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Forum

Quantifying the Magnitude of Biological Invasions Using Total Biomass

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Abstract

Biological invasions rank among the greatest anthropogenic threats to global biodiversity and ecosystem functioning, but measuring and comparing their relative magnitudes across regions and taxa remains challenging. The absence of a unified metric hinders scientific advancement, public awareness, and policy development. We propose a simple, standardized metric to quantify and communicate the magnitude of biological invasions: total biomass of nonnative species. This metric approximates the amount of native biomass co-opted, displaced, consumed, or replaced by the populations of invasive species. We illustrate how this metric can be applied to different research themes and contexts such as temporal and spatial invasion dynamics, management strategies, and invasion forecasts. Although not a metric for impact, this magnitude will be useful to quantify the extent of impact of invasive populations. Total biomass can provide a common currency to assess the magnitude of biological invasions, facilitating comparisons, syntheses, and innovations across invasion science.

Keywords: conservation, displacement, invasive species, management, quantitative metric

Biological invasions rank among the leading global challenges of the Anthropocene, capturing international attention and provoking extensive research (IPBES 2023). A biological invasion is the intentional or unintentional transportation of species outside their natural ranges by human activities into new regions where they establish and spread (Le Roux 2021, IPBES 2023). Biological invasions are responsible for rapidly expanding ecological and socioeconomic damage across the globe (Diagne et al. 2021, IPBES 2023). However, the awareness of, as well as the commitment and capacities to address, biological invasions are still lower than other planetary-scale drivers of biodiversity erosion (Courchamp et al. 2017). A pervasive reason for this mismatch is the diversity of invasive species (those that are responsible for biological invasions) and the damage they inflict across various sectors (ecological, health, social, and economic) that are quantified with different currencies (IPBES 2023). This multiplicity and heterogeneity complicate our capacity to capture and quantify the magnitude of invasions. Consequently, finding a common unit that enables compilation and standardization of data across taxonomic groups, regions, and at different scales will promote developing, comparing, interpreting, validating, and prioritizing management strategies, as well as building awareness among decision-makers and the public.

Although valuable, existing metrics such as the richness, abundance, distribution, and the rate of spread of invasive species present challenges when creating a generalizable, quantitative metric to standardize the magnitude of an invasion (Catford et al. 2012). In this article, we present a general solution to address these global challenges in understanding, managing, and communicating the magnitude of any biological invasion using a single and straightforward metric: biomass. By *magnitude*, we mean the overall scale of the physical presence of an invasive species within an ecosystem. We demonstrate how the total biomass of invasive species offers a common proxy of the magnitude of their invasion across different ecosystems and spatial scales. The intuitiveness of total biomass ensures its accessibility to a broad audience,

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from experts to nonexperts alike. Such accessibility can facilitate effective communication of the magnitude of biological invasions in a manner that transcends disciplinary boundaries. By drawing parallels with familiar metrics, such as tonnes of emitted carbon dioxide (Reed et al. 2022); tonnes of polluting plastic, oil, or heavy metals (Huang et al. 2018); tonnes of exploited fish stocks, timber, or bushmeat (Hughes et al. 2023); or even tonnes of anthropogenic waste (Elhacham et al. 2020), the invasive biomass metric integrates seamlessly into existing frameworks of other components of global change, fostering a transparent and informed discourse in scientific, political, policy, and public domains. This alignment with established environmental metrics could foster public acceptance and comprehension.

Biomass as a standard metric of invasion magnitude

In ecological terms, biomass represents the cumulative mass of living organisms within a specific community or ecosystem. This metric therefore encompasses the combined mass of organisms, be they plants, animals, or microorganisms, and can be used across multiple scales (e.g., individuals, populations, and communities) and in all habitats (marine, freshwater, and terrestrial). Biomass is commonly expressed in units of mass per spatial unit (area or volume), from which total biomass can be calculated for a given invaded range. In general, variation in biomass (e.g., across space or time) serves as an indicator of an ecosystem's health and efficiency of resource use because changes in total biomass can reflect changes in population dynamics or resource availability. Biomass also connects directly to many fundamental ecological concepts, such as ecosystem stability and energy flow (McCann 2000), and forms the basis for scaling laws comparing the traits of different species, which could be applied to impute missing biomass values (Hatton et al. 2019). Adopting biomass as a metric adds a layer of ecological relevance to invasion studies. Compared with metrics such as the abundance of invasive individuals, which is highly taxon-dependent, or geographical distribution, which often provides limited information regarding potential magnitude, biomass provides a more comprehensive understanding of the magnitude of an invasion in an ecosystem. Fundamentally, invasive biomass provides a means to gauge the overall productivity, energy flow, and ecological interactions that are potentially disrupted within an ecosystem.

We assume that in most cases, invasive populations do not fill empty niches (or ecological space) but necessarily co-opt the resources that would otherwise be incorporated into the total biomass of native species. If an invader becomes established, it is generally via an accommodation on the part of the native species (Briggs 2010). For example, we assume in practice that every tonne of the invasive velvet tree (*Miconia calvescens*) grows at the expense of less-competitive plants that it replaces in the Pacific islands, where it often forms dense, monospecific stands. Similarly, the population growth of any invasive deer, for example, is likely promoted at the expense of both native plants and competing native herbivores, even if one cannot easily disentangle the two. The concept is illustrated in figure 1.

