REVIEW
The Importance of Ecological Redundancy for Ecosystems Restoration
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1. Introduction

Ecological restoration is an activity that incorporates several concepts from different branches of ecology, for example, landscapes and mosaics, ecosystem functions and processes, population dynamics, species interactions, and genetic diversity [1]. Thus, as a science, restoration ecology is multidisciplinary and integrative. Another field of knowledge with which restoration shares some goals underlying biodiversity is conservation biology [2] and is precisely about one concept primarily linked to conservation biology, but that also directly affects restoration practices that this article addresses: ecological redundancy.

The concept of ecological redundancy was coined in the scope of conservation biology in the early 1990s [3] in an attempt to change the conservation focus of particular species (e.g., charismatic species such as African lion and giant panda) to a set of species that play vital functions in maintaining ecosystem integrity as a whole. As conservation biology is a discipline of crisis and as we do not have enough support to conserve each species in particular, conservation efforts directed towards one or fewer species could not effectively reduce the loss of biodiversity in general [3]. Therefore, if the focus was directed towards the aspects of biodiversity critical for maintaining ecosystems’ resilience, the loss of species (those already known and those still unknown) could be minimized [3].

In this context, it was suggested that species could be functionally grouped according to the function (or
functions) that they play in a given ecosystem. Take as examples the functional group of nitrogen-fixing plants in a grassland [9], herbs whose flowers provide resources to insects in impoverished environments (Saxifraga cotyledon on siliceous alpine cliffs [6], algae groups in coral reefs [7], and bird species dispersing seeds in forests [8].

Notice that in all cases, there is a set of species — a few or many species — performing the same role; fixing nitrogen, providing resources, and dispersing seeds. Ecological redundancy was coined to characterize species of a group that plays the same functions, meaning species with redundant roles [3]. Once the functional groups significant to ecosystem functioning were established, those composed of a few species performing the same function (a few redundant groups) would be priorities for conservation, precisely because if these species were eliminated, the system would lose resilience and increase the chances of another species also to become extinct [32]. The concept of functional redundancy is also applied in this context [10].

As with almost every new proposal in science, the idea of redundant species generated divergent opinions. Some argued that such a concept could suggest that redundant species would have fewer conservation efforts because some functional group species would be lost without harming the ecosystem’s functioning [11]. In other words, that ecosystems could naturally function with fewer species [12]. Others criticized the choice of the term redundancy, arguing that it may give margin to ambiguous and erroneous interpretations that some species are dispensable [13], and so it would be dangerous to utilize it in the conservation context [14].

Indeed, the word redundancy may sound strange at first sight and suggest some expendability or something unnecessary; however, this vision is distorted from the real base concept because the idea is just the opposite. Even when some species perform similar functions in the ecosystem (i.e., they are redundant), they differ regarding their necessities and adaptations to the environment. The critical point is that if the functional groups are conserved, meaning the species as a whole, or if any species become locally extinct, others with similar functions will persist so that the ecosystem functioning is not lost [9]. Thus, in this sense, the concept of redundancy was proposed, aiming to focus conservation efforts on aspects of biodiversity (in the functional groups) that are critical for maintaining ecosystem resilience [9].

Regarding this, a quite interesting point of view was proposed in the late 1990s in the light of engineering principles [15]. The study demonstrated that reliability, being the probability of a system to function under demand (in the study’s example, a machine), always increases if redundant components are added to the system. Thus, ecosystems with more redundant species are more “reliable” because if a component is lost (a species), another belonging to the same functional group would cover such a gap, and the system could remain to function [15]. At the heart of this concept, the conservation of redundant species (those with equivalent roles) might enhance ecosystem resilience and assist in maintaining its original functions [9].

2. Ecological Redundancy in Restoration

What about restoration ecology? How might ecological redundancy affect restoration practices? As previously stated, restoration incorporates many ecological and conservation concepts, and it is an excellent opportunity to test ecological theories [16]. Bringing the concept of ecological redundancy and incorporating it into restoration practices may bring forth exciting consequences, such as the possibility to create or improve the resilience of ecosystems undergoing restoration and enhance their chances of perpetuation in a changing environment [17].

