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Cryptic function loss in animal populations

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The essential functional roles performed by animal species are lost when they become locally extinct, and ecosystems are critically threatened by this decline in functional diversity. Theory that links function, diversity, and ecosystem stability exists but fails to assess function loss that occurs in species with persistent populations. The entire functional role of a species, or a critical component of it, can be lost following large population declines (functional extinction), following population increase, or after behavioural adaptations to changes in the population, community, habitat, or climate. Here, we provide a framework that identifies the scenarios under which 'cryptic' function loss can occur in persistent populations. Cryptic function loss is potentially widespread and critically threatens ecosystem stability across the globe.

Loss of function without the loss of species

Ecosystem stability depends on the maintenance of ecological functions performed by species within communities [1]. When species become locally extinct, the functional roles they performed are lost and the associated reduction in functional diversity is considered to be among the most significant concerns for ecosystem stability [2]. However, function loss also occurs in the absence of local extinction, when species undergo population declines (called functional or ecological extinction), in stable populations following behavioural changes and even under population increases (Box 1). In these cases, the affected species maintains visible populations and the function loss is rarely identified until the negative repercussions cascade through the ecosystem. These 'cryptic' function losses are likely to be more prevalent in disturbed ecosystems than those associated with local extinction, because anthropogenic disturbances affect the abundances of species, and behaviour of animals, more often than they affect the presence or absence of species [3]. Yet cryptic function loss is not considered in assessments of functional diversity, which will overestimate the resilience of ecosystems following disturbance [4]. Identifying cryptic function loss events is essential for understanding how ecosystems across the globe will respond to the diverse and intense disturbances facing them, and to effectively assess the relationship between functional diversity and ecosystem stability.

It is not all or nothing: partial function loss

Global change can cause both partial and complete function losses in persistent animal populations and considering only cases where all functions are eliminated will greatly overestimate functional diversity within an ecosystem. Functional extinction (synonymous with ecological extinction, see Glossary) is defined as occurring just before local extinction [5], resulting in the loss of all functions. However, this term is also used when a partial population decline triggers the loss of a 'single' function, while other functions performed by the animal are maintained. Presumably the loss of all functions would have the greatest overall impact on ecosystems, but species perform discrete functions, which involve different subsets of interacting organisms. Hence, the consequences of losing one function will operate independently of another. For example, hawksbill turtles in the Caribbean were once important

Glossary

Cryptic function loss: a loss in the function of a species that is hidden by its continual presence in the ecosystem.
Ecological extinction: the reduction of a species to such low abundance that although it is still present in the community it no longer interacts significantly with other species. Used as a synonym for functional extinction.
Ecological function: a service a species provides in an ecosystem, such as pollination or predation. A single species can have more than one ecological function.
Ecosystem stability: the ability of an ecosystem to maintain its structure, biomass, and function over long periods of time and despite disturbances.
Function loss: a loss in all functions, one function, or part of a function, performed by an individual in response to a driver of global change.
Functional behaviour: behaviour or set of behaviours that allow a species to perform a certain function in the ecosystem.
Functional diversity: the array of roles or functions found within a population or community.
Functional extinction: synonymous with ecological extinction.
Functional redundancy: an overlap in the functional traits of species within ecosystems, so that the resilience of the ecosystem is not threatened by the loss of species.
Habitat: the physical space where species coexist and find resources to survive.
Global change: human-induced disturbances that impact ecosystems across a large part of the globe.
Persistent species: species whose populations still exist within an ecosystem.
Species networks: the interactions that occur between a species and other species or the environment. When combined together these form a complex web of links, which sustain the ecosystem.

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Box 1. A framework for cryptic function loss

Empirical research shows that function loss can occur independently of local extinction, but these examples have not been organized conceptually to reveal the pathways by which cryptic function loss can occur. Here, we provide a framework that describes direct drivers of function loss in animal populations, and the conditions under which it can occur.

Population decline is the most widely recognized driver, causing function loss when it changes behaviour, or when a threshold abundance is required for function to be effective (Figure I). There are an increasing number of studies that indicate that partial function loss can occur 'without population decline'. Most of these occur when functional behaviour is directly altered by global change. These effects are probably the most prevalent in current ecosystems, but have never been formally considered as sources of function loss.