Invasive biomass as a unified metric also fosters comparison among species of different sizes. Smaller, but more abundant species do not necessarily represent a smaller global biomass relative to larger species across plants and animals. For example, the total biomass of annelids is estimated to be around one hundred times higher than that of birds worldwide (Bar-on et al. 2018), even if individuals of the latter are over one hundred times heavier on average. Tonnes of biomass can quantify both temporal and spatial invasion dynamics and can compare regions and taxa, forecast the magnitude of potential invasions, or track the efficacy of management actions. Below, we provide several empirical examples spanning habitats, realms, and regions that illustrate the use of total biomass for quantifying the magnitude of biological invasions. Table 1 summarizes these examples, with the calculation mode from the data contained in the cited reference.

Illustrating the use of invasive biomass

In the following section, we explore how invasive biomass can be characterized across biological, spatial, and temporal gradients, and how these insights translate into actionable value for management, policy development, and stakeholder engagement.

Comparison among taxa

Total biomass can be used to compare the invasion magnitude among taxa from anywhere across the tree of life (but see box 1 for the special case of pathogenic microorganisms). Communicating these magnitudes is challenging, particularly for small taxa where size has precluded research and management in contrast to larger, more charismatic taxa (Carlton 2009). For example, a single invasive zooplankton species (*Cercopagis pengoi*) in Lake Ontario can reach a total biomass of 9700 tonnes during the summer (Makarewicz et al. 2001; table 1). This figure aligns with the biomass of the much larger red fox (*Vulpes vulpes*) in Australia (9960 tonnes; table 1) or of the even larger chital deer (*Axis axis*) in Australia (8340 tonnes; table 1). Other total biomass values across taxa of different sizes indicate that invasions span different orders of magnitude among yellow crazy ants (*Anoplolepis gracilipes*) on Christmas Island (46 tonnes), mice (*Mus* spp.) on Gough Island (864 tonnes), brown tree snakes (*Boiga irregularis*) in Guam (2200 tonnes), giant African snails (*Achatina fulica*) in New Caledonia (19,000 tonnes), water hyacinth (*Pontederia crassipes*) in the Guadiana River on the Portuguese–Spanish border (200,000 tonnes), feral donkeys (*Equus asinus*) in Australia (1,250,000 tonnes), or the warty comb jelly (*Mnemiopsis leidyi*) in the Black Sea (91,368,000 tonnes), which in each case is the potential amount of biomass in the ecosystem that would otherwise be incorporated into native species (table 1).

Comparing two invasive species directly using biomass can be straightforward and more ecologically relevant than comparing abundance estimates. For example, comparing two invasive predators in Australia—the red fox and feral cat (*Felis silvestris catus*) on the basis of their respective abundances gives a biased impression of the magnitude of invasion for each species: there are approximately twice as many cats (2.8 million individuals) as foxes (1.6 million). However, their total biomasses indicate a similar magnitude of invasion (8500 tonnes for cats versus 9900 tonnes for foxes; table 1). Furthermore, it is more tractable and ecologically relevant to compare the total biomass of different invasive species than to compare abundances, which can be misleading or unfeasible (such as for plants, where the concept of individuality is not always relevant; Clarke 2012). For example, there are about 1 million feral camels in Australia, and 2.6 times more feral goats. However, the total biomass co-opted by camels is 406,000 tonnes, whereas that of goats is less than half that amount (186,000 tonnes), because a camel weighs on average about 10 times more than a goat. Because of its gen-

