Typology of the ecological impacts of biological invasions

Laís Carneiro[1], Boris Leroy[2], César Capinha[3,4], Corey J. A. Bradshaw[5,6], Sandro Bertolino[7], Jane A. Catford[8,9], Morelia Camacho-Cervantes[10], Jamie Bojko[11], Gabriel Klippel[1], Sabrina Kumschick[12,13], Daniel Pinchera-Doñoso[14], Jonathan D. Tonkin[15, 16], Brian D. Fath[17,18], Josie South[,19,20], Eléna Manfrini[1], Tad Dallas[21], Franck Courchamp[1]

[1] Université Paris–Saclay, CNRS, AgroParisTech, Ecologie Société Evolution, 91190, Gif-sur-Yvette, France

[2] Biologie des Organismes et des Ecosystèmes Aquatiques, Département de l’Adaptation du Vivant, Museum National d’Histoire Naturelle, France

[3] Centro de Estudos Geográficos, Instituto de Geografia e Ordenamento do Território, Universidade de Lisboa, Rua Branca Edmée Marques, Lisboa, Portugal

[4] Laboratório Associado Terra, Lisboa, Portugal

[5] Global Ecology | Partuyarta Ngadluku Wardli Kuu, College of Science and Engineering, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia

[6] Australian Research Council Centre of Excellence for Indigenous and Environmental Histories and Futures, Cairns, Queensland, Australia

[7] Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Torino, Italy

[8] Department of Geography, King’s College London, 40 Aldwych, London, WC2B 4BG, United Kingdom

[9] Fenner School of Environment & Society, The Australian National University, Canberra, Australian Capital Territory 2600, Australia

[10] Invasive Species Ecology Lab, Institute of Marine Sciences & Limnology, Universidad Nacional Autonoma de Mexico, Mexico

[11] National Horizons Centre, Teesside University, United Kingdom

[12] Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa

[13] Kirstenbosch Research Centre, South African National Biodiversity Institute, Cape Town, South Africa

[14] School of Biological Sciences, Queen’s University Belfast, Belfast, BT9 5DL United Kingdom

[15] School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand

[16] Te Pūnaha Matatini Centre of Research Excellence, University of Canterbury, Christchurch, New Zealand

[17] Department of Biological Sciences, Towson University, Towson, Maryland, USA

[18]Advancing Systems Analysis Program, International Institute for Applied Systems Analysis, Laxenburg, Austria.

[19] Water@Leeds, School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS29JT, UK
[20] South African Institute for Aquatic Biodiversity, Somerset Street, Makhanda, 6140 South Africa
[21] Biological Sciences, University of South Carolina, South Carolina, USA

Corresponding author: Carneiro, L. (lais.olicar@gmail.com)

Abstract

Biological invasions alter ecosystems by disrupting ecological processes that can degrade biodiversity, human health, and cause massive economic burdens. Existing frameworks to classify the ecological impacts either miss many types of impact or conflate mechanisms (causes) with the impacts themselves (consequences). We propose a comprehensive typology of 19 types of ecological impact across six levels of ecological organisation. This allows more accurate diagnosis of the cause of impact and can help triage management options to tackle each impact-mechanism combination. We integrated the typology with broad ecological concepts such as energy, mass, and information flow and storage. By highlighting cascading effects across multiple levels, this typology provides a clearer framework for documenting, and communicating invasion impacts, thereby improving management and research.

The need for a comprehensive impact typology

Biological invasions can occur when a species is introduced into an area where it is not native [1]. Once the alien (or non-native) species is established and spreading in the new environment, they are classified as ‘invasive’, often with many documented **impacts** (see Glossary) on biodiversity and society [2,3]. **Invasive species** are recognized as one of the major causes of native population declines and species loss, as well as habitat degradation and erosion of ecosystem functioning and services [3]. Due to the variety of these impacts, past efforts have been made to classify them, serving as the basis for impact documentation by researchers, prioritisation by practitioners and international institutions like the International Union for Conservation of Nature (IUCN), and global assessments on biological invasions [3–5]. Despite these advancements, current impact classifications are limited in scope and precision regarding the typology of impacts, reducing their overall applicability (see Supplementary material Table S1).

