

### **Opinion**

# Typology of the ecological impacts of biological invasions

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

Biological invasions alter ecosystems by disrupting ecological processes that can degrade biodiversity, harm 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, it is classified as 'invasive', often with many documented **impacts** (see Glossary) on biodiversity and society [2,3]. **Invasive species** are recognised 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 Table S1 in the supplemental information online).

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 categorises impacts based on six ecological **mechanisms** and on six socioeconomic 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

### Highlights

Biological invasions are one of the main drivers of change in biodiversity, because of the various ecological impacts of invasive species.

However, our understanding of impacts is currently limited because existing classifications of impacts in the field of biological invasions are neither exhaustive nor structured, and they confuse causes (mechanisms) and consequences (impacts)

We introduce a comprehensive typology of 19 impact types across six levels of biological organisation, ranging from individuals to ecosystems, which can be used to contextualise, rank and quantify the ecological impacts of invasive species.

This structured typology of impacts represents an exhaustive standardisation of the description and reporting of impacts of biological invasions to facilitate the understanding and management of biological invasions.

<sup>1</sup>Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Société Evolution, 91190, Gif-sur-Yvette, France <sup>2</sup>Laboratoire de Biologie des Organismes et des Écosystèmes Aquatiques-BOREA, Muséum national d'Histoire naturelle (MNHN), SU, CNRS, IRD, UA, F-75005 Paris, France <sup>3</sup>Centro de Estudos Geográficos, Instituto de Geografia e Ordenamento do Território, Universidade de Lisboa, Rua Branca Edmée Marques, Lisboa, Portugal



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 the Centre for Agriculture and Bioscience International (CABI)'s Invasive Species Compendium are valuable for cataloguing invasion-related data, but their species-specific approaches can lead to inconsistencies in the categorisation 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 standardisation of impact studies on GISD, which is the current home for systematically collated EICAT assessments. While these original frameworks, databases, and others [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 realised 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 organised.

### 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 reduced primary production and resource depletion for native species [13], and disease transmission negatively affecting 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

<sup>4</sup>Laboratório Associado Terra Lisboa Portugal

<sup>5</sup>Global Ecology | Partuyarta Ngadluku Wardli Kuu, College of Science and Engineering, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia

<sup>6</sup>Australian Research Council Centre of Excellence for Indigenous and Environmental Histories and Futures Cairns, Queensland, Australia <sup>7</sup>Department of Life Sciences and Systems Biology, University of Turin, Via Accademia Albertina 13, 10123 Torino,

<sup>8</sup>Department of Geography, King's College London, 40 Aldwych, London, WC2B 4BG, UK

<sup>9</sup>Fenner School of Environment & Society, The Australian National University, Canberra, Australian Capital Territory 2600, Australia

<sup>10</sup>Invasive Species Ecology Lab, Institute of Marine Sciences & Limnology. Universidad Nacional Autonoma de Mexico, Mexico City, Mexico <sup>11</sup>National Horizons Centre, Teesside University, Darlington, DL1 1HG, UK <sup>12</sup>Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Stellenbosch, South Africa

<sup>13</sup>Kirstenbosch Research Centre, South African National Biodiversity Institute, Cape Town, South Africa

<sup>14</sup>School of Biological Sciences, Queen's University Belfast, Belfast, BT9 5DL UK

<sup>15</sup>School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand <sup>16</sup>Te Pūnaha Matatini Centre of Research Excellence, University of Canterbury, Christchurch, New Zealand <sup>17</sup>Department of Biological Sciences, Towson University, Towson, MD, USA <sup>18</sup>Advancing Systems Analysis Program, International Institute for Applied Systems Analysis, Laxenburg, Austria <sup>19</sup>Water@Leeds, School of Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS29JT, UK <sup>20</sup>South African Institute for Aquatic Biodiversity, Somerset Street, Makhanda, 6140, South Africa <sup>21</sup>Biological Sciences, University of South Carolina, Columbia, SC, USA

\*Correspondence: lais.olicar@gmail.com (L. Carneiro).