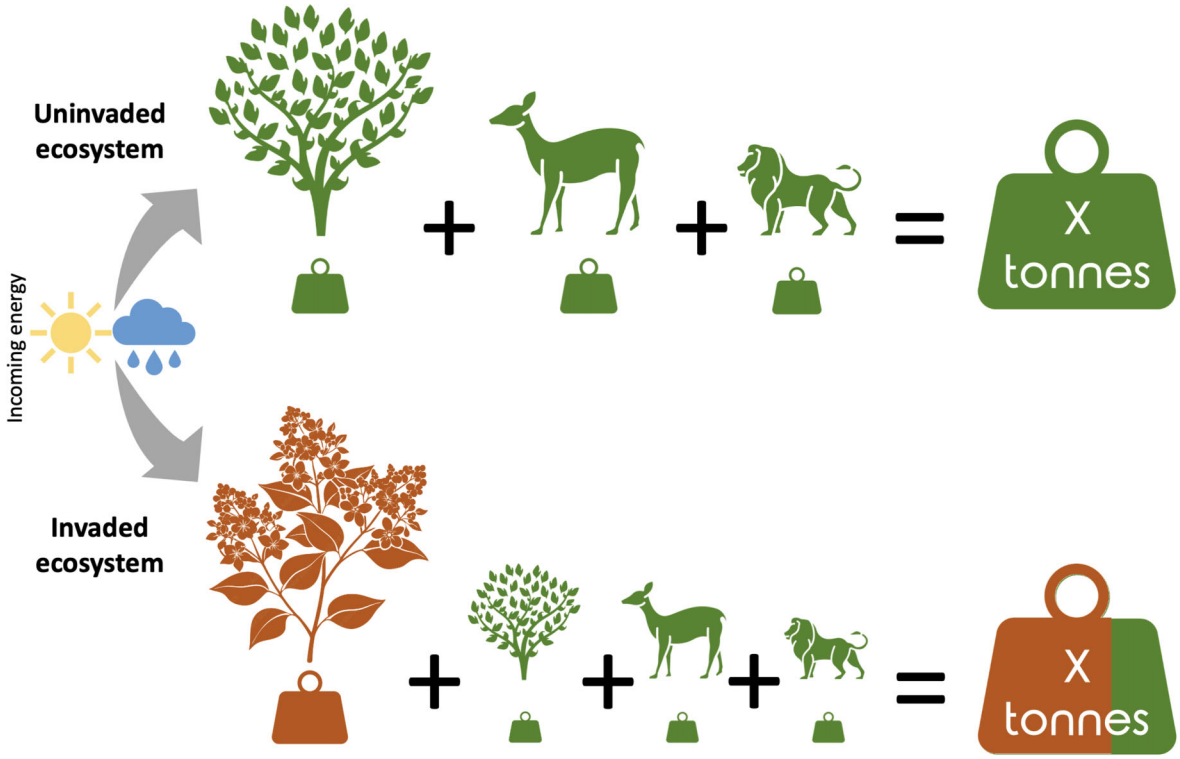

Figure 1. Total biomass accumulated by organisms in an uninvaded (top) and an invaded (bottom) ecosystem, represented by three trophic levels: producers (plant icon), primary consumers (herbivore), and secondary consumers (predator). The size of organisms represents the total biomass of the populations of the corresponding organisms. In this illustration, the quantity of energy (e.g., sunlight; sun icon) and precipitation (cloud) transformed into biomass is the same in the two ecosystems, so that the presence of an invasive species (in orange) might not affect the total biomass (weight icon), but decreases the biomass of the native species (in green). The total biomass of the invasive species represents the magnitude of the invasion. The magnitude of the invasion is distinguishable from the severity of the invasion, which would be the proportion of the total biomass that is contributed by the invasive populations.

eralizability, the total biomass of several invading taxa in a single region can be combined to reflect the total invasion biomass at a broader spatial scale. The combined biomass co-opted by all large invasive herbivores in Australia is well over 3.5 million tonnes, for about 6 million animals of differing average body mass (figure 2).

Comparing regions and spatial scales

Comparing invasion magnitudes among biomes, realms, and geographic regions is possible using total biomass. For instance, total biomass estimates demonstrate the magnitude of feral pig (*Sus scrofa*) invasions in Australia (270,000 tonnes), which is half the amount for the same species in the United States (591,000 tonnes; table 1). In fact, there is no a priori reason not to sum invasive populations of distant taxonomic groups in the same way: the total biomass of the Nile perch (*Lates niloticus*) and of the water hyacinth in Lake Victoria can be aggregated to reflect the overall magnitude of invasion in that ecosystem, which can then be compared to the magnitude of invasions of other species in other lakes or even of different habitats. In that context, studies can (and often should) use biomass per unit of area or volume to make meaningful comparisons. In any invasion, there are biomass differences among regions or heterogeneities within regions, compounded by variation in carrying capacities. This implies that, as in any extrapolation, upscaling the regional footprint of an invasion cannot be done to national scales without correcting for local specificities.

Temporal and spatial trends

The temporal and spatial scales at which an invasion is studied depend on the study itself, and it is possible to collect fine-resolution data to account for temporal or spatial heterogeneity. Calculating the total biomass of invasive populations allows meaningful assessments of temporal variation in the magnitude of invasions. Incorporating total biomass in studies also enables better assessment of spatial trends in the magnitude of invasions, exemplified by the grey squirrel (*Sciurus carolinensis*) in the United Kingdom (table 1) or the invasion of the Asian hornet (*Vespa velutina*) in France (figure 3). The Asian hornet was introduced to France in 2004 from a single queen (Arca et al. 2015). The spread of its descendants has been regularly monitored by spotting nests, providing a unique database that allowed the reconstruction of the spatial progression of the population over 15 years (Barbet-Massin et al. 2018, Robinet et al. 2019). Because the average biomass of the individuals within a nest and the overall density of nests are available (e.g., Requier et al. 2023), one can deduce the spatiotemporal dynamics of the total biomass of the invasive population (figure 3). These data resemble a typical invasion curve, which illustrates invaded area, impact, and management difficulty over time (Ahmed et al. 2022). When coupled with information on total biomass, potent tools such as species distribution models can provide data on the potential of current and future invasions. For example, species distribution models can estimate that the biomass of inva-

Table 1. Examples of total invasive biomass for some invasions, as detailed in the main text.

