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Ecosystem Services and Global Ecology

Edited by Levente Hufnagel





ECOSYSTEM SERVICES AND GLOBAL ECOLOGY

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Meet the editor



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He has more than 160 scientific publications (in both aquatic and terrestrial ecological aspects of plants, animals, and microbes, at community as well as population level) and more than 700 independent citations. Dr. Hufnagel is a participant in several large ecological research and development projects, having significant experience in multidisciplinary cooperation (with more than 180 coauthors in different publications). As the supervisor of several PhD, BSc, and MSc theses, and as editor-in-chief of an international scientific journal indexed by Web of Science and Scopus, he has wide supervising and editing experience. Dr. Hufnagel graduated from Eötvös Lorand University with a Master's degree in Ecology and Evolutionary Biology and a PhD degree in Hydrobiology. He also graduated from Szent István University with a PhD degree in Agricultural Science.

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Preface

Our book, *Ecosystem Services and Global Ecology*, provides a very stimulating report and overview of the frontiers of natural and social aspects of ecosystem services throughout the world.

It consists of two sections: the first section looks at natural and the second section at societal and human ecological aspects of ecosystems and their services. The first section has five chapters concerning collapsing ecosystems, invasive species, benthic macroinvertebrate communities, watersheds, and plant anatomical patterns from a worldwide viewpoint.

In the second section we can read about the mapping of ecosystem services, community well-being, urban ecology, and some historical aspects.

In my opinion every chapter is very useful and original.

I am sure that this book will be very interesting to everybody—researchers, teachers, students, or others interested in the field—who would like to gain insight into the area of ecological research.

> **Levente Hufnagel, PhD habil** Szent István University, Hungary

Natural Aspects of Ecosystem Services

Introductory Chapter: Evaluation Methods of Ecosystem Services and Their Scientific and Societal Importance in Service of Solving the Global Problems of the Humankind

Levente Hufnagel, Ferenc Mics and Réka Homoródi

Additional information is available at the end of the chapter

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1. Introduction

Reduction of ecosystem services plays a key role in the group of phenomena that is called global ecological crisis. Population explosion has resulted in overpopulation of our planet. Energy source of this overpopulation has been fossil fuels (coal, mineral oil and natural gas) produced by the biosphere over millions of years during the history of the Earth. Exploiting and burning of these natural resources have decreased living conditions of subsequent generations and have started a global climate change at the same time. However, it is more important that urban areas and agricultural land have extended in place of natural ecosystems, causing them to decrease drastically and malfunction, which has resulted in a biodiversity crisis, mass species extinction. Besides these, the global ecological crisis includes industrial, agricultural, traffic and residential pollution, which have damaged abiotic components of habitats, that is, air, soil and water. Deteriorating ecological conditions have caused social problems directly and indirectly, such as epidemics, poverty and humanitarian crises. Besides these, pollutant and nature-destroying economic activities increase wealth and income inequality among people, which results in further social tensions (crime, terrorism, riots and wars). At the same time, problems are aggravated by favorable processes whose disadvantages are not considered at first. Increasing scientific research has led to an information explosion. Due to this, experts have been forced back to a more and more narrow intellectual space; our excellent scientific specialists are less and less able to have an overview of their own wider discipline

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and, especially, the whole science, and thus, they are less and less able to solve complex problems and avoid them if possible. In the database Web of Science, which is the collection of scientific articles of the highest level, there are only 224 articles with the expression "global problems" in their title (at the time of writing this text), whereas 59,957 articles can be found with Drosophila (name of a fruit fly) in their title. Thus, researchers prefer more than 250 times dealing with molecular effects of any gene of a tiny fly to the complex study of the burning problems of our time. Of course not the scientific research is the only source of our knowledge, but the global usability of local ecological knowledge also depends on scientific and social science research [1, 2]. Not even the scientific world is dealing with solving the global ecological crisis; however, it might be even graver that if scientists presented suitable solutions, there would be currently nobody to execute them. Mankind is struggling not only with overpopulation crisis, environmental crisis, biodiversity crisis, social crisis and information crisis but lacks global coordination as well, which would be essential for political guidance. Mankind does not have a central legislative and executive power necessary for saving the whole Earth, but decision-making processes are split up among 195 nation states, among which the probability of substantial consensus approaches zero even in the most important questions.

Land cover change research has an important role in understanding the intensity and dynamics of real global processes [3–7]. The Land-Cover and Land-Use Change (LCLUC) Program launched by the National Aeronautics and Space Administration (NASA) is studying natural and human-induced changes of the vegetation of the Earth and consequences of environment transformation processes and attempts to forecast natural disasters considering the Earth as a single complete system, with the help of satellite images, using the tools of NASA and combining them with laboratory and modeling work [8].

Survival of mankind and sustainability of the society depend on ecosystem services provided by natural ecosystems. Only a healthy biosphere is able to regulate the climate of the Earth and keep it in a range suitable for us.

1.1. Ecosystem services

Goods which mankind receives from the natural environment, from properly functioning ecosystems are called ecosystem services. These goods contribute to the survival and well-being of people directly or indirectly. Ecosystem services can be divided into four different groups [9].

Provisioning services: food, biofuels, genetic diversity, medicinal plants (natural pharmaceuticals), ornamental materials.

Regulating services: climate regulation, water purification, river regulation, erosion prevention, pollination.

Supporting services: water and nutrient cycling, photosynthesis and primary production, soil formation (pedogenesis).

Cultural services: spiritual and religious enrichment, esthetic values, recreation and tourism.

Value of ecosystem services can be expressed in money, which indicates preferences of the users and helps to determine how much resource to expend in order to maintain or restore an ecosystem [10]. Protection of intact ecosystems helps to increase resilience against adverse effects of climate change [11]. Biodiversity, that is, diversity of life maintains and restores services. Ecosystems have certain resilience, of course; however, their ability to provide services to mankind is decreasing due to harmful human activities. This is caused by the fact that ecosystem services are less known or their importance is underestimated in political decisions [12]. They are so essential for life that people consider their existence as evident, and it is difficult to imagine that mankind can destroy these as well [13]. Ecosystem services affect each other and connect to each other in a rather complex way, and if humans use one of the services, they affect the others too [14]. For example, if the maximum yield is aimed for with intensive agriculture, this has a negative effect on the water and nutrient cycling of the area. In recent decades, the most important changes in ecosystem services have been caused by a continuous decrease in the area of intact ecosystems [15]. Between 1997 and 2011, a damage of 4.3–20.2 trillion USD was created globally due to the fact that the area of intact, properly functioning ecosystems was decreasing, and they were replaced by artificial ecosystems [16]. Urbanization is increasing, more and more people live in cities in the world. Where the soil is not covered by asphalt and concrete, plants and animals may appear and ecosystems may form. These can be alleys along the roads, parks, artificial creeks and lakes as well as gardens. Ecosystem services are present here as well, which influence people's life positively. For example, removing dust from the air, microclimate regulation and providing more attractive environment for residents [17].

2. Evaluation methods of ecosystem services

Experts more and more often encounter the problem that the value of a certain area, ecosystem or species has to be estimated. They have to decide how to handle a certain area and what to do with plants and animals, for example, whether a forest has to be left in its natural state or has to be cultivated. In this case, the value of that forest has to be estimated. In the academic literature, there are two approaches regarding the value estimation of natural ecosystems, the anthropocentric and the biocentric one. According to the first one, anything in nature can be as valuable as it benefits mankind. However, according to the second approach, everything in nature has an inner value, independently from its benefits for mankind [18]. Supporters of the anthropocentric approach mean that since humans are the dominant species on the Earth, they have the right to determine the value of anything [18]. According to the other approach, nature has direct (use) and indirect (nonuse) values [19]. According to the Millennium Ecosystem Assessment, goods provided by nature can be divided into four categories: provisioning services (e.g., fishing, timber), regulating services (e.g., climate and flood regulation), supporting services (e.g., pollination, pest control) and cultural services (e.g., tranquility, inspiration) [20]. Since the 1960s, more and more attention is paid to ecosystem value assessment in the academic literature [21]. Since first mentioning ecosystem services in 1983, the number of articles related to these and that of their citations has been rising steeply [22]. Ecosystems provide a wide range of goods and services to mankind, which are essential for the well-being of people [23]. In order to protect ecosystems, politicians should ensure that human activities are sustainable and resources are distributed fair and efficiently [24]. Decisions of politicians and the public opinion certainly strongly influence the value and usefulness of a certain service, thus value assessment of the services is rather contradictory [25]. Some people think that it is not possible or does not make sense since economists should not give a value to incomprehensible things such as esthetics and long-term ecological benefits [26]. Thus, there can be significant differences, contradictions between economical and ecological assessments [27]. It is especially important in western countries to give a value to natural ecosystems, where great importance is attached to high productivity in economical decisions [28]. Furthermore, monetary expression of ecosystem services does not necessarily mean that these can be considered as market products or private properties [29]. For example, pollination and water regulation cannot be in private property, everybody can benefit from them; however, they cannot belong to anybody [30]. This should definitely be included in political decisions, although translation of ecosystem services assessment into suitable financial mechanisms is not completely solved yet [31]. Since it is difficult to match them with economical processes or factory goods, they have only little weight in political decisions [32]. However, economical assessment of the services and their benefits is highly important because of the control of the services [33]. Attitude toward the assessment of services is best represented by the water-diamond paradox. Water is essential for life, still little value is attached to it, diamond is not important to maintain our quality of life at all; however, it has a great monetary value [34].