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 diversity 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) that drive distinct ecological impacts, each one with cascading consequences. Recognising 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 impacts on abiotic factor and at the ecosystem level.

We first reviewed the literature on existing ecological impact typologies (Table S1). These studies exhibit varying levels of organisation, from extensive lists of impacts and broad ecological categorisations (e.g., [6,21-23]) to detailed impacts focused specifically on plants (e.g., [10,24]). Some studies address other taxonomic groups [25], 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** [26], we did two rounds of voting and incorporated suggestions for improvement and refinement [27]. 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). The typology is meant to identify and categorise the different types of impact. 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, users should consider the spatial scale or degree of aggregation when using the typology, especially if it is meant for comparative purposes.

Besides the ecological levels of organisation, we also categorised 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

### Glossarv

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 restricted to a specific ecosystem or habitat.

Beta diversity: the variation in species composition among 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 in which 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; it is estimated with metrics similar to those used for alpha diversity.

Impact (consequence): any measurable change in ecological, economic, or social systems resulting from an invasive species [16]. The typology concerns only ecological impacts.

Invasive species: a non-native species that is transported beyond its natural biogeographic range. When it establishes and spreads (i.e., stages of the invasion process) it is usually referred to as an invasive species. Here we consider that any species can cause impacts regardless of 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



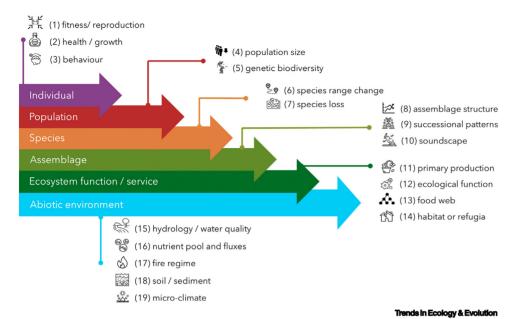


Figure 1. Nineteen impact types of invasive species categorised across six ecological levels. Each impact type is numbered and represented by an icon and label, illustrating its position within the ecological hierarchy. The arrows indicate increasing levels, from individual-level impacts to broader abiotic effects, highlighting how impacts can accumulate and propagate across scales. All scales are connected to each other and the impacts can have multiple connections between each other

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.

### Cascading impacts

Invasive species can directly induce one or multiple types of impact within invaded ecosystems, often with interrelated repercussions across impact types (e.g., [28,29]) (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 [30–33]. However, alien or invasive parasites can have their own impacts, both on local species and the invader (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.



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

Impact type	Definition	Ecological concept	Typically measured variable	Examples of impact description	Refs
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 of survival, mating success, and fertility.	Mass, information flow	Reproductive success, survival rates	Miconia calvescens reduces fertility of understorey trees in Tahitian rainforests	[51]
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.	[52] [53]
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 foraging time when in presence of invasive fish Capreolus capreolus. Decreased feeding and increased vigilance of European roe deer (Capreolus capreolus) when near introduced fallow deer (Dama dama).	[54] [55] [56]
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).	[57] [58]
Genetic diversity (5)	Reduction in genetic variation and diversity within populations and species resulting from hybridisation, 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 ( <i>Barbus barbus</i> ) in central Italy causes genetic introgression, threatening native barbels <i>B. plebejus</i> and <i>B. tyberinus</i> Widespread introgression between native Oreochromines and Nile tilapia ( <i>Oreochomris niloticus</i> ) in the Middle Zambezi Basin has caused almost the complete loss of <i>Oreochromis mortimeri</i> in Lake Kariba.	[59] [60]
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	[48]

(continued on next page)



Table 1 (continued)

Impact type	Definition	Ecological concept	Typically measured variable	Examples of impact description	Refs
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 <i>Boiga irregularis</i> 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 <b>gamma diversity</b> indices	Fish faunas across continental USA have become more similar because of widespread introductions of cosmopolitan species In Australian grasslands, dominant invasive grasses, <i>Bromus diandrus</i> and <i>Avena fatua</i> , altered community composition and reduced the cover of native species. Litter leachate of invasive blue gum <i>Eucalyptus globulus</i> reduces more biodiversity of understorey plants compared to its native range.	[61] [62] [63]
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, USA 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	[64]
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 resulted in lower song diversity and greater song similarity among yearlings. Invasive cane toads (Rhinella marina) disrupt the communication systems of native frogs.	[65–67]
Ecosystem function	n/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.	[68] [69]
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, decompo- sition rates, nutrient cycling rates), species interactions	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.	[70] [71]