Common name	Species	Region Invaded	Original data	Average body mass	Invasion biomass (tonnes)
hottentot-fig	*Carpobrotus edulis*	Cavado estuary	8.6 kg/m^2 (1)		33
yellow crazy ant	*Anoplolepis gracilipes*	Christmas Island	1.86 g/m^2 over 2500 ha (2)		46
house mouse	*Mus musculus*	Gough Island	266 individuals/ha (3)	35.7 g (3)	864
Asian hornet	*Vespa velutina*	France	1.08 nest/km^2 (4); 6185 individuals/nest (5)	386 mg (5)	1403
grey squirrel	*Sciurus carolinensis*	United Kingdom	2,700,000 individuals (6)	545 g (7)	1472
brown tree snake	*Boiga irregularis*	Guam	4 kg/ha (8)		2196
hog deer	*Axis porcinus*	Australia	105,000 individuals (8,9)	37.4 kg (7)	3932
banteng	*Bos javanicus*	Australia	8000 individuals (11)	636 kg (7)	5087
chital deer	*Axis axis*	Australia	120,000 individuals (8,9)	69.5 kg (7)	8340
feral cat	*Felis catus*	Australia	2,600,000 individuals (12)	3.0 kg (13)	8498
red fox	*Vulpes vulpes*	Australia	1,660,000 individuals (14)	6.0 kg (15)	9960
fishhook waterflea	*Cercopagis pengoi*	Lake Ontario	34,361 µg/m^3 (16)		up to 9700 during the summer
Sambar deer	*Cervus unicolor*	Australia	75,000 individuals (8,9)	177.5 kg (7)	13,314
rusa deer	*Cervus timorensis*	Australia	255,000 individuals (8,9)	66.3 kg (7)	16,926
giant African snails	*Achatina fulica*	New Caledonia			19,000 (17)
fallow deer	*Dama dama*	Australia	420,000 individuals (8,9)	57.2 kg (7)	24,034
water hyacinth	*Pontederia crassipes*	Deepor Beel	6.0 kg/m^2 (18)		28,621 (18)
swamp buffalo	*Bubalus bubalis*	Australia	150,000 individuals (19)	825 kg (7)	123,750
red deer	*Cervus elaphus*	Australia	525,000 individuals (8,9)	240.8 kg (7)	126,455
goat	*Capra hircus*	Australia	2,600,000 individuals (20)	71.4 kg (7)	185,512
water hyacinth	*Pontederia crassipes*	Guadiana River			200,000 (21)
horse	*Equus caballus*	Australia	400,000 individuals (22)	514.1 kg (23)	205,648
common carp	*Cyprinus carpio*	Australia			205,774 (24)
feral pig	*Sus scrofa*	Australia	3,200,000 individuals (25)	84.5 kg (7)	270,304
camel	*Camelus dromedarius*	Australia	1,000,000 individuals (26)	406.0 kg (27)	406,000
feral pig	*Sus scrofa*	United States	7,000,000 individuals (28)	84.5 kg (7)	591,301
smooth cordgrass	*Spartina alterniflora*	China	1490.6 g/m^2 (29,30)		838,852
donkey	*Equus asinus*	Australia	5,000,000 individuals (24)	250 kg (7)	1,250,000
water hyacinth	*Pontederia crassipes*	Shanghai			1,680,000 (31)
warty comb jelly	*Mnemiopsis leidyi*	Black Sea			91,368,000 (32)

[1]Meyer et al. (2023). [2]Abbott (2005). [3]Cuthbert et al. (2016). [4]Rome et al. (2015). [5]Requier et al. (2023). [6]Matthews et al. (2018). [7]Greenspoon et al. (2023). [8]Rodda et al. (1999). [9]Australia (2023). [10]Moriarty (2004). [11]Bradshaw et al. 2007. [12]Legge et al. (2017). [13]Fleming et al. (2020). [14]Stobo-Wilson et al. (2022). [15]Dyck and Strahan (2008). [16]Makarewicz et al. (2001). [17]Tiller (1982). [18]Rajora et al. (2023). [19]Albrecht et al. (2009). [20]Parkers et al. (1996). [21]Scalera et al. (2012). [22] Australia (2011). [23] Cozzi et al. (2013). [24]Stuart et al. (2021). [25]Hone (2019). [26]Saalfeld and Edwards (2010). [27]Boujenane (2019). [28] Lewis et al. (2019). [29]Zheng et al. (2018). [30]Liu et al. (2018). [31]Chu et al. (2006). [32]Mutlu et al. (1994).

Box 1. Special case of pathogenic microorganisms

The total biomass of invasive pathogenic microorganisms (e.g., viruses, bacteria) or even of disease-inducing macroparasites, presents a special case (Warren et al. 2023), in which their total biomass might not necessarily represent the magnitude of their invasions. For example, a single person infected with COVID-19 (which has been considered an invasive species; Nuñez et al. 2020) carries a total number of virions (1 billion to 100 billion virions) weighing between 1 microgram and 0.1 milligram (Sender et al. 2021). Across the total human population at any given time, there might only be several kilograms of virions present; this does not adequately reflect the magnitude of their presence across the world. In such cases, it could be feasible to highlight the total biomass of individual hosts that are affected by these organisms, rather than the total biomass of the infecting organisms themselves. For example, in recent years the annual number of pines that have died because of the pine wilt disease caused by the pinewood nematode (*Bursaphelenchus xylophilus*) invasion in China was over 20 million, amounting to a biomass of about 3.74 million tonnes of dead Masson pines (*Pinus massoniana*), or 600 million pines in the last 40 years, equivalent to 112.2 million tonnes for an average individual (*P. massoniana*) tree weighing about 187 kilograms (Huang et al. 2015, Dong et al. 2022). Similarly, it would be interesting to assess the overall biomass of all amphibians affected by chytrid fungus (*Batrachochytrium dendrobatidis*) (Fisher and Garner 2020), crayfish affected by crayfish plague (*Aphanomyces astaci*) (Svoboda et al. 2017), or several tree species dying from infection of the panglobal plant pathogen (*Phytophthora cinnamomi*) (Shakya et al. 2021). For pathogenic microorganisms, not only would the total biomass of affected hosts align better with other invasive species, it would also reflect the magnitude of invasions more directly. Although the numbers are often lacking, dedicated research would be relevant in this regard. These cases would be the only exceptions to the use of invasive biomass but would nevertheless respect the principle of affected native biomass.

