

# Concepts of keystone species and species importance in ecology

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**Abstract:** This paper discussed the keystone species concept and introduced the typical characteristics of keystone species and their identification in communities or ecosystems. Based on the research of the keystone species, the concept of species importance (SI) was first advanced in this paper. The species importance can be simply understood as the important value of species in the ecosystem, which consists of three indexes: species structural important value (SIV), functional important value (FIV) and dynamical important value (DIV). With the indexes, the evaluation was also made on species importance of arbor trees in the Three-Hardwood forests (*Fraxinus mandshurica*, *Juglans mandshurica*, and *Phellodendron amurense*) ecosystem.

**Key words:** Species importance; Keystone species; Structural important value; Functional important value; Dynamical important value

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## Introduction

Keystone species concept has been focused by ecologists and conservation biologists since its introduction by Robert T. Pain in 1969. By now, however, identification of the keystone species in communities or ecosystems is not effective, especially in nature, for example, in forests and grasslands, even in a functional group. Many scientists focused on keystone species researches. Tanner and Hughes (1994) applied a method of sensitivity analysis of a matrix of transition probabilities to quantify the relative importance of each species in a coral reefs community at Heron island, Australia, and they successfully identified "keystone" species (species group) in complex assemblages, but then this method is difficult to be applied in territory ecosystems. Traditional perturbing experiment can only be applied in a simple ecosystem or semi-artificially controlled ecosystem. So far, we have not found a real objective, comprehensive and quantitative method to identify keystone species in a natural ecosystem. The problem is how to define and quantify species "importance" in an ecosystem or community. Species importance concept can help us understand and quantitatively analyze species roles, and then identify and evaluate the keystone species in nature.

## Concept of keystone species

The term of keystone species was first introduced by Robert T. Pain in 1969, and originally applied to a top predator. The keystone species was defined as: The species composition and physical appearance in a community or ecosystem were greatly modified by the activities of a single native species in the food chains. These individual populations are the keystones of the community. The structure, integrity of the community and its unaltered persistence through time are determined by their activities and abundances (Pain 1969). Walker (1992) called those species that are important to an ecosystem "driver", and other species -- "passengers". Jones *et al.* (1994) and Lawton (1994) gave the concept of ecosystem engineers, considered that some species directly or indirectly affect other species, by causing physical state changes in biotic or abiotic materials, and thus lead to changes of ecosystem structure and function. Keystone species play a critical role in determining community structure. Removal of keystone species causes massive changes in species composition and other ecosystem attributes. For instance, removal of sea otters leads to an increase in sea urchins (*Strongylocentrotus* sp.), and hence leads to the disappearance of kelp beds, that in turn changes wave action and siltation rates, with profound consequences for other inshore flora and fauna (Estes and Palmisano 1974). In this familiar example, the species sea otter that was traditionally regarded as the keystone has major effects because it changes the impact of one engineer (urchin) on another (kelp), with knock-on effects on other species in the web of interactions.

Later, the term of keystone species has been broadly

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applied to many species at many tropic levels, and we can divide the usages of keystone species into five types (Table 1).

**Table 1. Categories of presumed keystone and the effects of their effective removal from a system**

Keystone category	Effect of removal	Organisms
Predator	Increase in one or several predators/consumers/competitions, which subsequently extirpates several prey/competitor species	Starfish (Paine 1966, 1969), sea otters (Duggins 1980), fire ants (Risch and Carroll 1982)
Prey	Other species more sensitive to predation may become extinct; predator population may crash	Arctic hares (Holt 1977), snowshoe hares (Holt 1984)
Plant	Extirpation of dependent animals, potentially including pollinators and seed dispersers	Hummingbird pollinators, mammalian dispersers (Wilcox and Murphy 1985)
Link	Failure of reproduction and recruitment in certain plants, which potential subsequent losses	Palmnuts, figs, nectar (Gilbert 1980; Terborgh 1986)
Modifier	Loss of structures/materials that affect habitat type and energy flow; disappearance of species dependent on particular succession habitats and resources	North American beaver (Naiman <i>et al.</i> 1986); Brazilian termite (Redford 1984)

As used by Paine and many other ecologists, there are two typical characteristics of keystone species. First, their presence is crucial in maintaining organization and diversity of their communities and ecosystems. Second, it is implicit that these species are exceptional, relative to the rest of community in their importance.