Table 1. (continued)

Impact type	Definition	Ecological concept	Typically measured variable	Examples of impact description	Refs
ood web (13)	Changes in the structure and dynamics of food chains and trophic interactions.	Energy, mass	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.	[72] [73] [74]
labitat 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 and loss of sheltering refugia for aquatic organisms following habitat alteration by invasive species	[75] [76]
Abiotic environment	t				
Hydrology/water quality/soil moisture (15)	Changes related to water-related factors such as hydrology, water quality, and soil moisture.	Energy, mass	Water quality (e.g., pH, nutrient concentration), soil moisture content, hydrological regimes	Higher water use by invasive plants (e.g., tamarisk, mesquite, <i>Prosopis</i> ) can reduce soil moisture, runoff, and baseflow.  Macrophytes (e.g., <i>Salvinia</i> , Eurasian watermilfoil, <i>Sagittaria</i> ) 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 ( <i>Dreissena polymorpha</i> ).	[77] [78]
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.	[79]
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.	[80] [81]

(continued on next page)



Table 1. (continued)

Impact type	Definition	Ecological concept	Typically measured variable	Examples of impact description	Refs
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.	[82] [83] [84]
Micro-climate (19)	Alterations in local or regional climatic conditions.	Energy	Temperature, precipitation, humidity, wind patterns, evapotranspiration rates, albedo, carbon dioxide concentration	Invasive plant Impatiens glandulifera alters temperature and soil humidity.  Dense stands of Ammophila arenaria reduce temperatures and available light.	[85] [86,87]

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

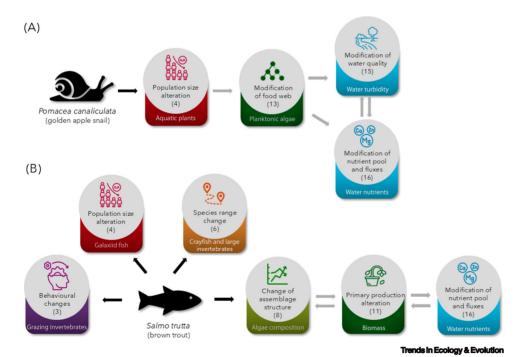


Figure 2. Examples of connections between more proximal (black arrows) and more distal (grey arrows) impacts of biological invasions. The colours for each impact type represent one of the six ecological scales provided in Figure 1, as do the numbers associated with impact types. (A) The golden apple 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 [41]. (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 [42].



### 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 [43], including a microbiome (mutualistic or commensal microbes) or a pathobiome (parasites), into new environments [44]. When parasites co-invade with their invasive hosts, they might impact only their invasive host or also infect native hosts, potentially becoming 'invasive' themselves [45]. 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 [45,46].

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 [47], 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 [48,49]. 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 [50]. 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 (Table S2 in the supplemental information online).

in turn increased the incidence of pathogenic insect-borne diseases such as malaria in humans living nearby [34]. 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 ([35], and reviewed in [36]). 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 not only degrade ecosystem function and services [37,38], 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) [29]. 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 [39]. 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 [29,40].

### 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

### Outstanding questions

Quantify connections. How strong are the connections between different impact types and their associated mechanisms? Are certain types of impacts more frequently linked to specific mechanisms?

Quantify impacts. Can a rigorous typology promote the quantification of ecological impacts of biological invasions?

Patterns in impact relationships. Are there discernible patterns in the relationships between different types of impact (e.g., consequence chains), or can all configurations be observed?

Relative importance of impact types. Are some types of impact inherently more important than others? If yes, how does this ranking vary based on habitat or the taxonomic group of the invasive species?