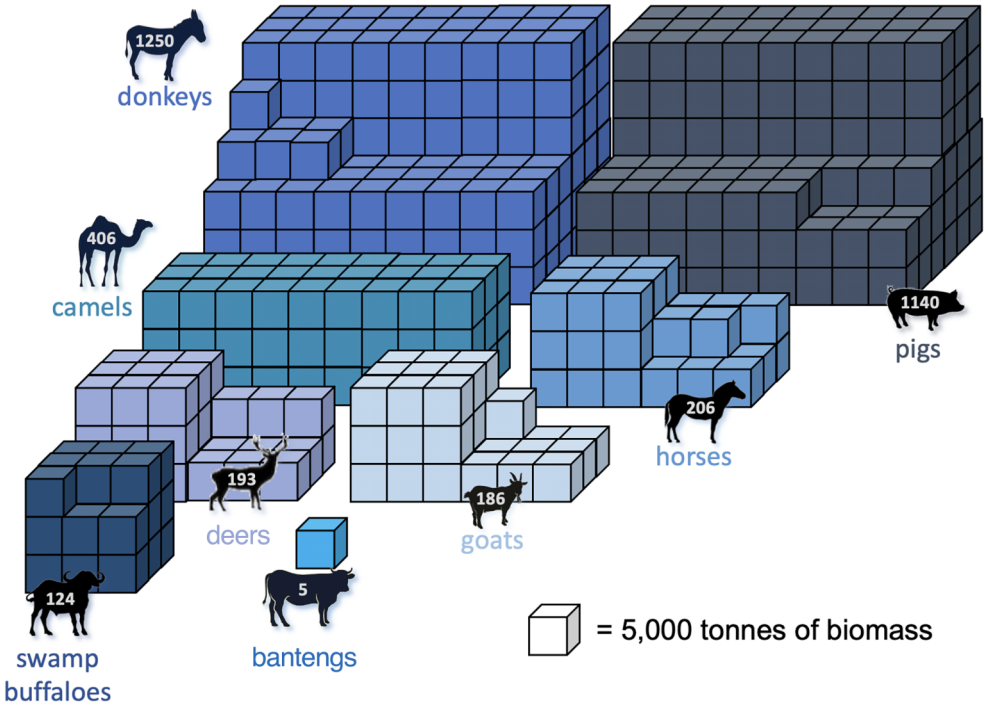

Figure 2. Total biomass of the populations of invasive large herbivores in Australia. Each pile of blocks represents the biomass of all individuals of these species in Australia, with block units of 5000 tonnes each. The number on each animal silhouette represents the total biomass of their populations, in thousands of tonnes. Large herbivores we considered are > 30 kilograms per individual: feral pigs, *Sus scrofa*; horses, *Equus caballus*; donkeys, *Equus asinus*; camels, *Camelus dromedarius*; goats, *Capra hircus*; six species of deer (hog, *Axis porcinus*; chital, *Axis axis*; fallow, *Dama dama*; red, *Cervus elaphus*; rusa, *Cervus timorensis*; sambar, *Cervus unicolor*); bantengs, *Bos javanicus*; and swamp buffalo, *Bubalus bubalis*. We did not find accurate data for feral cattle, *Bos taurus*, and feral sheep, *Ovis aries*. The data underlying this figure are provided in table 1 (and in the references).

sive feral pigs in the United States is around 591,000 tonnes (table 1).

Utility for management and policy

Total biomass is relevant for management because it can be used as a target for interventions. For example, 28,621 tonnes of water hyacinth were targeted for removal from Deepor Beel in India (table 1). Total biomass can be used to compare the cost-effectiveness of a management method: the management costs to remove 200,000 tonnes of water hyacinth along the Guadiana River on the Portuguese–Spanish border amounted to €14,680,000, which equates to only €74 per tonne, with more than 2500 tonnes removed per kilometer (table 1). In the Huangpujiang River and other areas in Shanghai, 1.68 million tonnes of water hyacinth were removed in 2002 alone (table 1). Moreover, total biomass limits could be set whereby policymakers impose quotas on the amount of invasions permissible to or from particular countries or industries (similar to carbon credits). Total biomass could also be applied to quantify the magnitude of