The best way to identify keystone species in a community or ecosystem may be perturbation experiments, whereby, the candidate keystone species are removed and the responses of a predefined assemblage of species are monitored. These tests require adequate experimental replication and careful definition of the relevant assemblage (MacMahon *et al.* 1978), and time scales should be considered.

About the importance of species in community, Mill (1993) advocated the concept of "community important value" and defined the community importance of a given species as the percentage of other species lost from the community after its removal, thus, we can draw out the relative community importance value of each species in the community.

How to understand the effects of species in an ecosystem or community, John H. Lawton summarized four hypotheses: First, the redundant species hypothesis, it suggests that there is a minimal diversity necessary for proper ecosystem functioning, but beyond that, most species are redundant in their roles (Walker 1992; Lawton *et al.* 1993). Second, the rivet hypothesis, which suggests that all species make a contribution to the performance of an ecosystem (Ehrlich *et al.* 1981), this hypothesis takes species as rivets holding a complex machine together. Third, the idiosyncratic response hypothesis, it suggests that ecosystem function varies when diversity changes, but the magnitude and direction of change is unpredictable. Finally, the null hypothesis, that ecosystem function is insensitive to species deletions or additions.

### Concept of species importance in ecology

Species is the basic structural unit of ecosystem. The structure, function and dynamics of ecosystem are closely related to its composed species, especially plant species, and it is the plant species that construct the ecosystem structure, fix sun energies, ensure matters circulation, present dynamics and provide ecosystem inner environment. But the role and acting intensity of each species in the ecosystem are different. How to clearly and objectively understand the species attributions and quantitatively measure their contributions in the ecosystem is fundamental and keystone for us to study the ecosystem.

Species importance is a common performance of species in the ecosystem. It is constructed by three indexes: structural important value (SIV), functional important value (FIV) and dynamical important value (DIV). Species structural important value is composed of important values of main-layer species, succession-layer species and generation-layer species. The species functional important value is composed of five measuring values: species biomass, species biomass energies, species net primary productivities, species growth production, and species leaf litter production. And species dynamical important value is calculated by Horn's Markov model (1975a, 1975b). The results of species importance of arbor trees in the Three-Hardwood forests ecosystem is as followed (Table 2).

### Discussion

In nature, ecosystem is changing constantly, and each succession stage has its own keystone species, so keystone species are varying as their ecosystem changes.

The role of species in ecosystem processes is mainly reflected in three aspects: structural importance, functional

importance, and dynamic importance. However, the impacts of species structural importance, species functional

importance and species dynamic importance on the ecosystem are not equal.

**Table 2. Species importance (SI) of arbor trees in the Three-Hardwood forests ecosystem**

Tree species	SIV	SIV Order	FIV	FIV Order	DIV	DIV Order	SI	SI Order
<i>Fraxinus mandshurica</i>	20.18	3	12.76	2	26.86	2	19.93	2
<i>Juglans mandshurica</i>	25.61	1	62.83	1	18.43	3	35.62	1
<i>Phellodendron amurense</i>	13.57	4	11.53	3	6.96	5	10.69	5
<i>Ulmus japonica</i>	21.64	2	3.30	5	29.05	1	18.00	3
<i>Acer mono</i>	12.99	5	1.61	8	17.67	4	10.76	4
<i>Tilia amurensis</i>	2.28	6	2.43	6	0.44	6	1.72	7
<i>Betula platyphylla</i>	1.58	8	1.65	7	0.30	7	1.17	8
<i>Populus davidiana</i>	2.10	7	3.90	4	0.28	8	2.10	6

**Notes:** SIV---structural important value; FIV---functional important value; DIV---dynamical important value; SI---species importance.

The best way to identify keystone species would be perturbation experiments whereby the candidate keystone are removed and responses are monitored. But such tests require adequate experimental replication, careful attention, and time scales should be considered. Traditional perturbing experiments may be only applied to a simple system or semi-artificially controlled system; it is difficult to be applied in natural ecosystems such as forests and grasslands.

Lack of a unit, objective and quantitative criterion of identifying keystone species leads to different keystone species in the same ecosystem by different scientists at the same time.

Redundancy is not surplus, thus this surplus is a kind of ecological redundancy. And just the redundancy results in stability, persistence and integrity of ecosystem.

Keystone species concept overstates the impacts of keystone species on many other species. In fact, several non-keystone species may have a greater contribution than a single keystone species.

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