Taxonomic group susceptibility. Are some native taxonomic groups or invaded habitats more (or less) sensitive to specific types of impacts?

Predictability of impacts. Are certain impacts more predictable than others. and if so, under what conditions? Do the same invasive species have similar impacts across their invaded



impact 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 standardised typology for ecological impacts has the potential to improve data harmonisation and interoperability across invasion biology databases and frameworks. By transitioning to an impact-centred typology, researchers can standardise 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 standardised 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 prioritisation 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).

### **Acknowledgments**

We thank the participants of the 2023 enKORE-INAS workshop within the Hi Knowledge initiative in Berlin, as well as those involved in the InvaPact I and II workshops, both funded by the AXA Research Fund Chair of Invasion Biology of Université Paris-Saclay, for their valuable input during early discussions that globally contributed to the development of this work. L.C., G.K., and E.M. also acknowledge the AXA Chair for supporting their salaries. B.L and F.C. were funded by their salary as French public servants. J.C. acknowledges funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No. [101002987]). J.S. acknowledges funding from UKRI Future Leaders Fellowship [Grant/Award Number: MR/X035662/1]. S.K. acknowledges the support of the Centre for Invasion Biology (CIB) at Stellenbosch University and the South African Department of Forestry, Fisheries and the Environment (DFFE).

### **Declaration of interests**

The authors declare no competing interests.

### **Supplemental information**

Supplemental information associated with this article can be found online at https://doi.org/10.1016/j.tree.2025.03.010.

- 1. Blackburn, T.M. et al. (2011) A proposed unified framework for biological invasions. Trends Ecol. Evol. 26, 333-339
- 2. Roy, H.E. et al. (2024) Curbing the major and growing threats from invasive alien species is urgent and achievable. Nat. Ecol.
- 3. IPBES (2023) Summary for Policymakers of the Thematic Assessment Report on Invasive Alien Species and their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. https://doi.org/10.5281/zenodo.
- 4. IUCN (2020) IUCN EICAT Categories and Criteria. The Environmental Impact Classification for Alien Taxa (EICAT), https://portals.iucn.org/library/node/4910 https://doi.org/10.2305/IUCN. CH.2020.05.en
- 5. IUCN (2020) Guidelines for Using the IUCN Environmental Impact Classification for Alien Taxa (EICAT) Categories Criteria, 1.1. https:// iucn.org/sites/default/files/2023-02/eicat-guidelines-final-v1.1.pdf
- 6. Nentwig, W. et al. (2016) The generic impact scoring system (GISS): a standardized tool to quantify the impacts of alien species. Environ. Monit. Assess. 188, 315
- 7. Hawkins, C.L. et al. (2015) Framework and guidelines for implementing the proposed IUCN Environmental Impact Classification for Alien Taxa (EICAT). Divers. Distrib. 21, 1360-1363
- 8. Kumschick, S. and Jansen, C. (2023) Evidence-based impact assessment for naturalized and invasive Australian Acacia species. In Wattles: Australian Acacia Species Around the World (Richardson, D.M. and LeRoux, J.J. and Marchante, F., eds). pp. 359-381, CABI



