that these wars also played key roles in the introduction and spread of many invasive organisms, as did the more localized conflicts that followed in the 20th and early 21st centuries. The phenomenon of the spread of invasive non-native species via military materiel remains relevant today, in the context of new types of warfare (asymmetric, hybrid, security operations, peacekeeping operations, and so forth). Even relatively small hostile actions require movements of troops, weapons, and supplies on a large scale in a short period of time between different geographical areas.

In facilitating invasion pathways, the role of war – as compared with international trade of plants and other goods – is probably minor, but it must still be considered important in part because it is largely unregulated. Furthermore, a large proportion of wars over the past several decades have been concentrated in regions that also host unique and diverse flora and fauna (Daskin and Pringle 2018), and the consequences of invasions in these regions may thus be particularly acute. In light of the devastation incurred by war, the introduction of invasive species (plants, animals, and pathogens) is likely to be considered a comparatively trivial form of collateral damage, but many invasions caused directly or indirectly by war have enduring effects on the ecosystems and economies of invaded countries. As such, the introduction of non-native species should be counted as among the ecological impacts of war, as characterized by Machlis and Hanson (2011), who noted that wars can have environmental impacts during the preparation phase (eg training camps and their effects on surrounding areas), during hostilities (eg direct habitat destruction in invaded areas), and during post-conflict activities (eg long-term landscape change or reconstruction operations). All three phases potentially promote the establishment and spread of invasive species either by increasing propagule pressure or by enhancing the invasibility of receiving habitats (Figure 5).

Given the potential influence of military activities in promoting biological invasions, it is reasonable to consider possible countermeasures. Several governments, notably those of Australia and the US, have instituted military-specific biosecurity risk management protocols and practices. Certain military movements have been identified as posing particularly high biosecurity risks, including military forces returning from overseas combat, peacekeeping, or humanitarian operations, as well as domestic and foreign defense forces participating in joint exercises and training (eg member nations of the North Atlantic Treaty Organization [NATO]; Cofrancesco *et al.* 2007; Inspector-General of Biosecurity 2018). Stringent biosecurity protocols for risk assessment and management have been instituted to reduce the likelihood of introducing non-native invasive species (Cofrancesco *et al.* 2007; Inspector-General of Biosecurity 2018). However, the measures described above are generally aimed at preventing introductions when armies return home, with little or no attention seemingly given to managing risks associated with species transported to other countries by armed forces during invasions or operating in peacekeeping and humanitarian missions or conducting exercises abroad.

In many respects the ways in which military biosecurity programs emphasize the exclusion of non-native taxa transported into the home country from abroad resemble the ways that nations also handle risks associated with international trade. Most

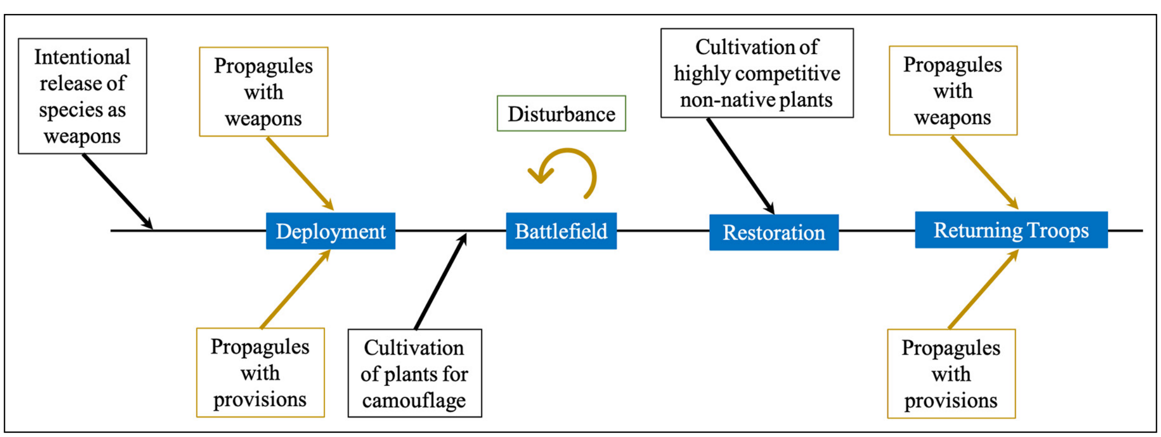

Figure 5. Conceptual depiction of how biological invasions are facilitated by military activity. The horizontal line represents the transition of a typical military incursion through successive phases, from left to right. Black arrows indicate instances of intentional facilitation of invasions, whereas gold arrows indicate instances of accidental facilitation.

national biosecurity agencies focus their efforts on exclusion of species from imports rather than exports (Ricciardi *et al.* 2021). However, international conventions, such as the International Plant Protection Convention and the International Convention for the Control and Management of Ships' Ballast Water and Sediments, have been established to implement standards that exporting countries are obliged to follow to minimize invasion risks to importing countries (David *et al.* 2015). Most aspects of these conventions generally or explicitly exclude international movement of goods as part of military activities. Indeed, as a generalization, invasion pathways associated with military actions are unregulated.