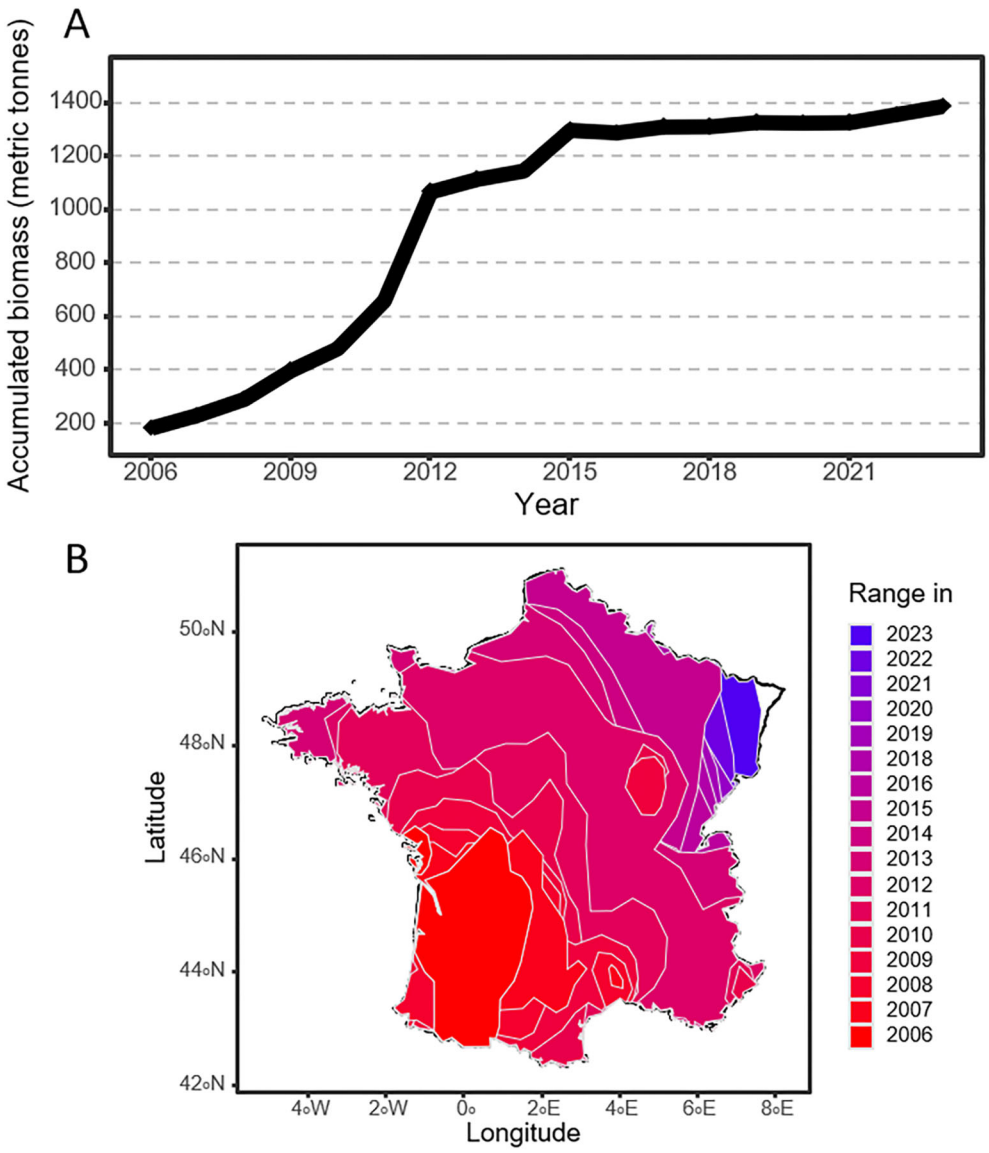

Figure 3. (a) Cumulative total biomass of the invasive Asian hornet (*Vespa velutina*) in France (table 1). (b) Spatial representation of the spread and total biomass of this species in France until 2023, from the oldest introduced region (southwest, red, lowest total biomass with about 200 tonnes), to the expanded invaded range until the northeast of France (blue, highest total cumulative biomass in 2023; about 1400 tonnes). The year indicated in the legend is the time of arrival of the hornet in the corresponding region.

flows of invasive species among source and recipient countries (e.g., Hudgins et al. 2023). Such standardization would allow prioritization of biosecurity and pathway management (however, see the caveat below regarding data-deficient regions). Furthermore, prioritizing areas for management could be facilitated using total biomass, where reactive removal could be most efficient in areas with the largest total biomass; although it is proactive, rapid eradication could be most efficient and cost-effective in areas with low total biomass (Finley et al. 2023). In China, the smooth cordgrass (*Spartina alterniflora*) has invaded several regions, accumulating approximately 839,000 tonnes of biomass, but with a heterogeneous distribution that provides an opportunity for spatial prioritization (figure 4 and table 1). Among other factors, the extent of invasions of these different regions could be a powerful metric for prioritizing conservation actions. Finally, many stakeholders currently struggle to articulate a meaningful indicator of biological invasions that will quantify and lower the current or potential environmental footprint of institutions, enterprises, or companies. In that context, the total biomass of invasions could be a practical metric, analogous to carbon footprint.

Communication benefits

Like established environmental drivers, invasive biomass can become a communication tool for raising public awareness. One of the issues complicating the message of invasions is the multiplicity of culprits: with over 35,000 invasive species worldwide, their sheer number and diversity ironically hinders a clear public understanding of the combined threat. Improving the way biological invasions are communicated by the media is therefore an effective tool in gaining support for management interventions (Courchamp et al. 2017). Stories are deemed noteworthy by news organizations when they satisfy specific criteria (Harcup and O'Neill 2001, 2017), such as relevance, magnitude, and qualifying as bad news (Harcup and O'Neill 2001, 2017), which all resonate with issues associated with biological invasions. Therefore, communica-