While mankind is receiving beneficial services from natural ecosystems, it is changing those, thus it is extremely important to monitor changes in their status continuously since their degradation influences the quality of life of mankind as well [35]. Ecological processes are endangered by human activities, destruction and transformation of habitats and pollution result in the disappearance of natural ecosystems all over the world [36]. Despite international, national and local environmental regulations, improvement of agriculture, industry and residential areas leads to further degradation and pollution of remnant intact natural vegetation [37]. In the future, these threats will be even graver since energy and raw material demand of mankind is continuously rising [38]. Nowadays, most people live torn away from nature and often consider nature protection as a barrier of industrial development; however, ecosystem services may change the point of view, and nature protection can drive the development [39]. Assessment of ecosystem services is also a tool for decision-makers, which helps to choose from alternative management options in order to reach multiple goals [40]. It is a system that links ecology to economy, which is why economical methods should be used for assessment of components of ecological systems [41]. There are several assessment methods which help to determine the monetary value of the services, although missing data make the work more difficult [42].

2.1. Direct market valuation methods

2.1.1. Revealed preference methods

2.1.1.1. Market price method

In some cases, value of the services can be directly measured based on the market price of goods, and these goods can be directly marketed. In these cases, the value is determined by how much they are paid for during the transaction. Thus, there is no need to use complicated methods. Such goods are, for example, sawn timber, firewood, fish and other foods. The value of the goods reflects the value of the ecosystem service. The advantage of this method is that it is simple to use since it considers available price, quantity and cost information, and simple

assumptions are needed. However, it has the disadvantage that several services cannot be directly marketed, and obtained information may be false and distorted; thus, the value of the service is false as well. Furthermore, it is not easy to use it in the case of large-scale changes influencing the stock and the demand on the service [43].

2.1.1.2. Production function method

This approach is used if a certain good or service is partly created by human work and partly by the contribution of an ecosystem. For example, several agricultural plants depend on pollination by insects and the value of pollination can be estimated based on the value and quality of the crops. Thus, this method has been developed to estimate indirect use values. It has the disadvantage that it is difficult to determine how tight the relationship is between ecosystem service and human contribution. Thus, this method is not often used. However, it is used to measure water quality and the change in that for example, considering lower costs of water purification, improving agricultural production data due to better pollination or improving soil quality. Thus, the quality of a marketable good has improved due to an ecosystem service. Another problem with this method can be that the researcher has to consider both human and machine contribution, which can lead to overestimation of the value of the ecosystem service. However, it has the advantage that theoretically it is rather suitable for evaluating ecosystem services since it is based on the assumption that the service and the economic advantage are strongly interconnected [44].

2.1.1.3. Cost-based methods

This method measures the value of ecosystem services so that it estimates the damage in case of loss of the service as well as it considers possible costs of substituting the ecosystem service. It is used to measure water quality and water purification costs, guard against soil erosion, storms and other natural disasters and protect natural habitats. These are not marketable goods, and the method reflects costs of creating the benefit and not the benefit itself. The method has the advantage that it supports the way the economy thinks about value and value creation. However, it has the disadvantage that in certain cases, cost of repairing the damages does not reflect the advantages obtained [45].

2.1.2. Random utility and travel cost methods

The travel cost method and the random utility method developed are based on the empiric assumption that people surely know their preferences; however, these are not always known for researchers. However, certain factors of preferences can be obtained using statistical methods. This method is mainly used to evaluate hobby fishing at lakes, rivers and seas. It measures the value of nonmarketable ecosystem services based on the money and time spent in order to get to the fishing or swimming sites. Time, money and the number of visits express the value of a site, fish and swimming [37].

2.1.3. Hedonic pricing method

This method measures the indirect value of ecosystem services, which is not marketable but can be estimated based on the observed value of a good. In order to determine the value, two goods

are necessary which are the same from most points of view but differ by certain environmental conditions, for example, traffic noise or distance from a park. Difference between monetary values of the goods can be interpreted as the willingness to pay for an ecosystem service. This method is often used to estimate the benefits or costs the environmental quality has (air pollution, water pollution, noise). This means that the environmental quality can also be estimated based on the price of houses. If there are two houses which are similar almost in every respect, however, air is more polluted in the surroundings of one of them, that one may cost less. The analysis reveals if changes in the environmental conditions affect the value of a market good [46].

2.2. Stated preference methods

2.2.1. Contingent valuation

This method measures the value of ecosystem services with surveys. Filled and submitted surveys show how much people are willing to pay for certain ecosystem services. In other words, it studies how people would behave in certain situations. Since these services cannot be marketed, the questions in the surveys ask what price respondents would pay in certain situations. The survey may contain options such as a new tax, an entrance fee to a national park, annual or monthly maintenance fee or a single charge. This method is widely used to assess the value of public goods. However, respondents are often not able to determine how much they would pay for a certain service. Thus, it is rather difficult to assess what an ecosystem is worth. Several respondents highly appreciate them but cannot attach monetary value to them and the answers also depend on the income of the individuals [47].

2.2.2. Conjoint analysis

This is also a commonly used and favored method and is based on surveys. The respondent has to answer questions regarding the characteristics of a good or service. For example, he has to choose between two options which describe possible characteristics of a park (distance from the house, size, vegetation and accessibility). Statistical analysis shows the relative importance of the different features for the respondents. It reveals the distance people are willing to cover to get there. Answers can be compared with answers given regarding other recreational opportunities [48].

2.3. Biodiversity as nonmonetary evaluation approach

Individual plants or animals, which constitute the biota together, can have characteristics which directly satisfy any demand of mankind. At the same time, biota and its role in supporting the biophysical cycles in the ecosystem benefit mankind indirectly [49]. It is necessary to maintain or restore the integrity of ecosystem services so that they persist and benefit mankind in the future as well [50]. Changing biodiversity and its effect on the functioning of the ecosystem have been a rather important field of ecological research in recent decades [51]. Due to landscape transforming human activities, habitats become fragmented, isolated, and dispersion ability of species may decrease. Thus, relationship among populations and viability of species also decrease, which may lead to extension [52]. If global average temperature increases by 2–3°C by the end of the century, 20–30% of all species will be endangered by

extinction [53]. Disappearance of certain species is able to change habitats physically as well, and biogeochemical cycles as well as productivity, structure and functioning of the ecosystems may also change [54]. Reduction of the number of plant species results in decreasing primary production and decomposition processes [55]. Even under stable conditions, a certain minimal number of species is necessary in order to maintain the stability of the ecosystem. Under changing conditions such as the present climate change, an even larger number of species would be necessary so that the community is able to react to changes resiliently [56].

3. Global ecological significance of ecosystem services research

Human activity is rapidly transforming the surface of the Earth, concerning biosphere, soil and water resources. This can be globally observed and changes the functioning of ecological systems. Due to this, climate changes as well because of the strong relationship between vegetation and atmosphere. Climate and vegetation mutually affect each other both locally and globally. Climate regulates the spatial distribution of vegetation types, whereas vegetation influences climate due to its physical characteristics (biogeophysical processes) and the gas exchange (biogeochemical processes) [57]. Between 1990 and 2009, 1.14 ± 0.18 Pg/year carbon was emitted to the atmosphere on average due to human activity and the disappearance of vegetation [58].