Pioneering endeavours such as the *Generic Impact Scoring System* (GISS) [6] and the *Environmental Impact Classification for Alien Taxa* (EICAT) [4,7] aim to assess the impacts of biological invasions systematically. These frameworks provide valuable tools to classify invasive species based on impact magnitude. The GISS categorizes impacts based on six ecological **mechanisms** and on six socio-economic sectors, while EICAT focuses on impacts on native biodiversity through 12 mechanisms. These frameworks have been applied to many taxa globally, and the EICAT has been adopted as a global standard by the IUCN [4]. Despite this wide usage, the latter only considers documented impacts of invasive species on native species — impacts on ecosystem processes and abiotic changes alone are not captured (e.g., [8]). Furthermore, it is not unusual for studies to refer to both mechanisms of impacts (e.g., predation by the invasive species) and the resulting types of impact (e.g., native prey population decline) under the broad label of *impacts*. However, these are structurally different: *mechanisms* represent the cause while types of impact reflect the consequences. This conflation of cause and consequence creates an inconsistent typology that can hinder clear assessment and communication. Existing databases such as the Global Invasive Species Database (GISD) and CABI's Invasive Species Compendium are valuable for cataloguing invasion-related data, but their species-specific approaches can lead to inconsistencies in the categorization of ecological impacts. CABI's Invasive Species Compendium, for example, provides a range of ecological, economic, and social impact outcomes based on varied sources, which makes cross-taxa comparisons difficult. However some progress has recently been made with standardization of impact studies on GISD, which is the current home for systematically collated EICAT assessments. While these original frameworks, databases. and others (see [9,10]), have been instrumental in advancing our understanding of the severity of invasion impacts, there is a need for a comprehensive and standardised typology that also clearly separates ecological impacts from causal mechanisms.

Based on the growing empirical evidence for the diverse impacts of biological invasions, we have developed an exhaustive typology of ecological impacts, scaled across levels of biological organisation from individuals to ecosystem functions. We then discuss how mechanisms acting across different levels of this hierarchy link the 19 types of impacts and clarify the distinction between causes and consequences. Such a typology brings research, management, and stakeholder communication closer to a more precise and unified understanding of the effect of biological invasions.

Identifying and disentangling impact types

A major barrier to standardising impact assessments is the complexity and the interconnected nature of impacts across the different levels of biological organisation and associated ecosystem processes. Different impacts can occur simultaneously across multiple ecological scales, from individuals to ecosystems, and act on both biota and the non-living (abiotic) environment. For example, the loss of a local population of native species can trigger the loss of associated ecosystem functions [11]. Additionally, the effects of biological invasions are realized through various mechanisms (causes) that are often mixed with the impact types themselves (consequences). To address these challenges, distinct but complementary aspects of invasion impacts need to be assessed and organized.

Separating cause from consequence

To identify and measure the impacts of invasive species accurately, one must distinguish the mechanisms driving these impacts from the resulting impacts themselves. A species can disrupt native ecosystems with various *mechanisms* leading to *impacts*, such as direct predation leading to population collapse[12], competition leading to primary production reduction and resource depletion for native species [13], and disease transmission leading to negative effects on health, growth, or reproduction of individuals[14]. We define these disruptive interactions as ‘mechanisms’ *sensu* [7], and their consequences as ‘impacts’. For example, the brown tree snake (*Boiga irregularis*) in Guam [15] caused the extinction of local fauna through direct predation. In that case, species loss is the *impact*, and predation is the *mechanism*. However, many studies use these two concepts interchangeably by listing for example ‘predation’ by an invasive species as an ‘impact’, which conflates the two phenomena. If the impact could instead be measured systematically as the *consequence* (impact definition *sensu* [16]) of the predation in this case (e.g., altered behaviour of individuals, abundance declines, extinction, etc.), it would clarify the much-needed distinction between these two concepts [17]. Predation by invasive species such as European red foxes (*Vulpes vulpes*) and feral cats (*Felis catus*) in Australia exemplifies how the same mechanism can produce various impacts, from abundance declines to range retractions, and even extinctions of native species [18]).