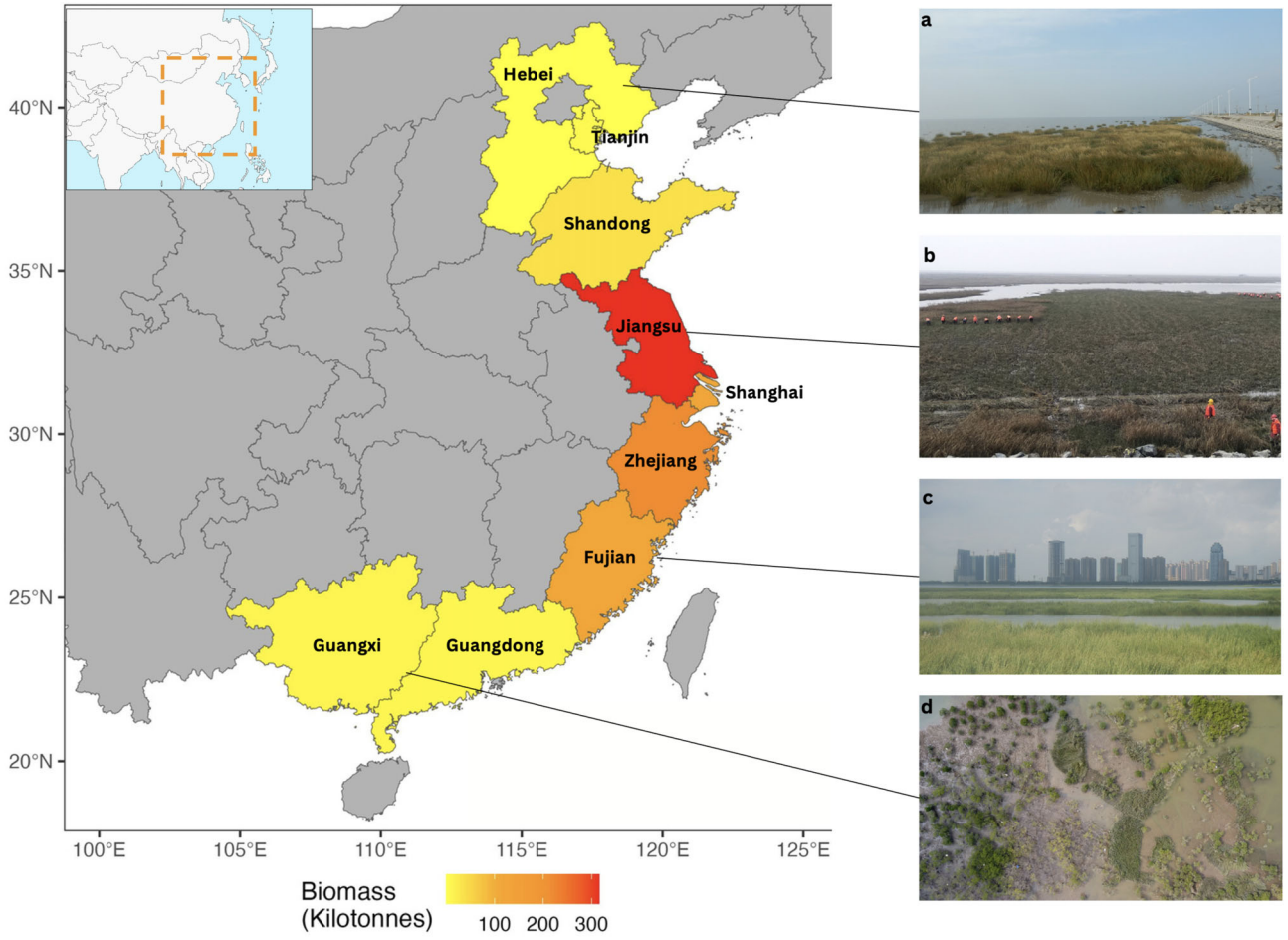

Figure 4. Total biomass of the invasive smooth cordgrass (*Spartina alterniflora*) in different coastal Chinese provinces. The sequence of photos corresponds to the provinces: (a) Hebei (Image: Xiao Xu), (b) Jiangsu (Image: Zhaohui Zhang/China Dialogue Ocean), (c) Fujian (Image: Xiao Xu), and (d) Guangxi (Image: Lianghao Pan).

tion about biological invasions should strive to address the relevance aspect (i.e., stories familiar to the audience) and focus on context-specific issues. Through quantification of the problem, a metric such as total biomass should also emphasize the magnitude of the bad news that biological invasions potentially cause in local ecosystems. Another issue is the paradox faced by the increasingly environmentally conscious public in their perception of the fight against invasive species to protect native biodiversity. The complexity of ecological processes involved in biological invasions is also an obstacle to public understanding of the risks (Courchamp et al. 2017). The quantification of the total biomass diverted by invasive species from native species could address these barriers, providing a clearer appreciation and stronger support for management.

Connection to impact metrics

Total biomass does not quantify the impact of an invasion on native species or ecosystems *per se*, just as the total tonnage of exploited timber or the total mass of discarded plastic does not necessarily quantify their ecological impacts. Nevertheless, a natural extension of using biomass as a standard metric of the *magnitude* of species invasions is that biomass might also help establish a standard currency of the potential impacts of species invasions. Indeed, total invasion biomass might have a quantifiable relationship to other metrics, such as economic costs, or negative ecological impacts. For instance, total biomass is suitable to be used to compare the per-unit effects of invasions in ecological or socioeconomic terms (e.g., impact per tonne)—for example, by using a population-level measure to upscale the per-unit effects of invasions (Parker et al. 1999, Dickey et al. 2020, Latombe et al. 2022). Furthermore, recent approaches have assessed ecological impacts per kilogram of traded goods between country pairs (Borgelt et al. 2024), and a similar premise could be used to determine the impact per kilogram of biological invasion. Whereas economic costs have been standardized (Diagne et al. 2020), ecological impacts and health effects have yet to be standardized for similar comparisons. For these latter effects, total biomass could be used to develop statistical links between all other socioeconomic and ecological dimensions of invasions.