Ecological processes happen on a longtime scale, thus, damages caused by human activity will be perceptible even after decades or centuries. On a geological time scale, climatic changes were related to the changes of the Earth's orbit around the Sun, which caused large changes in the vegetation. For example, forests disappeared in Iceland due to the so-called little ice age and the Sahara, which had rich flora and fauna previously, turned to the currently known desert 6000 years ago [59]. On a shorter time scale, extreme weather events, fires, overgrazing and human activities transformed the landscape into new ecosystems, while Pleistocene megafauna became extinct [60]. In the last 300 years, human influence became extensive and intensive globally [61]. Phenomena such as deforestation, extension and intensification of agricultural areas, desertification and urbanization can be globally observed. Significant reduction of natural vegetation results in changing climate regionally and globally, deteriorating water quality, air pollution, habitat fragmentation, decreasing biodiversity, species extinction and spreading diseases [61]. In the last 2000 years, mankind reduced plant biomass by 45% through its landscape-transforming activity, the third of which disappeared during the twentieth century [62]. Human activities change soil composition, soil-forming processes, quantity and quality of water and climate [62]. After eradication of vegetation, soil is eroded, degraded, which causes irreversible changes in ecological systems and the climate [63].

Human influence on the nature is not uniform, there are still intact areas (the Amazon Basin and the Congo Basin); however, destruction will be continued in the future and the effects of these harmful processes will be perceivable in these areas with relatively intact vegetation as well [64]. Reduction of natural vegetation results in decreasing value of the connected ecosystem services, such as biodiversity, climate regulation, carbon storage capacity and water supply [65, 66]. Change in vegetation coverage is a rather significant factor, it influences ecological systems and climate and thus human life as well [67].

The fact that rapid reduction of natural vegetation might be a serious problem and would affect the quality of human life through climate change emerged some decades ago. Disappearance of vegetation and appearance of agricultural and other artificial areas have changed the albedo of areas, that is, energy exchange between the surface and the atmosphere and the climate. Due to the continuously rising human population, demand on land is also rising. This is the most decisive cause of the further degradation of natural vegetation and loss of habitats and this poses the largest threat to biodiversity. The loss is especially large in tropical regions, where biodiversity is the highest. Between 1980 and 2000, half of the new agricultural areas was created in place of cleared, previously intact forests and 28% of them in place of secondary forests [68]. Land use certainly has economic benefits and fosters the development of the countries; however, it also has a significant negative impact on the whole planet and mankind. Agriculture supplies mankind with food, thus, this activity transforms the environment to the greatest extent and contributes to greenhouse gas emission. Loss of natural vegetation and the connected ecosystem services is a problem of the same significance as food supply of mankind and economic development, maintaining and increasing the quality of life. Thus, a compromise should be agreed regarding what has to be protected and preserved and what has to be developed considering synergetic and complementary effects which may emerge.

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Characteristics of Collapsing Ecosystems and Main Factors of Collapses

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Abstract

The synergistic effects of direct human perturbations and climate change have been causing the mass extinction of species. Here, I present the deterministic factors of collapses in present ecosystems. I captured and synthesized the key deterministic traits and processes before a collapse in the peer-reviewed literature. The results of the literature review show that deterministic factors can be used as early warning signals of collapses. The literature also suggests that we have entered the middle stage of global mass extinction, which may be irreversible.

Keywords: climate change, human perturbation, collapse, mass extinction, biodiversity loss, early warning signals, positive feedback

1. Introduction

The synergistic effects of direct human perturbations and climate change have been causing the mass extinction of species. The current extinction rate is about 100–1000 times the background rate. The local biodiversity intactness in terrestrial ecosystems is perhaps already beyond the planetary boundary on more than half of the world's land surface [1]. About 70% of the forests are within 1 km of the forest edges, which reduces biodiversity by 10–70% [2]. According to the IUCN Red List of Threatened Species [3], 10–30% of the world's amphibian, bird and mammal species are threatened by extinction. Wilson [4] suggests that half of the species will face an extinction by 2100. Nonlinearities, positive feedbacks, abrupt collapses and regime shifts are being observed globally. The rate of temperature increase, ocean acidification, sea level rises, anoxic ocean dead zones and extinctions make the recent mass extinction



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comparable with the "Big Five", even with the greatest End Permian extinction event, which wiped out 90% of species [5].

It is essential to explore all the phenomena and processes, which define the recent mass extinction to detect vulnerable ecosystems and predict the tipping points of collapses. It would be important to determine the stages of the extinction to make better predictions. Here, I present the deterministic factors of extinctions which characterize the first stage of mass extinctions. I identify the deterministic factors and their effects in recent ecosystems based on peer-reviewed literature. The results suggest that the effects of deterministic extinction traits are manifold and cascading. They represent the starting point of extinctions hence they can be used as early warning signals of collapses.

2. Triggers of recent mass extinction

The triggers of extinction can be classified into two groups, namely direct and indirect human effects. Indirect human effects usually refer to the ongoing anthropogenic climate change. The first stage of recent mass extinction is dominated by mainly direct human effects, however, climate change is becoming a contributor of sudden collapses as well.

2.1. Direct human effects

Direct human effects such as deforestation, hunting, pollution, alter the environment directly through human activities. They can be traced back to as early as the Upper Paleolithic (50–10 ka) when modern humans expanded their ranges throughout Eurasia and started to exert a great impact at a larger scale. At that time their social groupings, artifacts, tools, communication skills became much more sophisticated and specialized than before. These changes made humans more effective hunters. The increased human pressure probably contributed even to the great Pleistocene megafaunal collapse (14.8–13.7 ka) as well [6]. Development and population growth have always reinforced each other throughout the whole history. The main corner steps of this process were the appearance of agriculture (approx. 10 ka), the age of discovery (fifteenth to eighteenth century) followed by the industrial revolution (1760–1840). The global population is now over 7 billion and it is increasing by more than 80 million per year [7]. This huge pressure is manifested as direct human effects which have triggered a global mass extinction. Species and their habitats are disappearing leading to a great biodiversity loss and homogenized landscapes. Tylianakis et al. [8] pointed out that habitat modifications can alter the food web structure, decreases the evenness of interaction frequencies and increases the abundance of parasitoids. Habitat alteration and fragmentation induce processes which would not happen under normal circumstances. For instance, habitat alteration can enhance hybridization. Just to give an illustrative example, in the USA male wolves have difficulties in finding conspecific mates because of deforestation. Therefore in deforested areas they tend to pair with female coyotes which are abundant there. The genetic transfer of coyote mitochondrial DNA into wolves can give rise to a new species but it can also cause the collapse of gray wolves [9] which are critical keystone species. Without their top-down control, biodiversity starts to decline. Overhunting also affects biodiversity and biomass. It modifies the trophic structure and the species interactions. Sudden collapses and delayed extinctions are present in the ecosystems at the same time as a result of direct human perturbations.

2.2. Indirect human effects

Indirect human effects usually refer to the ongoing anthropogenic climate change. Indirect human effects are, actually, the consequences of direct human activities and they are almost as old as direct effects if we accept the hypothesis that Paleolithic humans were one of the main triggers of the Late Pleistocene megafaunal extinction as the extirpation of megaherbivores had an effect on the climate via vegetational and atmospherical changes [10]. Later, the spread of agriculture and the industrial revolution accelerated climate change dramatically. Agriculture modifies the climate in many ways. It is a great emitter of greenhouse gases, it increases radiative forcing through landcover alteration and it contributes to desertification. However, industrialization catalyzes the anthropogenic climate change even more. Since the mid-nineteenth century, the CO₂ level has risen from 280 to 400 ppm. By 2100, CO, may reach 700–800 ppm which means 3–4°C temperature increase [11]. Climate change creates feedback loops. As a result of temperature increase and ice-albedo feedback mechanism, the Arctic ice is melting. Such events usually indicate mass extinction boundaries between geologic eras according to the paleological records. Climate change increases the number of extreme events, such as severe droughts, extreme precipitation, floods, heat waves and probably hurricanes. The changes are so rapid that the wildlife may not be able to adapt and in the end it will collapse. It is important to note that direct and indirect effects act synergistically reinforcing the positive feedback loops. Direct effects decrease biodiversity and biomass. They weaken the connections in ecosystems. Hence, they increase the overall proneness to stochastic events.

3. Deterministic factors of extinctions

The deterministic factors of extinctions initiate collapses, which suggests that they could be used as early indicators of dramatic changes. Species with several deterministic factors are under the greatest threat. These species are often adapted to specific circumstances therefore they are severely hit by climate change. Their extinction brings about disrupted species interactions, ecosystem functions and trophic structure. Vulnerability, co-extinctions, homogenization and positive feedback loops are the main consequences. Here, I review the deterministic factors of collapses based on literature. I also investigate the severity of their effects in recent ecosystems.

3.1. Environmental factors

Climatic changes and pollution create unfavorable environmental conditions which make species prone to collapses.