Beyond predation, other mechanisms such as competition also cause impacts. For example, non-native fish compete with native species, reducing **alpha** and **beta diversity**, altering food-web structure, and thereby decreasing ecosystem functionality[19]. In plants, competing mechanisms such as allelopathy can cause impacts that cascade from the population to the ecosystem level, potentially driving long-term changes in community structure and ecosystem processes [20]. These two cases are good examples of different mechanisms (predation and competition) drive distinct ecological impacts, each one with cascading consequences. Recognizing these differences is essential because each impact-mechanism might require a distinct mitigation and management response.

Categorising all existing impact types

To establish a unified standard for classifying ecological impacts of invasions, we need a typology that is both comprehensive and straightforward. This typology should consist of well-defined impact types, each fitting into a few distinct and easily understandable categories. For widespread adoption, the scheme needs to be compatible with most published studies and reach a consensus among experts of biological invasions. Currently, there is no synthesis fulfilling all these criteria; the EICAT is arguably the closest, but it is limited to impacts on native biodiversity and excludes *de facto* impacts on abiotic factor and at the ecosystem level.

We first reviewed the literature on existing ecological impact typologies, (see Supplementary material Table S1). These studies exhibit varying levels of organisation, from extensive lists of impacts and broad ecological categorisations (e.g., [21–24]), to detailed impacts focused specifically on plants (e.g., [10,25,26]). Some studies address other taxonomic groups, collectively providing a comprehensive but scattered overview of the diverse impacts of invasive species.

Building on this previous research, we compiled all existing impact types, regrouping similar ones under broader categories to create a comprehensive, simple, and mutually exclusive list. After extensive discussion and deliberation, we developed a proposed list of impact types, which we then presented to 60 leading experts in the field. Using a **Delphi process** [27], we did two rounds of voting and incorporated suggestions for improvement and refinement [28]. Once we achieved a consensus, we identified the biological levels of organisation at which these impacts can occur (but to which they are not limited). Our assessment revealed that the impacts are expressed through 19 distinct types across six levels of ecological organisation: (*i*) individual/organism, (*ii*) population, (*iii*) species, (*iv*) **assemblage**, (*v*) ecosystem, and (*vi*) abiotic environment. Each of these 19 impact types operates primarily at one of these six levels, although they can cascade to affect other levels and even other impact types (Figure 1, Table 1). Note that the typology is meant to identify and categorize the different types of impacts. However, a given category of impact can occur at different scales – for example, assemblage-level structure change can occur in a local community or at the scale of an entire region. The typology can be applied regardless of the spatial or temporal scale, and either works for single studies or data aggregation. Naturally, the spatial scale or degree of aggregation should be taken into consideration by users when using the typology, especially if it is meant for comparative purposes.

Besides the ecological levels of organization, we also categorized each type of impact into one of the four main components of systems ecology: energy, mass, information flow, and information storage (Table 1). For example, invasive species can disrupt energy flow by altering primary production or trophic dynamics, or affect mass by modifying nutrient cycles and habitat structure. Similarly, shifts in information flow such as behavioural changes or species interactions, and in information storage such as the loss of genetic diversity, highlight how these impacts span different dimensions of ecosystem functioning. Framing invasion impacts within these ecological components enhances comparability across studies and aligns invasion biology with broader ecosystem theory, making it easier to integrate invasion impacts into ecosystem models, conservation planning, and environmental impact assessments.

Table 1: Types of impacts of invasive species, with their respective terms, definitions, ecological concepts, and associated variables to measure them, with examples. The impact types are also separated into the six ecological levels. Despite some impacts being identified in only one ecological level, they might affect others.

Impact type	Definition	Ecological concept	Typically measured variable	Examples of impact description	References
Individual					
fitness and/or reproduction (1)	Change in individual reproductive capacity and overall individual fitness in native species that can influence population dynamics. Fitness or reproductive success is a combination	mass, information flow	reproductive success, survival rates	*Miconia calvescens* reduces fertility of understorey trees in Tahiti rainforests	[29]