- 9. Bernardo-Madrid, R. et al. (2022) Consistency in impact assessments of invasive species is generally high and depends on protocols and impact types. NeoBiota 76, 163-190
- 10. Vila, M. et al. (2019) A review of impact assessment protocols of non-native plants. Biol. Invasions 21, 709–723
- 11. Tronstad, L.M. et al. (2010) Introduced lake trout produced a four-level trophic cascade in Yellowstone Lake, Trans. Am. Fish. Soc. 139, 1536-1550
- 12. Wiles, G.J. et al. (2003) Impacts of the brown tree snake; patterns of decline and species persistence in Guam's Avifauna. Conserv. Biol. 17, 1350-1360
- 13. D'Antonio, C.M. and Mahall, B.E. (1991) Root profiles and competition between the invasive, exotic perennial, Carpobrotus edulis, and two native shrub species in California Coastal Scrub. Am. J. Bot. 78, 885-894
- 14. Tompkins, D.M. et al. (2002) Parapoxvirus causes a deleterious disease in red squirrels associated with UK population declines. Proc. R. Soc. Lond. B 269, 529-533
- 15. Savidge, J.A. (1987) Extinction of an island forest avifauna by an introduced snake. Ecology 68, 660-668
- 16. Ricciardi, A. et al. (2013) Progress toward understanding the ecological impacts of nonnative species. Ecol. Monogr. 83, 263-282
- 17. Jeschke, J.M. et al. (2014) Defining the impact of non-native species Conserv Biol 28 1188-1194
- 18. Legge, S. et al. (2023) Loss of terrestrial biodiversity in Australia: magnitude, causation, and response, Science 381, 622-631
- 19. Moi, D.A. et al. (2021) Non-native fishes homogenize native fish communities and reduce ecosystem multifunctionality in tropical lakes over 16 years. Sci. Total Environ. 769, 144524
- 20. Wardle, D.A. et al. (1998) An ecosystem-level perspective of allelopathy. Biol. Rev. 73, 305-319
- 21. Blackburn, T.M. et al. (2014) A unified classification of alien species based on the magnitude of their environmental impacts. PLoS Biol. 12, e1001850
- 22. Kumschick, S. and Nentwig, W. (2010) Some alien birds have as severe an impact as the most effectual alien mammals in Europe. Biol. Conserv. 143, 2757-2762
- 23. Nentwig, W. et al. (2010) A generic impact-scoring system applied to alien mammals in Europe. Conserv. Biol. 24, 302-311
- 24. Vilà, M, et al. (2011) Ecological impacts of invasive alien plants; a meta-analysis of their effects on species, communities and ecosystems, Fcol. Lett. 14, 702-708
- 25. Cameron. E.K. et al. (2016) Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. Glob. Ecol. Biogeogr. 25, 596-606
- 26. Hasson, F. et al. (2000) Research guidelines for the Delphi survey technique. J. Adv. Nurs. 32, 1008-1015
- 27. Mukherjee, N. et al. (2015) The Delphi technique in ecology and biological conservation: applications and guidelines. Methods Ecol. Evol. 6, 1097-1109
- 28. Volery, L. et al. (2023) A general framework to quantify and compare ecological impacts under temporal dynamics. Ecol. Lett. 26,
- 29. Peller, T. and Altermatt, F. (2024) Invasive species drive crossecosystem effects worldwide. Nat. Ecol. Evol. 8, 1087–1097
- 30. Scheele, B.C. et al. (2019) Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. Science 363, 1459-1463
- 31. Skerratt, L.F. et al. (2016) Priorities for management of chytridiomycosis in Australia: saving frogs from extinction. Wildl. Res. 43, 105-120
- 32. Lips, K.R. (2016) Overview of chytrid emergence and impacts on amphibians. Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci. 371, 20150465
- 33. Fisher, M.C. and Garner, T.W.J. (2020) Chytrid fungi and global amphibian declines. Nat. Rev. Microbiol. 18, 332-343
- 34. Springborn, M.R. et al. (2022) Amphibian collapses increased malaria incidence in Central America\*, Environ, Res. Lett. 17.
- 35. Bartomeus, I. et al. (2008) Contrasting effects of invasive plants in plant-pollinator networks. Oecologia 155, 761-770
- 36. Parra-Tabla, V. and Arceo-Gómez, G. (2021) Impacts of plant invasions in native plant-pollinator networks. New Phytol. 230, 2117-2128