3.1.1. Climate

Climate change alters the whole physical environment. It changes the precipitation pattern, increases the number of extreme weather events (fires, droughts, tsunamis and tropical cyclones). Climate change affects biogeochemical cycles and intensifies positive feedbacks [12]. Sea ice extent decreases, glaciers retreat, sea level rises. Ice cover retreating can increase volcanism and the number of intense earthquakes [13, 14]. Oceans suffer from extreme heat events, acidification, perhaphs slowing thermoline circulation [15] and oxygen depletion. All these changes reduce fitness and fertility. Climate change affects abundance, species richness and it can even drive genetic changes [16]. At local scale, vulnerable species respond to climatic changes with quick collapses [17].

3.1.2. Pollution

Pollution is also a main contributor of extinctions. Air, water and soil pollution severely affect the wildlife. Agriculture, industry, transportation and the commercial sector emit harmful materials, noise and excess light. Even everyday people produce an immense amount of waste. EU statistics show that a single person generates half a ton of municipal waste per year and only 50% of the waste is recycled [18]. Chemicals are getting more and more potent, but also more destructive in many cases. Pollution significantly alters the physical and chemical characteristics of the environment. Local pollution can easily turns into regional disaster. Air, water and soil communicate with each other, which means that soil contaminants can get into the water and the air, and from the air toxic contaminants can deposit in the soil and water again making pollution a large-scale problem. The consequences of pollution are manifold. It causes ozone depletion, acid rain, algal bloom, anoxic marine dead zones, waste accumulation and soil depletion. Contaminated plants and animals show reduced fitness, fertility and shortened lifespan. Pollution damages ecosystems and disrupt their functions. Unfortunately, the rate of pollution will probably keep increasing because of global population growth and short-term economic interests [18].

3.1.3. Habitat destruction

Pimm and Raven [19] suggest that habitat destruction is the primary reason for species extinction. Anthropogenic activities (agriculture, industry and urbanization) are the main causes of habitat destruction. Biodiversity hotspots which are the most species-rich regions on Earth are declining rapidly. Tropical forests once covered about 14% of the Earth [20]. Today they occupy less than half of the original area. About 70% of species live in tropical forests [21]. According to Myers [22], 66% of plant species and almost 69% of bird species will disappear if Amazonian forests are restricted to only parks and reserves as a result of deforestation. Deforestation also affects carbon balance. According to Baccini et al. [23], tropical forests are becoming a net carbon source as a result of deforestation and from reductions in carbon density, and this way they cannot dampen the effects of climate change any more. Wetlands which provide vital ecosystem services are also threatened. They are one of the most biologically diverse ecosystems. They clean fresh water by filtering pollutants and neutralizing harmful bacteria, and they prevent devastating floods. They serve as carbon sink and shoreline stabilizer, as well. More than one-third of wetlands have been lost globally [24]. Europe has suffered the greatest loss: more than 60% of European wetlands have been destroyed [25]. Coral reefs are also one of the most diverse ecosystems on Earth. They harbor 25% of marine species [26]. They offer several important ecosystem services, such as tourism, fisheries and shoreline protection. Coral reefs are vulnerable to climate change, fishing and pollution. As of 2005 data, about 20% of coral reefs have been lost so far [27]. However, not only direct habitat destruction, but also indirect disturbances can lead to disturbed habitats and species loss [28, 29]. Ecosystems are melting globally. Main consequences are the loss of biodiversity, the loss of valuable ecosystem services, landscape degradation, increased vulnerability to stochastic events, altered carbon cycles and disrupted climate regulation.

3.2. Geographical factors

The literature suggests that the extinction rate decreases with increasing elevation under the effect of human pressure.

3.2.1. Lower elevations

Due to ongoing climate change and human pressure, a lot of marine and terrestrial habitats have become vulnerable to extinction. Species distribution has changed a lot during the modern historical period. The lower elevations are the most accessible to the ever-growing human population. As a result, many species which are targets for overhunting and/or have poor environmental tolerance have already disappeared from these regions [30]. Lomolino and Channell [31, 32] explain these changes in geographical distribution with their 'contagion model'. They suggest that anthropogenic disturbances spread like a 'contagion' and only populations which live along the edges of historical ranges can survive. The remnant populations with a small number of individuals are at a great risk of extinction as they probably live under suboptimal conditions and they usually have no potentials to migrate to optimal habitats because they are poor dispersals or they have narrower environmental tolerance [30].

3.2.2. Mid and high elevations

Species living at higher altitudes may be at risk too because they have small geographical ranges and they have nowhere to migrate [30]. Upward shifting of other species also puts pressure on them. The changing climate is becoming unfavorable as well. Warm and/or dry conditions can cause stress and shifts in phenology [16, 33] and the spread of pathogens [34]. Though recent studies suggest that middle-elevation species are affected more than the ones living at high-altitude because pathogens thrive at higher temperatures [34, 35]. Lowland species pressure, direct human effects and climate change-induced pathogens altogether jeopar-dize the more accessible mid-elevation regions.

3.2.3. Latitudes

The poleward shifts of species have been observed as a result of climate change during the recent decades [16]. The high latitudes are under great pressure. Tundra is warming twice as fast as the global average [11, 36] resulting in intense permafrost thaw, carbon release and woody encroachment which make them extremely vulnerable [36]. Climate warming, the greenhouse gas release of permafrost, shrub expansion create a positive feedback loop which

turns tundra into boreal forest [37]. Low latitudes are also mentioned as vulnerable regions in the literature several times because of direct (overhunting, logging and pollution) and indirect effects (climate change-related heat susceptibility) [17, 28, 38]. Regime shifts, such as coniferous to a deciduous boreal forest, forest to savannas, steppe to tundra can be expected in the future [37, 39, 40].

3.2.4. Edges

It is a long-debated question if edge populations are more vulnerable to environmental changes than central populations. According to Merriam and Wegner [41], ecotones show higher extinction rates than core regions. Recent studies show that climate change may affect the core populations as well. Bennett et al. [42] created a model based on the observation of seaweeds and concluded that both central and edge populations can show the signs of heat susceptibility under recent climate change. They considered the thermal-safety margins of the populations and not the absolute temperature tolerances. According to their results, both core and edge populations displayed similar thermal stress anomaly. They pointed out that range contractions reflect the anomaly and not the variation in the absolute temperatures. Peres et al. [43] raise the question whether the core regions of Amazonia include intact forests or they are already disturbed. Indirect effects (e.g. selective logging and hunting) weaken the core regions and make them vulnerable to stochastic events.

3.3. Biotic factors at species level

Extinction traits have been studied for a long time. McKinney [44] suggests based on fossil and modern data that specialization is a main factor in extinction. He mentions *adaptation to narrow range of temperature, specialized diet, large body size, low fertility, slow maturation, long lifespan, complex morphology and behavior, limited mobility and migration* as individual extinction traits. Many of them are typical characteristics of K-selected species. The list can be extended by general drought/heat susceptibility and hidden failures based on recent literature on climate change.

3.3.1. K-selected species traits

Numerous studies of recent mass extinction focus on the ongoing loss of large-bodied species. At this point of extinction, the main driving factors of their extinction are direct human perturbations, such as overhunting and habitat destruction. Most ecosystems, both terrestrial and marine systems are affected, which gives rise to concerns. Large animals usually have an important role in ecosystems. Many of them are keystone species and ecosystem engineers providing important ecosystem services. They maintain biodiversity whether they are apex predators or mutualistic seed dispersals. The loss of large-bodied species initiates the disappearance of positive species interactions. Climate change also affects large animals. Climate change-induced body size shrinkage has already observed in terrestrial and marine systems as well [16]. The main problem is that large animals cannot be replaced by small ones [45], and this way important ecosystem functions will disappear for good [46].

One of the most affected large-bodied animals is megaherbivores which are keystone species in terrestrial ecosystems [47]. Historical and modern data and models show that the loss

of megaherbivores causes altered ecosystem structures and functions [6, 48, 49], and even a collapse [50]. Megaherbivores are threatened by several factors acting synergistically, such as hunting, habitat loss via human overpopulation, agricultural land use and deforestation [51]. Climate change also has a negative effect on large-bodied herbivores. Woody encroachment ceases their habitats, decreases their biodiversity and biomass in the long term [49]. Disappearing herbivores means decreasing environmental heterogeneity [52], which can make the ecosystems more vulnerable to stochastic events and it can also brings about the collapse of carnivores [49, 50].

The loss of large apex consumers has an effect on the herbivory intensity, and thus the abundance and the composition of plants, which can result in a regime shifts [53]. Without topdown control, the patterns of invasion, diseases, wildfire, biogeochemical processes and carbon sequestration alter [54]. Nevertheless, it is important to note that carnivores are not strong keystone species anymore because of their low abundance in terrestrial ecosystems, therefore their positions in food webs are already replaced by other species in many cases [47]. This fact also suggests that large carnivores solely cannot be used as effective early warning signals of vertebrate collapse [55]. However, de Thoisy et al. [55] also concluded that apex predators can be effective bioindicators of a forest collapse but only combined with forest structure, phenology and vertebrate community.