	of survival, mating success, and fertility.				
health and/or growth (2)	Change (e.g., inhibition, increasing) of growth and adverse impacts on the physical condition of individual organisms.	energy, mass	health indices (e.g., disease prevalence, physiological stress), growth rates	Impact of *Carpobrotus edulis* on native plants. This experimental study shows the impact at different stages of plant growth. The presence of invasive insects carrying non-native fungal pathogens can reduce growth and vigour of forest trees	[30] [31]
behavioural (3)	Shifts in the actions, activities, and responses exhibited by individual organisms or populations.	mass, information flow	behavioural observations, activity patterns, habitat use	Native squirrel (*Sciurus vulgaris*) activity reduced following infection by non-native parasites (*Strongyloides robustus*). Native topminnows (*Skiffia bilineata*) reduced their foraging time when in company of invasive fish *Capreolus capreolus* decreased feeding and increased vigilance when near introduced fallow deer (*Dama dama*)	[32] [33] [34]
Population					
population size (4)	Reductions or increases in the number of individuals within populations of native species.	mass	population abundance, population growth rates, recruitment rates	Crayfish (*Aphanomyces astaci*) plague can cause large mortality events in crayfish in invaded streams and lakes. Reduction of population size of ground-nesting birds by the American mink (*Neogale vison*).	[35] [36]
genetic diversity (5)	Reduction in genetic variation and diversity within populations and species resulting from hybridization, introgression, and genetic assimilation processes. This occurs when genetic diversity within a population decreases due to factors such as genetic drift or reduced gene flow, leading to decreased adaptability and resilience.	information storage	genetic diversity indices, gene flow rates, genetic differentiation	Invasion of the invasive European barbel (*Barbus barbus*) in central Italy causes genetic introgression, threatening native barbels *B. plebejus* and *B. tyberinus* Widespread introgression between native Oreochromines and Nile Tilapia (*Oreochomris niloticus*) in the Middle Zambezi Basin has caused almost the complete loss of *Oreochromis mortimeri* in Lake Kariba.	[37] [38]

Species					
species range (6)	Shifts in the geographical distribution of species, including expansions, contractions, or shifts in habitat occupancy.	mass	geographic distribution, habitat suitability, dispersal ability	Contraction of the range of a native animal species due to competition with invasive species; replacement of *Sciurus vulgaris* by S. *carolinensis*	[39]
species loss (7)	Decline or disappearance of native species within a particular ecosystem or geographical area.	mass, information storage	species richness, community composition	Predation by *Boiga irregularis* extirpated bird species from Guam	[12]
Assemblage					
assemblage structure (8)	Alterations in the diversity and abundance of species within assemblages, which can scale from local communities to large-scale species pools.	energy, information storage	alpha, beta and gamma diversity indices	Fish faunas across continental United States have become more similar because of widespread introductions of cosmopolitan species In Australian grasslands, dominant invasive grasses, *Bromus diandrus* and *Avena fatua*, altered community composition and reduced the cover of native species Litter leachate of invasive blue gum *Eucalyptus globulus* reduces more biodiversity of understorey plants compared to its native range	[40] [41] [42]
successional patterns (9)	Involves alterations to the temporal sequence and trajectory of ecological succession within ecosystems.	energy, information flow	successional stage, vegetation composition, community turnover rates, disturbance regime	Invasion of many non-native plant species in old fields in Tennessee disrupts native species interactions and accelerates successional patterns by shifting native co-occurrence from structured to random, and promotes the dominance of non-native woody species that alter forest development	[43]
soundscape (10)	Changes in the acoustic environment.	information flow	acoustic diversity, sound intensity, sound frequency, temporal patterns of vocalisation, species composition, species richness, species evenness, community diversity indices	Invasion of spotted knapweed (*Centaurea stoebe*) in savannahs reduced habitat quality for chipping sparrows (*Spizella passerina*), leading to fewer older song model birds and resuled in lower song diversity and greater song similarity among yearlings. Invasive cane toads (*Rhinella marina*) disrupt the communication systems of native frogs.	[44,45] [46]