About five years after the publication of the term ecological redundancy, restoration practitioners had already alerted the scientific community on the necessity to know about functional redundancy in the regional species pool, which could be used in projects whose objective would be to restore ecosystem functions [16]. However, given the great diversity of species in natural ecosystems, determining the functional groups and which species are redundant is not easy. This idea seems to be even more improbable in high diversity regions (such as the tropics), and this was another aspect of the concept that received criticism because a high level of knowledge would be necessary to know which species are redundant [14].

However, it is essential to highlight that only a subset of species from the total regional pool is used in restoration plantations. For example, in the Brazilian Atlantic Forest, the average number of tree and shrub species produced in nurseries of São Paulo state (the pioneering Brazilian state in forest restoration) for restoration purposes is about 80 species [19]. On the other hand, only one forest remnant in this same biome may have about 250 tree species [20]. Thus, considering that restoration practitioners work with a subset of species and that ecosystems under restoration frequently harbor simpler communities than natural ones [18,21], the restoration practices have not only the potential to incorporate the concept of ecological redundancy, but also to test and adapt it (when necessary), and to assist in determining the functional groups.

Indeed, by analyzing some restoration models, we can notice that they naturally consider ecological redundancy. For instance, there are models which utilize a set of colo-
nizers (the functional group of pioneers) and late species (the functional group of non-pioneers) in different proportions, either by planting or sowing \cite{22,23}. Other models employ a functional group of filling and another of diversity, with the first being a set of fast-growing species and the second being long-lived ones \cite{24}. Other times, a functional group of nitrogen-fixing species can be favored to improve the soil’s nutritional quality \cite{25}, and fleshy fruit trees can be planted to attract seed dispersal fauna \cite{26}. Note that there are redundant species in all cases because one must keep in mind that complementarity increases the project’s chances of success. If any species do not establish themselves or become extinct in the area, another with a similar function might develop its role, and the ecosystem functions will still be guaranteed.

If, on the one hand, redundancy occurs indirectly in the models, on the other, studies carried out in ecosystems under restoration which explicitly incorporate and test the ecological redundancy concept are still scarce. To prove this, I performed a search in the Web of Science® database in March 2021 using the key terms ‘ecological redundancy’ AND ‘restoration.’ The search resulted in 153 documents; but when I refined the search for studies that in some way considered the ecological redundancy of species in restoration sites, this number drops to only 14 documents (Table 1). The ecological