As a result of human pressure, large-bodied animals are becoming rare. The populations of large-bodied species are getting smaller and smaller mainly because of overhunting. Some rare and large-bodied species are experiencing collapse through hybridization. Kleindorfer et al. [56] observed that female individuals of rare, large-bodied tree finch species paired with smaller and common finch species in the Galápagos Archipelago. They suspect that the population of large-bodied species collapsed under the conditions of hybridization. They also assume that the hybrids gained fitness benefits. Vaz Pinto et al. [57] studied human-induced interbreeding between large-bodied, sympatric antelopes in Angola. Hybridization between sympatric species never happens under normal circumstances, therefore it is a strong sign of a decline. As a result, parental species almost collapsed and the hybrids also showed reduced viability and fertility.

3.3.2. Specialized diet

Recent studies show that specialized diet can lead to an extinction cascade even if the consumers can shift their diet. Gilljam et al. [58] modeled predator-prey co-extinctions with network model based on antagonistic natural and computer-generated food webs. They concluded that it is an effective short-term survival strategy for specialized predators to switch to a new prey after the extinction of the only previous prey. However, it can lead to the overexploitation of the novel prey in the long term, for example, if the predator is more mobile and the prey is rare. Gilljam et al. [58] noted that some external stochastic factor is also needed besides predation to trigger prey extinction. According to the authors, climate change-induced extreme weather events affect preys more than predators. Switching diet can improve the survival prospects but only in the short term [52]. In the long term, climate change affects negatively most specialized species, therefore diet shift only postpone the extinction of species.

3.3.3. Heat/drought susceptibility

Considering climate warming, sternothermy, which is the adaptation of species to a narrow range of temperature, can be an *Achilles' heel of susceptible species*. *It is projected that the sea surface temperature may rise by* 3° C *by the end of this century. Marine organisms living near the Equator, especially sessile species, are under great threat as they are adapted to a very narrow range of temperature* [59]. Perry and Morgan [17] observed the extinction of the most abundant reef-building species on the southern Maldives reefs. This species was the less tolerant to the changes in temperature, thus the most vulnerable to warming events. The mass mortality of the fast-growing, most abundant species brought about the secondary extinction of other species and a complete collapse. However, mobile tropical species are also jeopardized. Rummer et al. [59] conducted an experiment to test the thermal tolerance windows of tropical fish species. They pointed out that even relatively small temperature rise (2–3°C) can lead to local extinctions. They also suggest that species slow in adaptation will move to higher latitudes.

Climate change-driven seasonal changes in precipitation and temperature affect several ecosystems all around the world. Brookshire and Weaver [60] investigated biomass decline of grasslands in the Greater Yellowstone Ecosystem for 40 years. According to their results, the grassland production decreased by more than 50%, mainly because of a drop in late summer rainfall. Even drought-resilient forest types produce canopy collapse due to extreme drought and heat events [61]. Mortality as a result of heat susceptibility is not a stand-alone phenomenon. It can trigger co-extinction especially if keystone species, symbiotic species are involved. Kikuchi et al. [62] carried out an experiment on a pest insect and its heat-susceptible bacterial symbiont. They pointed out that mid-summer extreme heat can cause a significant decline in the insect population because of the collapse of its symbiont vulnerable to heat stress.

3.3.4. Hidden failures

Species might have some hidden failures which are revealed only when the environmental conditions change significantly. Torres-Ruiz et al. [63] reported on the hydraulic failure of tropical trees in the Amazonia. The synergistic effect of highly vulnerable xylem tissues and the more frequent and extreme droughts because of climate change results in forest dieback.

3.3.5. Endemic or relict species with weak dispersal capacity

Species restricted to geographic locations are threatened by both direct and indirect human effects as they have nowhere to migrate. Sandel et al. [64] investigated the relationship between Late Quaternary climate change velocity and the presence or absence of endemic species. They found that endemics, especially weakly dispersing amphibians, disappeared in high-velocity regions. Areas with low-velocity preserved small-ranged species. Sandel et al. [64] modeled future climate change and found discrepancies between the patterns of past and future climate change, which suggests that past low-velocity areas with a high number of endemic species may become high-velocity regions. For example, the western part of Amazonia and Central Africa which hosts many endemic and rare species may face great climatic changes in the future, according to the authors. Bergstrom et al. [35] observed the rapid collapse of a Sub-Antarctic
alpine ecosystem after the loss of keystone endemic cushion plant. Climate change-modified climatic conditions. It decreased summer water availability, increased wind speed, sunshine and evaporation, which increased stress in cushion plants. Bergstrom et al. [35] suspect that the increased environmental stress made the plants more susceptible to pathogens.

3.4. Biotic factors at population level

3.4.1. Abundance

Significant changes in abundance traits are typical signs of extinction. Small ranges as a result of hunting, deforestation and fragmentation, low abundance, decreased population growth rates [16], seasonal population aggregation [43] can increase extinction proneness. Although the global overall aboveground biomass has increased during the recent years [65], a decrease in the abundance at local and regional scales can be experienced. The main drivers are still direct human disturbances; however, climate change-related abundance changes have also been reported.

Common species are becoming rare [66], which decreases resilience and increases the vulnerability to collapse. Barbosa et al. [67] conducted a field experiment to test the effects of reducing the abundance of a common species in an association of arthropods and an abundant shrub. The species richness and the abundance of other species did not change during the experiment; however, they experienced higher parasitism, lower connectance, interaction evenness and robustness. Winfree et al. [68] modeled plant-pollinator networks and they concluded that abundance is one of the most important drivers of extinction, and abundant species are the most persistent. Abundance is even more important factor than diet breadth. They also simulated what happens if an abundant species disappear first. They experienced a quick secondary extinction. Perry and Morgan [17] also pointed out that climate change can affect abundant species badly. They observed climate change-driven bleaching which caused a collapse on the southern Maldives reefs. The mass mortality of the fast-growing, most abundant species brought about the secondary extinction of other species and a complete collapse. The most abundant species was the most vulnerable to warming events, so the less tolerant to changes in temperature.

Brookshire and Weaver [59] studied a native C3 grassland in the Greater Yellowstone Ecosystem using historical records (1969–2012) to investigate the effects of climate change. They documented a more than 50% decrease in the above-ground net primary production. They blamed the decreased late-season precipitation and higher temperatures for the drought-driven production decline. They noted that CO_2 fertilization could not counterbalance the negative effects of droughts. They also pointed out that drought affects some species more seriously [59, 69]. Perennial forbs showed a greater drought susceptibility, which resulted in local extinctions with no recovery. The increased drought also caused a long-term oscillation of higher frequency in production.

3.4.2. Population cycles

Cornulier et al. [70] reported on the dampening of small herbivore cycles in several European ecosystems because of decreased winter population growth. Small herbivores provide

important ecosystem functions, thus their population collapses are worrying. The authors blame climatic drivers for the increased frequencies of low amplitudes.

Barnes et al. [71] observed the local extinction of echinoid *Paracentrotus lividus* after a cycle collapse. *Paracentrotus lividus* is a keystone species which maintains trophic and food web structure as well as biodiversity. They graze algae, and thus they keep coral reefs healthy. The loss of keystone species results in regime shift and homogenization. The population showed an increased level of fluctuation since the 1920s before its collapse during the 1980s. During the collapse, old individuals became dominants. About 20 years after the collapse no individuals were found. The reason for the collapse is likely to be an increased variation of sea surface temperature with episodes of great increase which inhibited spawning.

3.4.3. Strong Allee effects

Pollinators are suffering in many ways under climate change. Dennis and Kemp [72] modeled a hive collapse due to a strong Allee effect. They concluded that strong Allee effect combined with environmental stressors (climate change, pathogens, pesticide and mites) can lead to the collapse of hives.

3.5. Biotic factors at community level

3.5.1. Positive species interactions

Facilitation or positive species interactions promote species co-existence. Facilitation maintains biodiversity and provides important ecosystem functions. It increases resilience and works as a buffer under stress [73]. Intensive direct human perturbations and climate change susceptibility of species lead to disrupted positive species interactions. The loss of positive species interactions are the signs of large-scale extinction [74].

According to the stress-gradient hypothesis, the frequency of facilitation increases with stress in plant communities. He and Bertness [75] emphasize that facilitation is enhanced and not competition under increasing physical and biological stresses. Exceptional cases are weak stress, non-limiting sources, stresses outside the niche, simultaneous multiple stresses and temporally dependent effects. Typically, dispersal-limited invertebrates and plants use facilitation to expand their species ranges. As direct human perturbations and climate change act synergistically, positive species interactions are under great threat.