Ratified by the United Nations in 1976, the Environmental Modification Convention (ENMOD) prohibits the military use of environmental modification technologies that have widespread or long-lasting effects but does not mention the use of invasive species as weapons (Yuzon 1996). Likewise, the Convention on the Prohibition of the Development, Production and Stockpiling of Bacteriological and Toxin Weapons and on their Destruction (also called the "Biological Weapons Convention", BWC) bans the military use, development, production, acquisition, transfer, and stockpiling of biological weapons (Huigang *et al.* 2022). Initially signed by 103 countries in 1975 and now adopted by 183 countries, BWC targets microbes and chemicals. Neither ENMOD nor BWC specifically cover the use of invasive species as weapons, and regulation of military practices that facilitate the accidental or intentional relocation of invasive species appears to be largely beyond the scope of existing agreements. Consequently, efforts to reduce the risk of biological invasion from military activities might possibly be addressed in the future by expanding an existing international convention or by creating a new convention. At present, scientific reviews of the environmental effects of war have paid only scant attention to biological invasions; for example, Lawrence *et al.* (2015) mentioned invasive species only once. As we have shown here, the ways in which military activity impacts biological invasions have been largely understudied. Better integration of current knowledge about this phenomenon is needed to develop a more comprehensive synthesis of the diverse ways in which human activities impact the biosphere. In the meantime, biological invasions will likely continue to be one of many undesirable consequences of war. An improved understanding of their effects can only provide additional motivation for those working to achieve lasting global peace.

Acknowledgements

The authors thank A Baldazzi, Director of the "Museo della Linea Gotica" Castel del Rio (Bologna, Italy), for use of the photographs in Figure 4. This project received funding from the European Union's Horizon 2020 Program for Research and Innovation under grant agreement #771271 "HOMED". AML acknowledges funding from grant EVA4.0, #CZ.02.1.01/0.0/0.0/16_019/0000803 from OP RDE. DMR received support from the DSI-NRF Centre of Excellence for Invasion Biology, Mobility 2020 project #CZ.02.2.69/0.0/0.0/18_053/0017850 (Ministry of Education, Youth and Sports of the Czech Republic) and long-term research development project RVO 67985939 (Czech Academy of Sciences).

Data Availability Statement

Data are already published and publicly available, with those items properly cited below.

References

Anderson F. 2000. Crucible of war: the Seven Years' War and the fate of empire in British North America, 1754–1766. New York, NY: Knopf.

Binggeli P. 2001. The human dimensions of invasive woody plants. In: McNeely JA (Ed). The great reshuffling: human dimensions of invasive alien species. Gland, Switzerland: International Union for Conservation of Nature.

Black J. 2009. War – a short history. London, UK: Bloomsbury Academic.

Caldas MM and Perz S. 2013. Agro-terrorism? The causes and consequences of the appearance of witch's broom disease in cocoa plantations of southern Bahia, Brazil. *Geoforum* **47**: 147–57.

Casagrande RA. 1987. The Colorado potato beetle: 125 years of mismanagement. *Bull Entomol Soc Am* **33**: 142–50.

Chalk P. 2004. Agroterrorism: what is the threat and what can be done about it? Santa Monica, CA: Rand Corporation.

Cofrancesco AF, Reaves DRJ, and Averett DE. 2007. Transfer of invasive species associated with the movement of military equipment and personnel. Vicksburg, MS: Engineer Research and Development Center.

Coles SL, DeFelice RC, Eldredge LG, and Carlton JT. 1999. Historical and recent introductions of non-indigenous marine species into Pearl Harbor, Oahu, Hawaiian Islands. *Mar Biol* **135**: 147–58.

Cristinzio M, Marziano F, and Vernau R. 1973. La moria del platano in Campania. *Riv Patol Veg* **9**: 189–214.

Crosby AW. 1986. Ecological imperialism: the biological expansion of Europe, 900–1900. Cambridge, UK: Cambridge University Press.

Daskin JH and Pringle RM. 2018. Warfare and wildlife declines in Africa's protected areas. *Nature* **553**: 328–32.

David M, Gollasch S, Elliott B, and Wiley C. 2015. Ballast water management under the Ballast Water Management Convention. In: David M and Gollasch S (Eds). Global maritime transport and ballast water management. Dordrecht, the Netherlands: Springer.

Diamond J. 1998. Guns, germs, and steel: a short history of everybody for the last 13,000 years. London, UK: Vintage.

Drake DR and Hunt TL. 2009. Invasive rodents on islands: integrating historical and contemporary ecology. *Biol Invasions* **11**: 1483–87.