Ecosystem function/ service					
primary production (11)	Changes in the rate and magnitude of biomass production by primary producers (e.g., plants, algae) within ecosystems.	energy, mass	biomass accumulation, photosynthetic rates, primary productivity	Reduction in plant biomass production due to competition with invasive plants. Increase in algal blooms leading to enhanced primary production in aquatic ecosystems affected by invasive species.	[47] [48]
ecological function (12)	Impairment or disruption of ecosystem processes, such as nutrient cycling, pollination, or decomposition.	energy, mass, information flow, information storage	functional diversity indices (e.g., functional richness, evenness, divergence), rates of ecological processes (e.g., pollination rates, decomposition rates, nutrient cycling rates), species interactions, trophic dynamics	Extirpation of native pollinator species due to competition with invasive pollinators, resulting in reduced pollination services and decreased reproductive success for native plant species. Disruption of soil microbial communities by invasive plant species with allelopathic traits, reducing nutrient cycling rates and impairing soil fertility.	[49] [50]
food web (13)	Changes in the structure and dynamics of food chains and trophic interactions.	energy	trophic interactions, food chain length, energy flow	Disruption of native insect-plant interactions by invasive herbivores. Alteration of predator-prey dynamics in aquatic ecosystems due to introduction of invasive fish species. Invasive lake trout (*Salvelinus namaycush*) disrupt and reorganise lake trophic pathways and outcompete bull trout (*S. confluentus*) despite bull trout shifting resource consumption patterns.	[51] [52] [53]
habitat or refugia (14)	Deterioration, substitution, or disappearance of critical habitats or refuge areas for native species.	mass	habitat quality, habitat availability, habitat complexity	Degradation of nesting habitats for native bird species due to invasive vegetation encroachment loss of sheltering refugia for aquatic organisms following habitat alteration by invasive species	[54] [55]
Abiotic environment					
hydrology / water quality /	Changes related to water-related factors such as	energy, mass	water quality (e.g., pH, nutrient	Higher water use by alien plants (e.g., tamarisk,	[56] [57]

soil moisture (15)	hydrology, water quality, and soil moisture.		concentration), soil moisture content, hydrological regimes	mesquite, *Prosopis*) can reduce soil moisture, runoff, and baseflow. Macrophytes (e.g., *Salvinia*, Eurasian watermilfoil, *Sagittaria*) can increase flood risk by reducing flow velocities and water passage. Invasive plants (e.g., willows, poplars) and animals (e.g. beavers, coypu, carp) can alter channel form and hydraulics, changing flow patterns and flood risk. Dissolved oxygen declines in the Hudson River associated with invasion of zebra mussel (*Dreissena polymorpha*).	
nutrient pool and fluxes (16)	Changes in the availability, cycling, and distribution of nutrients.	energy, mass	nutrient concentrations (e.g., nitrogen, phosphorus), nutrient cycling rates, soil nutrient content	Introduced hippopotamus as ecosystem engineers in Colombia, importing terrestrial organic matter and nutrients with detectable impacts on ecosystem metabolism and community structure in the early stages of invasion.	[58]
fire regime (17)	Changes in the frequency, intensity, and spatial patterns of wildfires.	energy, mass	fire occurrence, fire severity, fire spread rates	Alteration of fire frequency and intensity in grassland ecosystems invaded by flammable exotic plant species. Changes in fire spread patterns in forested areas following introduction of invasive shrub species.	[59] [60]
soil / sediment (18)	Changes in the physical, chemical, and biological properties of soil or sediment substrates	mass	soil properties (e.g., texture, pH), sediment characteristics, mineral concentrations, heavy metal bioavailability	Invasive plants altering soil chemistry. Increase in heavy metal bioavailability by plants. Changes in soil physical properties and geo-morphology.	[61] [62] [63]
micro-climate (19)	Alterations in local or regional climatic conditions.	energy	temperature, precipitation, humidity, wind patterns, evapotranspiration rates, albedo,	Invasive plant *Impatiens glandulifera* alters temperature and soil humidity.	[64] [65,66]

			carbon dioxide concentration	Dense stands of *Ammophila arenaria* reduce temperatures and available light.	