Different life histories may affect the responses given to stress. Michalet et al. [76] reviewed literature on plant responses in water-stress ecosystems. They pointed out that getting closer to a tipping point, facilitation either collapses or switches to competition in plant-plant interactions. More specifically, switching from facilitation to competition is the strategy of beneficiary species due to increasing environmental stress, while nurse plant species experience the collapse of facilitation.

In many cases, extinction traits and drivers act synergistically accelerating extinction processes. For instance, a large body is considered as a main determinant factor in mass extinctions in the literature [43]. In plant-animal mutualistic relationships, large-bodied animals are frequent interacting partners. They are threatened by overhunting worldwide, thus their ecosystem functions are also jeopardized. Large-bodied, seed-dispersing species are keystone species in tropical forests [27], hence their extinction brings about ecosystem degradation. Several studies show that the overhunting of large-bodied seed-dispersing species in the Amazonian forests generates long-term biomass depletion and biodiversity decrease because of the disrupted plant-animal mutualistic interactions [27, 28, 77, 78]. Large-bodied, seed dispersals cannot be replaced by small ones [27, 44, 74], because the large seeds of neotropical trees physically cannot be consumed by smaller species. Tropical giant trees are disappearing partly because of the indirect effects of seed dispersal extinction and partly because of the direct effects of logging. As a result, giant trees are replaced by pioneers, which along with other factors are triggering a positive feedback loop and regime shifts in tropical forests [79]. Without large animals, seed dispersal distances reduce and ecosystem functions degrade [45]. However, it is very difficult to detect the degradation of species interactions, especially in a seemingly intact forest. Pérez-Méndez et al. [77] suggest that reduced 'seed dispersal distances' can be used as an early warning signal of the collapsing mutualistic plant-animal relationships.

Besides direct human effects, climate change also influences mutualistic relationships. For example, climate change causes irregularities in flowering time, which evokes failures in pollination [16, 80]. Pollination is a key ecosystem function, therefore pollinator collapses bring about the loss of an important ecosystem service [81]. Pollinators usually peform an abrupt and great biodiversity loss, which is explained by nestedness [73]. As a result of climate change, droughts are becoming more extreme in some regions. Heat susceptibility can be a weak point of mutualistic relationships. Kikuchi et al. [61] carried out an experiment and pointed out that heat-susceptible symbionts can drive symbiotic relationships into a collapse.

As we can see, mutualistic relationships are threatened by both direct and indirect interactions globally [73], which results in collapses and positive feedback loops worldwide. It is important to assess the tipping point of mutualistic communities to be able to estimate the resilience of ecosystems. When tipping points are crossed, systems give abrupt, nonlinear responses, which eventually lead to a quick collapse. Close to tipping points, ecosystems tend to slow down (usually referred to as 'critical slowing down'). Dakos and Bascompte [82] suggest that capturing this phenomenon by statistical signals can help to predict tipping points. They propose that increasing variance and autocorrelation are the best statistical indicators to assess the tipping points of mutualistic communities.

3.5.2. Negative species interactions

3.5.2.1. Competition

Positive interactions decrease competition and maintain biodiversity [83]. While positive species interactions promote co-existence, competition usually triggers an extinction. Biodiversity decrease caused by human perturbations can increase competitiveness [84]. Recent mass extinction is the result of direct and indirect human perturbations ,which act synergistically. As human pressure does not reduce and global temperature is increasing, ecosystems are

under the pressure of several factors, which suggests that positive interactions are facing a great decline globally. If this tendency continues, Earth will become a homogenized system dominated by mainly negative species interactions.

It is important to note that competition is not always something 'destructive' but also has an important role in maintaining communities, even in the light of climate change. For example, increasing temperature can be beneficial for some pathogens and parasites which extend their species ranges under more favorable climatic conditions. Having non-host competitors in a community provides a dilution effect and reduces the number of infected host-species at a local scale [85].

The literature suggests that positive interactions collapse first if species cannot switch to competition [76]. Considering competitors, strong competitors have more chance to survive in most cases and they collapse later during extinction. Matusick et al. [61] conducted a field investigation and aerial survey in a Mediterranean-type eucalypt forest in southwestern Australia. The canopy collapsed in patches in the observed forest as a response to extreme water stress. The less competitive mid-story tree species collapsed first and they did not show any signs of re-sprouting.

However, stronger competitors can also fail if they perform well only under very specific environmental circumstances. Yu et al. [86] observed the collapse of a key species in a Mongolian semi-arid grassland during a long-term disturbance prevention. The species adapted the best to a narrow environmental niche that outcompeted other species within a community. However, long-term environmental changes hit this species first. In this case, the dominant key species was replaced by less competitive subdominant species.

In ecosystems which maintain high species richness, invaders are less competitive and less abundant [87]. Fragmentation as a direct human effect increases competition which in turn leads to biodiversity loss [87]. Decreased biodiversity and resilience foster the spread of invaders, generalized pathogens which are often strong competitors.

3.5.2.2. Predation

Predators, especially marine top predators are declining globally [88]. Predators have an important controlling role in healthy ecosystems. They maintain biodiversity and stabilize landscape, especially keystone species. Re-introducing wolves in the Yellowstone National Park greatly increased the resilience and re-balanced the whole ecosystem [89]. Sharks are also keystone predators. Without their strong top-down control, marine ecosystems would alter and shift to a homogenized system [88]. Predators literally keep diseases away as they can reduce the effectiveness of pathogens. Khalil et al. [85] studied a vole population, its non-host competitors and its predator in northern Sweden. They highlighted that the presence of competitors and the predator decreased the number of infected vole individuals within the population.

As a result of human perturbation, top-down control of predators either decrease or increase. Both of them can lead to biodiversity decrease. An increased top-down control usually triggers the collapse of preys. Gilljam et al. [57] created a model to investigate if a specialized predator can survive if it switches to a new prey after losing the only prey. They concluded that shifting a diet does not always help predators to survive, especially if the prey cannot escape or it is rare or the consumer is an efficient predator. Strong human perturbation can cause an increased top-down and a bottom-up control simultaneously, which leads to a long-term decline in both preys and predators [90].

3.5.3. Keystone species

Keystone species and their functions are disappearing. They are hit by both direct and indirect effects. Overhunting, hybridization and climate change [34] accelerate their extinction. Keystone species have important functions (e.g. seed-dispersing and pollination) in ecosystems. They maintain biodiversity. Their collapse, especially if they have strong top-down control, leads to regime shifts and homogenization. Megaherbivores, carnivores [46] and pollinators have key functions. Keystone species are threatened by the synergistic effects of deterministic extinction factors. For example, K-selected species traits, nestedness. Jordano [74] suggests that the disappearance of key mutualistic interactions is an early warning signal of extinctions.

4. Conclusions

Extinctions driven by deterministic factors are present in the ecosystems globally as a result of direct and indirect human effects. Both terrestrial and marine habitats are overexploited under the ever-growing human pressure. Considering environmental factors, species living at low elevations, low and high latitudes and/or in suboptimal habitats (e.g. at the peripheries of historical species ranges) are under greater threat than rest of the world. At the species level, K-selected species, especially large-bodied species, specifically large herbivores, carnivores are becoming rare mainly due to extensive hunting. Species adapted to a narrow range of temperature will probably collapse quickly, especially if they are not mobile, because of rapid climatic change. Seasonal changes in precipitation and temperature affect several ecosystems all around the world. Both grasslands and forests are suffering experiencing biodiversity and/ or biomass loss and collapses [91]. Hidden failures, which are revealed only during significant changes in environmental conditions, will enhance collapses. Endemic, rare and weak dispersing species in regions with the largest and quickest climatic changes will probably die out. At the community level, positive species interactions are already melting because of the high number of species loss. Species interactions and functions are disappearing. The abundance of predators has decreased dramatically because of overhunting. Small mammal population cycles are collapsing as a result of climate change. Populations experiencing Allee effect will probably have a tendency to collapse under climate change. Common species are becoming rare, which decreases resilience and increases the vulnerability to collapse. Studies show that abundant species are one of the most persistent, except in case of specialization. The extinction of abundant species can be followed by co-extinction and rapid collapse. Literature suggests that many keystone species have deterministic species traits, which can lead ecosystems to a sudden collapse. Further consequences of human activities in the ecosystems are genetic changes, hybridization, invasion, pathogens, shorter food chains, altered trophic structure, disrupted species interactions and general homogenization.