1. **Function loss with population decline**. The functional role of a species or a critical component of its function is lost following population decline (i.e., ecological or functional extinction). This occurs because:
   (i) the population of vulnerable species becomes too low to maintain interactions with other species (e.g., seabirds [9]);
   (ii) intraspecific variability within the population means that individuals do not contribute equally to population function; individual behaviour does not change but the collective behaviour within the population does (e.g., sheephead fish [19]); and
   (iii) there is an abrupt change in the behaviour or ecology of a species at different densities; in these cases, behaviour of individuals is dependent on population abundance (e.g., flying foxes [10]).
2. **Function loss without population decline**. Ecosystem changes affect the behaviour or ecology of a species and initiate a loss in function. Target behaviours are those that are dependent on, and altered by:
   (i) an increase in the population abundance of a species alters the balance between multiple functions of a species (e.g., deer [22]);
   (ii) alterations in the assemblages of interacting species (e.g., extinction of species with which they have trophic or nontrophic interactions with, introduction of new species) (e.g., grasshoppers [25]);
   (iii) changes in the habitat structure, resource distribution, or nonstructural conditions (e.g., zooplankton [38]); and
   (iv) climate change (e.g., moose [45]).

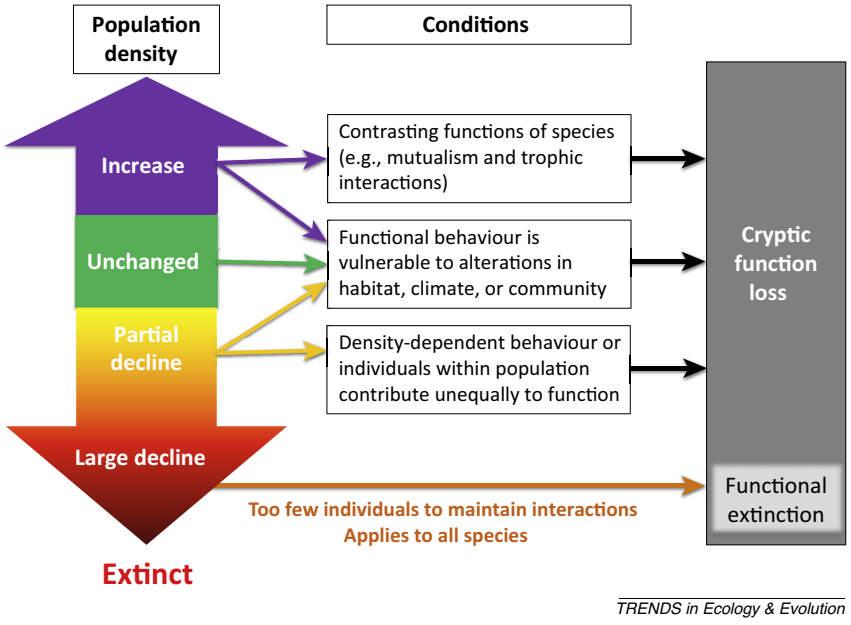

Figure I. Conditions under which cryptic function loss can occur at different population densities. The conditions promoting function loss are indicated for a population increase, unchanged population density, and a partial decline in population density.

predators of the sponge *Chondrilla nucula*, but turtle population declines of 75–98% have allowed this competitively superior sponge to overtake coral reefs and affect reef communities [6]. This functional extinction of turtles as predators has had effects that are independent of their functional extinction as herbivores [7].

Species also provide unique functional contributions under a broader ecological role and loss of 'part' of a function can also negatively affect ecosystems. For example, hawksbill turtles are predators of different animal species but, as we showed previously, the loss of the predation function for a single prey species can alter coral reef communities. Hence, entire functions do not need to be lost for ecosystem stability to be threatened and partial function losses must be incorporated into frameworks on functional diversity. In fact, as we will show, these partial function losses can accumulate within a species, and within a single community, having wide-reaching consequences for ecosystems.

Underlying causes of cryptic function loss in persistent animal populations

The most common cause of cryptic function loss in animal populations occurs when ecosystem change directly alters behaviours that are critical for maintaining a certain function. Ecological functions performed by animals are a consequence of daily activities such as searching for and consuming food, avoiding being eaten, seeking shelter, and pursuing mates. Hence, it is the ecological and behavioural attributes of animals that ultimately determine their