Cascading impacts

Invasive species can directly induce one or multiple types of impacts within invaded ecosystems, often with interrelated repercussions across impact types (e.g., [67,68]) (Figure 2), which can complicate the understanding of cumulative impacts in the absence of a structured typology. Ecological impacts can, however, be positioned along a gradient ranging from proximal to distal effects. At the proximal end, immediate consequences stem directly from the presence and activities of invasive species, manifesting as observable impacts in the short term (i.e., months to years). These initial impacts can cascade through ecosystems, generating diverse and increasingly complex ecological effects over time (Figure 2). For example, the introduction of a lethal pathogen can swiftly reduce native populations through disease transmission causing higher mortality, illustrating a direct and immediate impact. One example includes the introduction of invasive amphibians that carry and spread chytrid fungus (*Batrachochytrium dendrobatidis* and *B. salmandrivorans*) to native amphibian populations. This has occurred frequently in many parts of the world, causing the extinction of native populations [69–72]. However, alien or invasive parasites can have their own impacts, both on local species and the invader (see Box 1). More distal impacts are subsequent consequences that emerge from the cascading effects of the initial impact. The extinction of a native species due to a disease can alter altered food-web dynamics. Such changes can disrupt the trophic interactions and energy flow within the ecosystem, potentially shifting ecosystem functions or services. For example, when native amphibian populations began disappearing in Central America after the introduction of chytrid fungi, the resulting loss of predation on mosquito larvae and adults caused an explosion of mosquito populations; this in turn increased the incidence of pathogenic insect-borne diseases such as malaria in humans living nearby [73]. Over time, these functional disruptions can culminate in habitat modification because the altered processes reshape the physical environment and the structure of the biotic community, disturbing the energy, mass, information flow, and storage of the ecosystem.

The causal relationship between more proximal and distal impacts often spans ecological scales, especially where a decline in the abundance of native species populations (e.g., a flowering plant) can cascade to disrupt the population dynamics of interacting native species (e.g.. its pollinators), the structure of the community itself (e.g., diversity of insects), and even beyond to erode ecosystem function (e.g., pollination). For instance, invasive plants strongly influence plant-pollinator network structure ([74], and reviewed in [75]). The ecological scale at which impacts occur can also affect our perception of overall impacts, because structural changes are more easily perceived at broader ecosystem scales. For example, habitat degradation or changes in fire regime are generally more noticeable than changes to individual fitness or behaviour, or genetic changes in populations. Invasive species do not only degrade ecosystem function and services ([76,77]), they can also have more subtle effects across all ecological scales.

Invasive species can also affect ecosystems beyond their immediate environment by changing the flow of nutrients and species across boundaries (i.e., cross-ecosystem interactions) [68]. The invasive willow tree (*Salix spp.*) in Australia altered riparian vegetation structure, and increased leaf litter input and stream shading, reducing light availability and suppressing algal growth. This shift redirected the aquatic food web toward detritus-based energy pathways, leading to changes in fungal, algal, and macroinvertebrate communities. As a result, algal production declined, while detritivore macroinvertebrates became more dominant [78]. Although important, these cross-ecosystem interactions are currently understudied and the impact categorisation can support the identification of the range, connections, and breadth of these impacts occurring at all scales (see [68,79]).

Concluding remarks

Our aim here is to provide a clear and standardised terminology for classifying impacts across all ecological levels. We introduced a comprehensive typology encompassing 19 distinct types of impacts caused by invasive species, organised into six ecological levels. We also differentiated these impact types from their underlying causes, emphasising the ecological mechanisms through which invasive species affect native ecosystems, and outlined a gradient of proximal and distal impacts that often cascade through these systems. Recognising the full spectrum of these impacts and their interconnections is necessary to develop effective conservation and management strategies.

The adoption of a standardized typology for ecological impacts has the potential to improve data harmonization and interoperability across invasion biology databases and frameworks. By transitioning to an impact-centred typology, researchers can standardize how impacts like habitat degradation, disruption of nutrient cycling, or declines in population size are recorded, without focusing solely on the identity of the invasive species. Furthermore, adopting an impact-based framework could be instrumental in assessing the effectiveness of global biodiversity monitoring and management initiatives, such as the Kunming-Montreal Global Biodiversity Framework. Our typology provides a standardized foundation for ecological impact indicators that can be tracked over time across diverse ecosystems. Such a framework can also support decision-making by streamlining data reporting and making invasion impacts more directly comparable. This would ultimately support better prioritization of invasive species management by enabling clearer assessments, including quantification, of ecological impacts of invasions. Our typology can also complement existing frameworks such as the EICAT or the GISS offering researchers, managers, stakeholders and others a tool to organise and communicate the impacts of invasive species. We hope to standardise future research and facilitate clearer definitions and distinctions across studies, ultimately advancing the field of invasion biology (see Outstanding questions).