Essl F, Bacher S, Blackburn TM, *et al.* 2015. Crossing frontiers in tackling pathways of biological invasions. *BioScience* **65**: 769–82.

Ewel JJ, O'Dowd DJ, Bergelson J, *et al.* 1999. Deliberate introductions of species: research needs. Benefits can be reaped, but risks are high. *BioScience* **49**: 619–30.

Fletcher J, Bender C, Budowle B, *et al*. 2006. Plant pathogen forensics: capabilities, needs, and recommendations. *Microbiol Mol Biol R* **70**: 450–71.

Foxwell JWJ. 2001. Current trends in agroterrorism (antilivestock, anticrop, and antisoil bioagricultural terrorism) and their potential impact on food security. *Stud Confl Terror* **24**: 107–29.

Garrett B. 1996. The Colorado potato beetle goes to war. *Chem Weapon Conv Bull*: 2–3.

Geissler E. 1999. Biological warfare activities in Germany, 1923–45. In: Geissler E and van Courtland Moon JE (Eds). Biological and toxin weapons: research, development and use from the Middle Ages to 1945. New York, NY: Oxford University Press.

Gonthier P, Warner R, Nicolotti G, *et al*. 2004. Pathogen introduction as a collateral effect of military activity. *Mycol Res News* **108**: 468–70.

Grasso DV. 1951. Un nuovo agente patogeno del *Cupressus macrocarpa* Hartw. *L'Italia For e Mont* **6**: 62–65.

Gullino ML. 2021. Spores. Cham, Switzerland: Springer.

Haack RA, Britton KO, Brockerhoff EG, *et al*. 2014. Effectiveness of the International Phytosanitary Standard ISPM No 15 on reducing wood borer infestation rates in wood packaging material entering the United States. *PLoS ONE* **9**: 96611.

Haldane JBS. 1937. Science and future warfare. *Roy United Services Instit J* **82**: 713–28.

Huigang L, Menghui L, Xiaoli Z, *et al*. 2022. Development of and prospects for the Biological Weapons Convention. *J Biosafe Biosec* **4**: 50–53.

Hulme PE. 2021. Unwelcome exchange: international trade as a direct and indirect driver of biological invasions worldwide. *One Earth* **4**: 666–79.

Hulme PE, Bacher S, Kenis M, *et al*. 2008. Grasping at the routes of biological invasions: a framework for integrating pathways into policy. *J Appl Ecol* **45**: 403–14.

Humble LM. 2010. Pest risk analysis and invasion pathways – insects and wood packing revisited: what have we learned? *New Zeal J For Sci* **40**: 199–209.

Inspector-General of Biosecurity. 2018. Military biosecurity risk management in Australia. Canberra, Australia: Commonwealth of Australia.

Janovsky RM and Larson ER. 2019. Does invasive species research use more militaristic language than other ecology and conservation biology literature? *NeoBiota* **44**: 27–38.

Keegan J. 1993. A history of warfare. London, UK: Pimlico.

Lawrence MJ, Stemberger HLJ, Zolderdo AJ, *et al*. 2015. The effects of modern war and military activities on biodiversity and the environment. *Environ Rev* **23**: 443–60.

LeBlanc R. 2002. Another sneak attack, war heralded pallet in industry – World War II spurred use of pallet in material handling. *Pallet Enterprise*; www.palletenterprise.com/articledatabase/view.asp?articleID=681. Viewed 22 Dec 2022.

Leoni D. 2015. La guerra verticale. Uomini, animali e macchine sul fronte di montagna 1915–1918. Torino, Italy: Einaudi.

Leung B, Springborn MR, Turner JA, and Brockerhoff EG. 2014. Pathway-level risk analysis: the net present value of an invasive species policy in the US. *Front Ecol Environ* **12**: 273–79.

Lockwood JA. 2012. Insects as weapons of war, terror, and torture. *Annu Rev Entomol* **57**: 205–27.

Lopez J, Nicolas A, Bernard V, and Guillerat N. 2018. Infographie de la Seconde Guerre mondiale. Paris, France: Editions Perrin.

Lowney M, Schoenfeld P, Haglan W, and Witmer G. 2005. Overview of impacts of feral and introduced ungulates on the environment in the eastern United States and Caribbean. In: Nolte DL and Fagerstone KA (Eds). Proceedings of the 11th Wildlife Damage Management Conference. Bethesda, MD: The Wildlife Society.

Machlis GE and Hanson T. 2011. Warfare ecology. In: Machlis GE, Hanson T, Špirić Z, and McKendry JE (Eds). Warfare ecology: a new synthesis for peace and security. Dordrecht, the Netherlands: Springer.

Madden LV and Wheelis M. 2003. The threat of plant pathogens as weapons against US crops. *Annu Rev Phytopathol* **41**: 155–76.