- 37. Gallardo, B. et al. (2024) Risks posed by invasive species to the provision of ecosystem services in Europe. Nat. Commun. 15,
- 38. Peichar, L. and Mooney, H.A. (2009) Invasive species, ecosystem services and human well-being. Trends Ecol. Evol. 24. 497-504
- 39. McInerney, P.J. et al. (2016) Invasive willows drive instream community structure, Freshw. Biol. 61, 1379-1391
- 40. Kumschick, S. et al. (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations, BioScience 65 55-63
- 41. Carlsson, N.O.L. et al. (2004) Invading herbivory: the golden apple snail alters ecosystem functioning in Asian Wetlands. Ecology 85, 1575-1580
- 42. Townsend, C.R. (2003) Individual, population, community, and ecosystem consequences of a fish invader in New Zealand streams, Conserv. Biol. 17, 38-47
- 43. Bojko, J. et al. (2021) Invasive non-native crustacean symbionts: diversity and impact. J. Invertebr. Pathol. 186, 107482
- 44. Bass, D. et al. (2019) The pathobiome in animal and plant diseases. Trends Ecol. Evol. 34, 996-1008
- 45. Bojko, J. et al. (2023) Diagnosing invasive parasites. In Parasites and Biological Invasions (Boiko, J. and Dunn, A.M. and Blakeslee, A.M.H., eds), pp. 8-23, CABI
- 46 Dunn, A.M. and Hatcher, M.J. (2015) Parasites and biological invasions: parallels, interactions, and control, Trends Parasitol, 31, 189\_199
- 47. Lymbery, A.J. et al. (2014) Co-invaders: the effects of alien parasites on native hosts, Int. J. Parasitol, Parasites Wildl. 3, 171-177
- 48. Gurnell, J. et al. (2004) Alien species and interspecific competition: effects of introduced eastern grey squirrels on red squirrel population dynamics. J. Anim. Ecol. 73, 26-35
- 49. Rushton, S.P. et al. (2005) Disease threats posed by alien species: the role of a poxvirus in the decline of the native red squirrel in Britain. Epidemiol. Infect. 134, 521
- 50. Strauss, A. et al. (2012) Invading with biological weapons: the importance of disease-mediated invasions. Funct. Ecol. 26,
- 51. Meyer, J.-Y. and Florence, J. (1996) Tahiti's native flora endangered by the invasion of Miconia calvescens DC. (Melastomataceae). J. Biogeogr. 23, 775–781
- 52 Novoa A and González I. (2014) Impacts of Carpobrotus edulis (L.) N.F.Br. on the germination, establishment and survival of native plants: a clue for assessing its competitive strength. PLoS One 9, e107557
- 53. Vilcinskas, A. (2019) Pathogens associated with invasive or introduced insects threaten the health and diversity of native species. Curr. Opin. Insect Sci. 33, 43-48
- 54. Santicchia, F. et al. (2020) Spillover of an alien parasite reduces expression of costly behaviour in native host species. J. Anim. Ecol. 89, 1559-1569
- 55. Camacho-Cervantes, M. et al. (2019) Foraging behaviour of a native topminnow when shoaling with invaders. Aquat. Invasions
- 56. Ferretti, F. et al. (2011) Behavioural interference between ungulate species: roe are not on velvet with fallow deer. Behav. Ecol. Sociobiol. 65, 875-887
- 57. Brady, D.J. et al. (2024) The crayfish plague pathogen Aphanomyces astaci in Ireland. Microorganisms 12, 102
- 58. Niemczynowicz, A, et al. (2017) Non-native predator control increases the nesting success of birds: American mink preying on wader nests, Biol. Conserv. 212, 86-95
- 59. Zaccara, S. et al. (2021) Genetic and phenotypic displacement of an endemic Barbus complex by invasive European barbel Barbus barbus in central Italy. Biol. Invasions 23, 521-535
- 60. Gregg, R.E. et al. (1998) Introgressive hybridization of tilapias in Zimbabwe. J. Fish Biol. 52, 1–10
- 61. Rahel, F.J. (2000) Homogenization of fish faunas across the United States. Science 288, 854-856
- 62. O'Reilly-Nugent, A. et al. (2020) Measuring competitive impact: Joint-species modelling of invaded plant communities. J. Ecol.
- 63. Becerra, P.I. et al. (2018) Inhibitory effects of Eucalyptus globulus on understorey plant growth and species richness are greater in non-native regions. Glob. Ecol. Biogeogr. 27, 68-76