Glossary

Alpha diversity – The diversity of species within a specific habitat or ecosystem, often measured as species richness. It represents local biodiversity and the complexity of an ecosystem.

Assemblage – A group of species that coexist in the same geographical area, which can vary in spatial scale from local to regional. It includes communities, which are generally considered to be restricted to a specific ecosystem or habitat.

Beta diversity – The variation in species composition between different habitats, ecosystems, or geographical areas.

Delphi process – A structured, iterative method for expert consensus used in research and decision-making. It involves multiple rounds of anonymous surveys, where experts provide input, receive feedback, and refine their responses to reach a collective agreement.

Gamma diversity – The diversity of the whole region or area of interest, usually measured by pooling multiple samplings in the study area; estimated with similar metrics to alpha diversity.

Impact (consequence)– Any measurable change in ecological, economic, or social systems resulting from an invasive species (Ricciardi et al. 2013). The typology concerns only to ecological impacts.

Invasive species – An alien or non-native species that is transported beyond its natural biogeographic range. When it establishes and spreads (i.e., stages of the invasion process), they are usually referred as invasive species. Here we consider that any species can cause impacts regardless the stage of invasion and we refer to all of them as 'invasive species' throughout the text.

Mechanism – The process through which an invasive species exerts its impact.

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Declaration of interests

The authors declare no competing interests.

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Figure legends

Figure 1: Nineteen impact types of invasive species categorized across six ecological levels. Each impact type is numbered and represented by an icon and label, illustrating its position within the ecological hierarchy. The arrows indicate increasing levels, from individual-level impacts to broader abiotic effects, highlighting how impacts can

accumulate and propagate across scales. Note that all scales are connected to each other and the impacts can have multiple connections between each other.

Figure 2: Examples of connections between more proximal (black arrows) and more distal (grey arrows) impacts of biological invasions. The colours for each impact type represent one of the six ecological scales provided in Figure 1, as do the numbers associated with impact types. (A) The golden apple snail *Pomacea canaliculata* reduced the population of aquatic plants, which led to planktonic algae dominating the food web, and consequently a shift to turbid water by released nutrients [80]; (B) The introduction of brown trout *Salmo trutta* caused changes in invertebrate grazing behaviour, replaced the population of nonmigratory galaxiid fish, altered crayfish and large invertebrate distributions, and changed algal species assemblage structure, causing higher algal primary productivity, and consequently altering nutrient flux [81].

Box

Box 1: Invasive parasites: mediating native ecological influence and invasive host impact

Biological invasions often involve many organisms. Invasive plants, vertebrates, and invertebrates can carry symbionts [82], including a microbiome (mutualistic or commensal microbes) or a pathobiome (parasites), into new environments [83]. When parasites co-invade with their invasive hosts, they might impact only their invasive host or also infect native hosts, potentially becoming ‘invasive’ themselves [84]. By affecting the health of their invasive hosts, these parasites can reduce the host’s impact on the ecosystem, acting as a form of biological control on invasive populations [84,85].

Alternatively, invasive parasites can also infect native species, posing their own set of impacts. They can adversely affect native population size, health, and ecological roles [86] and in these cases, they have impacts similar to those that invasive hosts have directly on native species. However, in those cases, the literature should be (but rarely is) clear whether the invasive parasite or the invasive host is responsible for the impact on native species. For example, the grey squirrel not only outcompetes the native red squirrel through ecological competition, but the invader also carries squirrel poxvirus, which accelerates the red squirrel's decline upon infection [39,87]. The two viewpoints, that the invasive host is only the carrier of the invasive pathogen with the impact, or that the invasive host has the impact by spreading pathogens (i.e., via apparent competition), seem equally defensible, but the distinction should be clearly made. In our typology, we propose one type that corresponds to the former (typically the first effects, at the individual level), but also to the latter (changing species interactions).

Parasites can have a positive effect on the invasive host by affecting their native competitors or other enemies more, creating an invasional meltdown during which the invasive host is helped in its invasion by its parasite [88]. All three aspects make the impacts of invasive parasites more complicated cases, calling for additional clarity in reporting their impacts, or the impacts of their invasive hosts (see Supplementary material Table S2).