McNeely JA (Ed). 2001. The great reshuffling: human dimensions of alien invasive species. Gland, Switzerland: International Union for Conservation of Nature.

McNeely JA. 2005. Human dimensions of invasive alien species. In: Mooney HA, Mack RN, McNeely JA, *et al*. (Eds). Invasive alien species: a new synthesis. Washington, DC: Island Press.

McNeely JA. 2006. As the world gets smaller, the chances of invasion grow. *Euphytica* **148**: 5–15.

Novick D, Anshen M, and Truppner WC. 1949. Wartime production controls. New York, NY: Columbia University Press.

Pimentel D, Lach L, Zuniga R, and Morrison D. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* **50**: 53–65.

Prosser F. 2015. Effetti della prima guerra mondiale sulla flora del Trentino. *Rendiconti Online della Società Geologica Italiana* **36**: 105–09.

Ricciardi A, Aldridge DC, Blackburn TM, *et al*. 2021. How should invasion science adapt to an era of rapid environmental change? *Environ Rev* **29**: 119–41.

Rogers P, Whitby S, and Dando M. 1999. Biological warfare against crops. *Sci Am* **280**: 70–75.

Ruppenthal RG. 1995. United States Army in World War II, the European theater of operations, logistical support of the armies, vol I: May 1941–September 1944. Washington, DC: Center of Military History, US Army.

Stack J, Cardwell K, Hammerschmidt R, *et al*. 2006. The national plant diagnostic network. *Plant Dis* **90**: 128–36.

Stanaway MA, Zalucki MP, Gillespie PS, *et al*. 2001. Pest risk assessment of insects in sea cargo containers. *Aust J Entomol* **40**: 180–92.

Suffert F, Barbier M, Sache I, and Latxague E. 2008. Biosécurité des cultures et agroterrorisme: une menace, des questions scientifiques et une réelle opportunité de réactiver un dispositif d'épidémiovigilance. *Le Courrier de l'environnement de l'INRA* **56**: 67–86.

Suffert F, Latxague É, and Sache I. 2009. Plant pathogens as agroterrorist weapons: assessment of the threat for European agriculture and forestry. *Food Secur* **1**: 221–32.

Sumner J. 2019. Plants go to war: a botanical history of World War II. London, UK: McFarland.

Vernier F. 2014. Plantes obsidionales. L'étonnante histoire des espèces propagées par les armées. Strasbourg, France: Vent d'Est.

Wadge R. 2012. Archery in medieval England: who were the bowmen of Crecy? London, UK: The History Press.

Whitby SM. 2002. Biological warfare against crops. London, UK: Palgrave Macmillan.

Yuzon FJ. 1996. Deliberate environmental modification through the use of chemical and biological weapons: greening the international laws of armed conflict to establish an environmentally protective regime. *Am Univ J Int Law Pol* **11**: 793–846.

Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2640/suppinfo

FrontiersEcoPics

Blackbird dominance and habitat loss

Yellow-headed (*Xanthocephalus xanthocephalus*) and red-winged (*Agelaius phoeniceus*) blackbirds coexist in marshes across North America. Pictured here at Iona Beach Regional Park in Vancouver, British Columbia, males of each species compete for nesting areas. In wetlands across their overlapping ranges, yellow-heads are dominant over red-wings, pushing them out of valuable marsh real-estate to secure the best nesting places.

Unfortunately, since the construction of Vancouver International Airport in 1968 and its expansion in subsequent years, both species have lost substantial extents of marsh habitat. Given their dominant–subordinate relationship, one might expect that habitat loss should disproportionately impact the subordinate red-wings, since they get last choice at nesting habitat, which might limit their reproductive success. Today, however, Iona Beach supports a healthy and abundant population of red-wings, and usually hosts only a few yellow-heads. Indeed, over the past half-century, the population of yellow-heads at Iona Beach has decreased ~95%, down from an estimated 70 individuals in 1970 to only 1–3 nowadays (Campbell RW, Dawe NK, McTaggart-Cowan I, *et al*. 2001. The Birds of British Columbia. Volume 4. Royal British Columbia Museum Victoria. Vancouver, Canada: UBC Press).

Despite their dominance, the yellow-headed blackbirds of Vancouver have seemingly been more negatively impacted by habitat loss and degradation than their subordinate red-winged cousins. Does their dominant behavior make yellow-heads more vulnerable to change? Are red-wings more tolerant of anthropogenic disturbances? Over the next decade, the potential extirpation of yellow-headed blackbirds from Iona Beach calls into question which blackbird genuinely is the dominant species. Of course, none of this stops the remaining few yellow-heads from bullying the abundant red-wings out of prime nesting space. At least population decline has not adversely impacted their yellow-headed ego!

Isaac Eckert
McGill University, Montreal, Canada
doi:10.1002/fee.2691