- 64. Kuebbing, S.E. et al. (2014) Effects of co-occurring non-native invasive plant species on old-field succession. For. Ecol. Manag. 324 196-204
- 65. Ortega, Y.K. et al. (2014) Invasive plant erodes local song diversity in a migratory passerine. Ecology 95, 458-465
- 66. Barney, J.N. et al. (2024) A silent spring, or a new cacophony? Invasive plants as maestros of modern soundscapes. Front. Fcol. Fnviron, 22, e2729
- 67. Bleach, I.T. et al. (2015) Noisy neighbours at the frog pond: effects of invasive cane toads on the calling behaviour of native Australian frogs. Behav. Ecol. Sociobiol. 69, 675-683
- 68. Gordon, D.R. (1998) Effects of invasive, non-indigenous plant species on ecosystem processes; lessons from Florida, Ecol. Appl. 8, 975-989
- 69. Angeler, D.G. and Johnson, R.K. (2013) Algal invasions, blooms and biodiversity in lakes: Accounting for habitat-specific responses. Harmful Algae 23, 60-69
- 70. Morales, C.L. et al. (2017) Disruption of pollination services by invasive pollinator species. In Impact of Biological Invasions on Ecosystem Services (Vilà, M. and Hulme, P.E., eds), pp. 203-220, Springer International Publishing
- 71. Qu, T. et al. (2021) Invasive species allelopathy decreases plant growth and soil microbial activity. PLoS One 16, e0246685
- 72. Vázguez, D.P. and Simberloff, D. (2003) Changes in interaction biodiversity induced by an introduced ungulate, Ecol. Lett. 6. 1077-1083
- 73. Nõomaa, K. et al. (2022) Novel fish predator causes sustained changes in its prey populations. Front. Mar. Sci. 9, 849-878
- 74. Wainright, C.A. et al. (2021) Species invasion progressively disrupts the trophic structure of native food webs. Proc. Natl Acad. Sci. U. S. A. 118, e2102179118
- 75. Okoye, O.K. et al. (2020) Retraction of invasive Spartina alterniflora and its effect on the habitat loss of endangered migratory bird species and their decline in YNNR using remote sensing technology. Ecol. Evol. 10, 13810-13824

- 76. Nishijima, S. et al. (2017) Habitat modification by invasive crayfish can facilitate its growth through enhanced food accessibility. BMC Ecol. 17, 37
- 77. Catford, J.A. (2017) Hydrological impacts of biological invasions. In Impact of Biological Invasions on Ecosystem Services (Vilà, M. and Hulme, P.E., eds), pp. 63-80, Springer International Publishing
- 78. Caraco, N. et al. (2000) Dissolved oxygen declines in the Hudson River associated with the invasion of the zebra mussel (Dreissena nolymorpha) Environ Sci Technol 34 1204-1210
- 79. Shurin, J.B. et al. (2020) Ecosystem effects of the world's largest invasive animal. Ecology 101, e02991
- 80. Brooks, M.L. et al. (2004) Effects of invasive alien plants on fire regimes. BioScience 54, 677-688
- 81. Mandle, L. et al. (2011) Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. Biol. Invasions 13, 1815–1827
- 82. Weidenhamer, J.D. and Callaway, R.M. (2010) Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. J. Chem. Ecol. 36, 59-69
- 83. Li, J. et al. (2022) Interactions between invasive plants and heavy metal stresses: a review. J. Plant Ecol. 15, 429-436
- 84. Raizada, P. et al. (2008) Impact of invasive alien plant species on soil processes: a review. Proc. Natl Acad. Sci. India Sect. B-Biol. Sci 78 288-298
- 85. Buckli, B. et al. (2013) Invasion of Impatiens glandulifera affects terrestrial gastropods by altering microclimate. Acta Oecol. 47,
- 86. Barbour, M.G. et al. (1985) Marine beach and dune plant communities. In Physiological Ecology of North American Plant Communities (Chabot, B.F. and Mooney, H.A., eds), pp. 296-322, Springer, Netherlands
- 87. Dukes, J.S. and Mooney, H.A. (2004) Disruption of ecosystem processes in western North America by invasive species. Rev. Chil. Hist. Nat. 77, 411-437