Sudden collapses have a high priority in the literature. Frequently mentioned triggers of rapid collapses are, among others, nestedness in mutualistic communities, adaptation to a narrow range of environmental factor, keystone species with deterministic species traits. The extinction of abundant species can be followed by rapid and extensive collapse. It must be noted that deterministic factors tend to converge, which increases the probability of collapses. An ecosystem which is burdened with several deterministic extinction factors and belongs to a high-velocity region is under the greatest threat. That is why it is important to identify the early warning signals of collapses. Deterministic factors of extinctions and other factors which trigger sudden collapses are likely to be good indicators. Specialization at species level seems to be one of the most vulnerable extinction traits. According to the literature, carnivores, forest collapses. The collapse of mutualistic plant-animal relationships could be detected with reduced seed dispersal distances. Short-lived specialists respond to perturbation quickly, thus they can be considered as good early warning indicators, as well.

Mainly direct human effects dominate the first stage of recent mass extinction and it can be characterized by deterministic extinction factors which undermine the biodiversity and thus the resilience of ecosystems. In the next stage, which probably has already started, an increased number of stochastic events can be expected because of climate change. Stochastic events bring about the sudden collapses of the weakened ecosystems. Positive feedback loops both in climate (e.g. Arctic sea ice melting) and in ecosystems (e.g. forest collapses) are present. They are likely to indicate the onset of the middle stage of mass extinction, which may be irreversible [92].

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Non-Native Invasive Species as Ecosystem Service Providers

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Additional information is available at the end of the chapter

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Abstract

Non-native or alien species present a range of threats to native ecosystems and human well-being. Many such species have selective advantages over native species, such as faster growth and reproduction rates, higher ecological tolerance, or more effective dispersal mechanisms. However, these species are often inadvertently demonised without sufficient awareness of the ecological principles—disturbance, niche and competition—that contribute to species dominance in an ecosystem. Non-native species can provide services useful to humans, particularly in facilitating many contemporary needs of modern civilisation. In the present paper, the available records on the influence of non-native invasive species and the relationship between services lost and new services acquired due to their presence will be discussed.

Keywords: ecosystem service providers, new services, non-native invasive species

1. Introduction

An invasive alien species (IAS) is any species that is not native to that ecosystem and is capable of propagating itself, whose introduction causes or is likely to cause harm to the environment, economy, or human health [1]. IAS, as well as other species, are affected by climate changes. Predicted environmental changes, such as changing in precipitation and temperature, nutrient availability and soil disturbance, may enhance the susceptibility of habitats to invasion by non-native plant species [2]. Many studies have tried to predict future distributions of invasive species taking different approaches [2–4]. Since introduced species are more spread in disturbed ecosystems with reduced competition, it is crucial to consider the natural and

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human factors, such as economic activity, urbanisation, land use, overpopulation, migration, etc., associated with the occurrence of IAS [5]. In general, the invasion process is a complex series of events, reliant upon both the invasive capabilities of the species and the invasibility of the ecosystem [5]. Global environmental changes additionally complicate a continuous battle of governments and managers to detect and control invasive species [3].

The ecological influence of invasive alien species is manifested in different ways. Alien plant species inhabit the area of native species, alter the conditions in their habitat as well as the structure of their communities and interbreed with native species. Alien animal species can also compete for food and shelter with native species and transfer different diseases. Invasive species in general are highly adaptable to a new habitat, tolerate a wide range of climate



Figure 1. Negative effects of Ailanthus altissima on archaeological sites in Croatia.

conditions and usually occupy marginal and degraded habitats. They grow fast and have a high reproductive rate to ensure future survival. Although the economic cost of ecological damages caused by IAS is significant, their direct influence on human activities and sites is also relevant [3] (**Figure 1**). Some IAS also have a direct negative influence on human health, such as invasive allergens (e.g. *Ambrosia artemisiifolia* L.) [6], species that causes skin irritation [7], obstructions in freshwater traffic caused by water plants [8] or decreasing crop production caused by invasive weed species and diseases [9].

A fraction of established exotics become serious pests (e.g. the Eurasian zebra mussel *Dreissena polymorpha* Pallas), while others become well fitted and contribute to global and/or specific



Figure 2. Positive and negative effects of alien invasive species on the scale.

ecosystem services (e.g. the persimmon fruit *Diospyros kaki* L. in the Mediterranean area). For example, D. polymorpha has both numerous negative and positive effects on natural ecosystems. Negatives include the economic costs of damage due to clogged water pipes and the fouling of ship hulls and aquaculture cages. This mussel is a predator that significantly decreases plankton abundance as a result of filter feeding. Studies have shown that other filter feeding species may experience competition for resources in the presence of *D. polymorpha*. On the other hand, filtration as a feeding mode may increase water clarity and therefore improve habitat characteristics [10].

In rapidly changing environments, the effects of both non-native and native species may vary with time [11]. The truth is that most human and natural communities consist of both native and new species and new ecosystems are constantly being formed. Many eradication attempts have failed in the past [11], and we must accept novel ecosystems with dynamic living components. Moreover, sometimes, the eradication of one species will not result in the desired outcome because species interactions can be altered [12].

In this chapter, different aspects of the impacts of non-native invasive species are discussed in order to reopen the debate on new complex ecosystems that include both native and nonnative species (Figure 2) (Table 1).

Ecosystem services provided by invasive species				
Ecosystem service	Species	Origin	Reference	
Reducing environmental pollution and phytoremediation	Ailanthus altissima (Mill.) Swingle	China	[19, 89, 90]	
	Potamogeton illinoensis Morong	North America	[91, 92]	
	Artemisia vulgaris L.	Euroasia	[93, 94]	
Bioenergy	Panicum virgatum L.	Central and Eastern USA	[26–28]	
	Arundo donax L.	Euroasia	[95, 96]	
	Paulownia tomentosa (Thunb.) Steud.	China	[31, 38–40]	
	Jatropha curcas L.	Central America	[97–99]	
Art	Alliaria petiolata	Europe	[40]	
	(M. Bieb.) Cavara and Grande			
	Morus alba L.	North China	[100]	
	Lonicera maackii (rupr.) Maxim	Western Asia	[100]	
	Chamaedaphne calyculata (L.) Moench	Temperate and subarctic regions of the Northern Hemisphere	[100]	
	Mahonia bealei (Fortune) Carrière	China	[100]	
	Rosa multiflora	Eastern Asia	[100]	
	Thunb.			
	Hedera hibernica	Atlantic region	[44]	
	(G. Kirchn.) Bean			
Honey plants	Robinia pseudoacacia L.	North America	[52–54]	
	Impatiens glandulifera Royle	Pakistan to India	[60, 61]	

Ecosystem service	Species	Origin	Reference
Land reclamation and erosion control	Ailanthus altissima (Mill.) Swingle	China	[19, 63, 64]
	Casuarina equisetifolia L.	Malaysia, Vietnam, Australia and French Polynesia	[65, 69, 70]
	Crassostrea gigas Thunberg	Asia	[73, 74]
	Spathodea campanulata P. Beauv.	Africa	[101]
Fibre source	Ailanthus altissima (Mill.) Swingle	China	[18, 19]
	Spartina alterniflora Loisel	Atlantic coast of the South and North America	[102]
Medicinal use	Opuntia stricta (Haw.)	Caribbean region	[80]
	Ricinus communis L.	North-Eastern Africa	[80, 103]
	Datura stramonium L.	North America	[104, 80]
	Schinus molle L.	Peru	[80, 105, 106]
	Eriobotrya japónica (Thunb.)	China	[80, 107]
	Catharanthus roseus L.	Madagascar	[80, 108, 109]
	Ailanthus altissima (Mill.) Swingle	China	[83, 84, 86]
	Sambucus canadensis L.	North and Central America	[80]
	Melia azedarach L.	Australasia, Indomalaya	[80, 110–112]
	Argemone ochroleuca L.	Central America	[80]
Pharmaceutical use in agriculture	Ailanthus altissima (Mill.) Swingle	China	[9, 87]
	Chrysolina hyperici Forster	Europe and Asia	[113]
Ornamental	Paulownia tomentosa (Thunb.) Steud.	China	[31]
	Robinia pseudoacacia L.	North America	[48-50]
	Pueraria montana var. lobata (Willd.)	Asia	[114]

Ecosystem services provided by invasive species

Table 1. Overview of the most relevant ecosystem references provided by invasive species and related references.

2. The most common myths about non-native invasive species

There are several myths concerned with non-native invasive species.

The most widely spread myth is that **invasive species intend to dominate ecosystems and exclude others more than native species do.** The truth is that only a minority of species introduced to a habitat will spread on their own (naturalise) and only a small percentage of those will spread enough to be called invasive [13]. All species rely on certain conditions for survival; therefore, it is not simply the origin of a species that determines invasiveness, but the interaction between a species' traits and the community of which it is a part [14]. One such example is the domination of a forest by alien trees in Puerto Rico for the first three or four decades of the invasion. However, these forests are also a habitat in which native trees can begin to thrive again. This case will be further explained below in the chapter on land reclamation [15].