| ID | Biological community studied | Reference |
|----|-------------------------------|-----------|
| 01 | Vegetation on restored steep slopes | Monteiro J, et al. 2020. A tale of two green walls: A functional trait approach to assess vegetation establishment on restored steep slopes. *Restoration Ecology* 28:687–696. DOI: 10.1111/rec.13055 |
| 02 | Ground dwelling beetles within a disturbance gradient | Cajaiba RL, et al. 2020. Are primary forests irreplaceable for sustaining Neotropical landscapes’ biodiversity and functioning? Contributions for restoration using ecological indicators. *Land Degradation & Development* 31(4):508–517. DOI: 10.1002/ldr.3467 |
| 03 | Vegetation in urban savanna patches | Shackelford N, et al. 2019. Ten years of pulling: Ecosystem recovery after long-term weed management in Garry oak savanna. *Conservation Science and Practice* 1:e92. DOI: 10.1111/csp.92 |
| 04 | Insect communities at grasslands | Luong J, et al. 2019. Local grassland restoration affects insect communities. *Ecological Entomology* 44(4):471–479. DOI: 10.1111/een.12721 |
| 05 | Vegetation in restored grasslands | Tőlyesi C, et al. 2019. Recovery of species richness lags behind functional recovery in restored grasslands. *Land Degradation & Development* 30(9):1083–1094. DOI: 10.1002/ldr.3295 |
| 06 | Birds in vegetated patches of old-growth woodland, regrowth woodland, and restoration plantings | Ikin K, et al. 2019. Avian functional responses to landscape recovery. *Proceedings of the Royal Society B* 286:20190114. DOI: 10.1098/rspb.2019.0114 |
| 07 | Macroinvertebrates in lowland UK rivers | England J & Wilkes MA. 2018. Does river restoration work? Taxonomic and functional trajectories at two restoration schemes. *Science of The Total Environment* 618:961–970. DOI: 10.1016/j.scitotenv.2017.09.014 |
| 08 | Tree species pollination mode | Montoya-Pfeiffer PM, et al. 2018. Are the assemblages of tree pollination modes being recovered by tropical forest restoration? *Applied Vegetation Science* 21(1):156–163. DOI: 10.1111/avsc.12335 |
| 09 | Macroinvertebrate communities in a watershed | DeNicola DM & Stapleton MG. 2016. Using macroinvertebrates to assess ecological integrity of streams remediated for acid mine drainage. *Restoration Ecology* 24(5):656–667. DOI: 10.1111/rec.12366 |
| 10 | Vegetation in tropical forests | Garcia LC, et al. 2015. Flower functional trait responses to restoration time. *Applied Vegetation Science* 18(3):402–412. DOI: 10.1111/avsc.12163 |
| 11 | Macrobenthic communities in a mangrove | Leung YJS. 2015. Habitat heterogeneity affects ecological functions of macrobenthic communities in a mangrove: Implication for the impact of restoration and afforestation. *Global Ecology and Conservation* 4:423–433; DOI: 10.1016/j.gecco.2015.08.005 |
| 12 | Frugivorous birds and carnivorous mammals | Escribano-Avila G, et al. 2014. Diverse guilds provide complementary dispersal services in a woodland expansion process after land abandonment. *Journal of Applied Ecology* 51(6):1701–1711. DOI: 10.1111/1365-2664.12340 |
| 13 | Plants and insects in northern Europe | Devoto M, et al. 2012. Understanding and planning ecological restoration of plant-pollinator networks. *Ecology Letters* 15(4):319–328. DOI: 10.1111/j.1461-0248.2012.01740.x |
| 14 | Bee communities along the Sacramento River, California | Williams NM. 2011. Restoration of nontarget species: Bee communities and pollination function in riparian forests. *Restoration Ecology* 19(4):450–459. DOI: 10.1111/j.1526-100X.2010.00707.x |
communities studied included terrestrial vegetation and insects, birds, mammals, and aquatic macroinvertebrates (Table 1). The number of studies has increased in recent years, but further investigations are needed. Moreover, the studies have focused mainly on functional groups and functional redundancy.

The studies [27] and [28] can be cited as examples; the first shows how a functional species approach can assist in directing management decisions (mainly if the goal is to restore ecological functions) and giving recommendations to improve public policies linked to restoration. The second study found that ecological restoration by planting a highly diverse pool of species in the tropics can ensure the functional diversity of flowers of tree species in the medium term.

Other studies did not evaluate ecological redundancy explicitly, but they have indirectly noticed the influence of species redundancy in ecosystems under restoration. In the Mojave Desert (USA), the functional equivalence of exotic and native species as a source for bird nesting explained why avifauna species richness could be affected by vegetation structure and not by tree species richness [29]. In restored prairie wetlands, the difficulty in determining plankton as a recovery indicator was due to some species’ functional redundancy [30]. Thus, although ecological redundancy was proposed about three decades ago and is accepted as an essential component that maintains some ecosystem properties [31], it is still poorly considered in ecological restoration studies.

I suggest that future studies should consider the ecological redundancy clearly, especially in the coming years when ecosystem restoration should gain scale [32]. When considered, the concept of ecological redundancy and species replacement must be taken with care because it may give the idea that restoration projects always need to have high species richness, which is not valid. The natural diversity of each ecosystem must be respected. A high diversity of species can be employed in a broadleaf rainforest which is naturally diverse. However, the same should not be done in temperate or boreal ecosystems because they naturally contain few species due to environmental restrictions [33].