Limitations and caveats

As with any unifying metric aimed at capturing a range of complex processes, using total biomass to quantify invasion magnitudes comes with limitations. Most importantly, behind the inference that invading species co-opt native biomass lies the assumption that invasive species exclusively exploit existing niches rather than colonizing vacant or incompletely filled niches. It is plausible in some ecosystems that invasive species generate biomass that would otherwise not be produced by native species (e.g., Vall-llosera et al. 2016, Gonzàles-del-Pliego et al.

2023). Biomass is a proxy for the resources consumed by invasive species and, in that manner, for the work energy needed to maintain the population. However, it is not a measure of the work energy done on the ecosystem by the invasive species. Direct measurement of the impact is still undetermined. Similarly, biomass is incompletely transferred through the trophic web, because of energy losses from metabolism, heat, and incomplete digestion, for example. Therefore, the total biomass of a top predator will not completely reflect that of its prey consumed. This limitation might require the incorporation of a correction factor to make it suitable for research questions focused on comparing different trophic levels.

The biome-dependent nature of biomass production suggests the possible relevance of employing relative (to native) total biomass metrics for research purposes. For example, the total biomass co-opted in an invaded ecosystem that is highly productive could be more than that of a less-productive ecosystem, making the comparison of proportions more relevant. In this regard, the magnitude of the invasion is distinguishable from the severity of the invasion, which could be seen as the proportion of the total biomass that is contributed by the invasive populations. Likewise, understanding how total biomass is distributed among invaders and co-opted from native species could help interpret the relative complexity of invasions. Recognizing such sources of variability will enhance the metric's applicability across diverse ecosystems and reduce misinterpretations in assessments.

The temporal dynamics of invasive populations can further complicate estimates of total biomass. Changes in abundance are expected if a species is invading a new environment or in response to management interventions. It is important that each biomass estimate is associated with the time when it was measured, so that comparisons among regions and taxa can be made within the same time frame or at the same invasion stage. Moreover, populations of some species might experience large annual fluctuations, which can make it difficult to define the precise time of the year in which biomass should be estimated. For example, the abundance of invasive insects varies seasonally according to their developmental phenology (Ward et al. 2019), and some algae populations quickly grow by several orders of magnitude because of unpredictable increases in nutrient availability (Fang et al. 2019). In such cases, biomass estimates require assumptions informed by the species' biology as well as the dynamics of the specific invasion. These temporal and biotic contexts should be clear when reporting biomass estimates to permit comparability.

Finally, it is important to agree on a standardization of reporting to enhance the utility and generalisability of biomass as a metric. Methodological inconsistencies in biomass estimation—such as the use of fresh versus dry weight, differences in spatial scaling, and variability in sampling protocols—pose challenges to cross-study comparability. We recommend reporting fresh biomass per unit volume in aquatic environments and per unit area in terrestrial ecosystems. This reporting would ideally be accompanied by similar reporting of native biomass to account for ecosystem-specific productivity baselines.

Feasibility

Besides the average body mass of individuals, population-level estimates only need either the number of individuals in the population or its density and invaded area, which are all relatively straightforward to acquire. However, invasion science is subject to the same knowledge gaps that affect biodiversity and ecology research more generally—namely, Wallacean (distribution), Prestonian (abundance), and Raunkiærian (trait) data shortfalls (Hortal et al. 2015). Because of these shortfalls, the biomass approach is less readily applied to those invasive taxa most affected by knowledge gaps, such as cryptic invertebrates. However, reaching global estimates on the magnitude of invasions is achievable for many invasive species; the average individual body mass of many taxa has already been measured or estimated (e.g., Jones et al. 2009, Campione and Evans 2012, Kattge et al. 2019, Herberstein et al. 2022, Tobias et al. 2022, Froese and Pauly 2023), and open-science initiatives facilitate access to these traits (Gallagher et al. 2020). Several recent studies have evaluated the global biomass of different taxonomic groups (e.g., Bar-On et al. 2018, Schultheiss et al. 2022, Greenspoon et al. 2023). Concerted community efforts in reporting biomass of invaders can offset the current knowledge gaps for less-studied taxonomic groups.

Conclusions

Because of the difficulty in designing unified quantitative frameworks, we remain largely unaware of the varying extent of biological invasions globally. The metric we propose fills this gap by helping to quantify, compare, and communicate the magnitude of invasions. The total biomass of an invasive population, which can approximate the total biomass diverted from native species, can reflect the extent of any invasion by any taxonomic group in any invaded habitat. Although simple, intuitive, and useful, this metric has not been used as such. Recently compiled databases are already providing the necessary data for some taxonomic groups and we recommend adopting biomass as a starting point for the comparison of invasion magnitudes. Despite its many advantages, total biomass of an invader is limited to the magnitude of an invasion, and inference of impact on natives requires nuanced consideration. For a unified impact quantification, another metric is needed, and that could be linked to the magnitude of invasions through total biomass. The rigors of quantifying biological invasions are many, but a unified and comprehensive metric is an important step toward addressing this global challenge.

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