In such low-diverse communities, the chance that one or a few species play unique roles may be increased as the total pool is low, but the ecosystem still works properly. In the cases where a functional group is represented by one or few species (the so-called key-species), a high conservation value is attributed to them [34]. Many rare species support the ecosystem’s most vulnerable functions, even in ecosystems with high diversity (e.g., the tropics, coral reefs, and alpine regions). A vulnerable function is defined as a particular function exercised by few species and few individuals, and they have low functional redundancy [35]. In other words, there are many species with unique functions in the system. In ecological restoration, it is emphasized that identifying key species may also be a relevant task if we want to improve the success chances of projects because such species may not be replaceable or have no functional equivalents [36].

In this way, if the concept of ecological redundancy is direct and correctly incorporated into the restoration practices (i.e., taking into account that some species can play similar roles in the ecosystem and that some are unique representatives of specific functional groups (to identify key-species)), we can have more resilient restoration areas. It is expected that areas restored with this approach will be more resilient because some species’ functional diversity and equivalence increase ecosystem resilience [3,15,31].

Indeed, it has been already noticed that the use of functional groups for some ecosystems is an essential factor in developing restoration strategies [35], and it is suggested that restoration projects should generally include all desirable functional groups across a comprehensive plan [28]. With an ecological redundancy approach, more resilient and resistant ecosystems may be created, increasing success chances. Some ecosystem properties are initially insensitive to species loss due to redundancy. By having by having a range of species that respond differently to distinct environmental disturbances, the ecosystem processes can stabilize in response to the disturbances and abiotic variations [33].

3. Ecological Redundancy in the Monitoring

Beyond using ecological redundancy and its respective functional groups in planning restoration actions, it is also relevant to address them during the monitoring of already underway projects. Often three ecosystem attributes are evaluated in the monitoring, namely vegetation structure, species diversity, and ecological processes [36]. From the diversity attribute, it is possible to characterize the species, assign them into functional groups, and identify key-species. In ecological processes, the groups are already characterized, for example, colonizers (pioneer species), dispersers, or decomposers.

Another attribute that has been argued to be assessed is the socioeconomic function, such as the quantification of ecosystem services [37]. Even here, the ecological redundancy may be evaluated because there are groups
that integrate ecosystem services such as pollination and water supply maintenance. Functional groups obtained by monitoring may then be compared with those defined in the initial project goals or with reference ecosystems, and, if necessary, corrective measures can be proposed.

Even if functional groups’ distinction was not an initial objective of the project, its evaluation during monitoring may reveal relevant information and assist in management decision-making. For instance, a study evaluated the functional group of pollinating bees in remnant riparian forests (reference ecosystems) and restoration forests at the Sacramento River in the United States [38]. The results pointed out a reduced redundancy of pollinators visiting some plants in the restored sites. Since pollination is a vital function for most plants’ reproduction, and as there was little pollinators’ redundancy at the restoration sites, some corrective approaches can be proposed for improving this functional group (such as enrichment with resource-plants for pollinators) [38].

Either in the initial planning of a restoration project or management actions carried out after monitoring, restoration ecology aims to guarantee the ecosystem’s resilience in question [39]. One way to increase resilience is through ecological redundancy in the functional groups (or functional redundancy) because it will permit a range of responses to environmental factors while maintaining similar effects on ecosystem functions [40].

4. Conclusions

Throughout this article, I presented the real meaning of the ecological redundancy concept and how important it is to consider redundant species (functional groups, functional redundancy) in restoration practices. The environment is rapidly changing worldwide due to human activities, and ecological restoration is one of the useful tools we have to counteract. This work shows that few studies on ecological restoration have considered ecological redundancy directly. Resilience-based strategies are necessary to restore sustainable ecosystems, and ecologists should consider using ecological redundancy broadly.

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