The second myth implies that **all native species are good and useful and all from outside are invasive.** This is not true for several reasons. First, many local species could and would become invasive when introduced to another habitat [13]. On the other hand, invasiveness is linked to the role of human activity in spreading species and changing the environment. Any species' distribution relies on certain conditions for survival which must be met. Many species that we nowadays consider local have been relocated from around the world, both accidentally and intentionally. A few hundred years ago, European explorers brought turkeys, potatoes, corn, tobacco and tomatoes from America to Europe. In turn, species such as horses, cows, sheep, goats, pigs, wheat, soy and grapes were transferred from Europe and the Middle East to America. Plants used in horticulture for ornamental purposes also play a major role in the global spread of species. From these examples, we can see that non-native species should not always be targeted as something bad and unwanted.

Another myth considers ecosystems to be static organisations. There is also a false idea that ecosystems were previously rich in diversity and the introduction of an alien species is responsible for any such losses. Ecosystems are dynamic and are subject to many human and natural disturbances, including fires, climatic changes, flooding, tropical cyclones, construction, tree logging, mining and pollution. As ecosystems change, older inhabitants may die, thus creating a new niche for new organisms to move in. Successions, both primary and secondary, are natural changes in ecological communities which have happened in the past and which will continue to occur in the present and future. However, currently, these changes may be occurring faster due to disturbances, and we can expect an increased dynamism in natural processes.

3. Complete role of non-native invasive species

Biological invasions must be considered within the larger set of environmental issues [3]. Knowing the complex ecology and different potential harms and benefits to society, in general invasive species, can teach us important lessons about how we use the planet [13]. Some authors [16] state that alien species as newcomers in urban areas are not a threat to urban ecosystems; in contrast, there is a chance for increasing biological diversity and thus achieving conservation objectives [12]. In the past half century, biological invasions together with other related environmental problems have become interesting study subjects because they provide natural experiments at temporal and spatial scales [3]. There has been an explosive development in the science of invasion in recent years, and many symposiums, articles and books have been prepared. However, there is still substantial controversy regarding the role of invasions in natural as well as human-shaped environments.

4. Ecosystem services provided by invasive species

Not all non-native species are invasive. There are numerous examples of introduced organisms that are not a threat but have been beneficial. There are many systems trying to list and categorise biological services to humans. One of the most used is the Millennium Ecosystem Assessment from 2005 [17]. Its objective is to assess the consequences of ecosystem change for human well-being and create a scientific basis for environmental conservation and sustainable use of those systems. According to this system, ecosystem services are divided into four categories: provisioning, regulating, cultural and supporting. Invasive species can provide one or several of these services and make itself beneficial to the ecosystem [18]. It is sometimes difficult to isolate different services as there is continual interaction between them.

4.1. Environmental conservation

Non-native species can be useful catalysts for ecosystem restoration and increase the structural heterogeneity or complexity of an area. Such species can also function as biocontrol agents by limiting the spread of agricultural pests [12].

Some IAS, such as *Ailanthus altissima* (Mill.) Swingle, tolerate poor, dry soils, support relatively high levels of air pollution and may be able to sequester some pollutants [19].

Moreover, IAS are a good solution in disturbed sites. They can adapt rapidly to the novel ecological conditions due to their ability to tolerate and adapt to a broad range of biotic and abiotic conditions [12].

4.2. Bioenergy

The world's energy needs are growing every day, and according to the US Energy Information Administration (EIA) projections, between 2015 and 2040, the world's energy consumption will grow by 28% [20]. Conventional fuels such as natural gas, coal and nuclear energy are limited and unsustainable in the long run. In the USA, the US renewable energy initiative announced a new impetus for the identification of biofuel crops as important sources of energy [21].

In October 2014, the European Council set a new framework for climate and energy in which the EU committed to having 27% of energy obtained from renewable sources by 2030. One of the main energy policy targets of the European Union is to increase renewable energy sources by enhancing the development of biofuel cropping systems in order to produce biomass for energy [22]. Biofuel crops, particularly using non-native species, must be introduced with an understanding of possible risks to the environment. The policies may conflict because traits deemed ideal in a bioenergy crop are also commonly found among invasive species.

Before cultivation of biofuel crops, it is necessary to ensure that such plants do not "escape" from plantations and become invasive. Therefore, biofuel crops should be subjected to a Weed Risk Assessment (WRA) before cultivation [23]. There are many WRA systems used around the world to predict the invasiveness of a plant species [24]. The Australian WRA system has been tested in several countries since its introduction in 1997 and is internationally recognised as one of the best systems to determine the risk of invasion [24, 25].

A great number of plant species have been proposed for biofuel cultivation in different countries. *Panicum virgatum* L., commonly known as switchgrass, is native to most of the central and eastern USA [26]. Since the 1990s, there has been growing interest in using this plant for

bioethanol in California and the Pacific Northwest. This species could become invasive if it is not properly managed or due to changes in local climate parameters [27]. *P. virgatum* is known for its ability to improve soil quality, sequester carbon and mitigate greenhouse gas emissions [28]. It grows in a wide range of suitable habitats, from 5 to 25°C mean annual air temperature and 300–1500 mm mean annual precipitation, and has relatively low nutrient requirements [26, 28]. Such attributes make this plant very suitable for cultivating in marginal and highly disturbed lands with poor soil. Deep fibrous root systems, slow decomposition rates and root biomass make *P. virgatum* a great agent for carbon sequestration [29, 30].

Paulownia tomentosa (Thunb.) Steud., known as princess tree, is another proposed biofuel crop. *P. tomentosa* is native to eastern and central China where it is used as an ornamental tree. It was introduced to the USA in the 1840s and soon become very invasive, covering disturbed natural areas, forests and river banks [31, 32]. The first record of *P. tomentosa* in the EU was in the 1980s; currently, this species appears less invasive. The EU Regulation on invasive species did not include *P. tomentosa* on the list of Invasive Alien Species of Union concern [33] although recent studies have shown significant spread. The species population has been recorded in urban areas, along railways, and near industrial sites in several European cities in Austria, SW Germany, Switzerland, Italy and SW Slovenia [34–36]. In Croatia, it has also been noticed at several sites near large cities, but currently does not show traits of invasiveness [37].

P. tomentosa became important as a biofuel crop because of its fast growth rate and high wood quantity generated in a short time period [38]. Timber biomass contains high cellulose and hemicellulose concentrations which are the main source of ethanol production [39]. Therefore, this species is highly preferred for the production of raw material for biofuel [40]. Studies have shown that the calorific value of *P. tomentosa* timber biomass is higher than that of coal (20.90 and 14.64 kJ/g, respectively) and thus more environmentally friendly [38, 41].

4.3. Turning invasive species into art

Invasive weeds can be used as material for art activities. Invasive removal programmes of some weeds result in plants that are usually dismissed as unwanted. However, if the act of weeding can be replaced into an act of harvesting, it changes the purpose and gives it a new meaning. Some plants have strong and flexible fibres that can be used for natural basketry [42]. Another attractive example of artistic approaches to invasive species is their use in art photography, in which they are used for making paper on which the photos of the shadows of rare or threatened plants are printed [43]. Some artists use invasive species [white mulberry, *Morus alba* L.; Irish ivy, *Hedera hibernica* (G. Kirchn.) Bean; multiflora rose, *Rosa multiflora* Thunb.; Amur honeysuckle, *Lonicera maackii* (Rupr.) Maxim.; leatherleaf mahonia, *Mahonia bealei* (Fortune) Carrière] for the production of pigments, ink, wood blocks, paper or other kinds of fibre [44].

Sustainable or science art is a great tool to communicate complex scientific concepts, such as the complex relationships between native and invasive species, to the wider public. In that sense, IAS also can be used for public education on possible negative impacts of the spread of non-native species. Thus, attractive collages of invasive species prepared from invasive plant materials are a great example of art with an environmental message [45].

4.4. Honey plants

Insect pollination is an important ecosystem service to agriculture and horticulture [46]. In the past decade in Europe, studies have shown a decrease in wild pollinator diversity due to the use of pesticides, habitat degradation and climate change [47]. To help solve this problem, some invasive alien plant species can serve as pollination providers.

Robinia pseudoacacia L. also known as black locust, is a species native to North America where it was used to control erosion, for reforestation, and as an ornamental tree. Nowadays it has been widely naturalised all across Europe, South Africa, Asia, Australia and New Zealand [48–50]. Currently, in Europe, this species is not listed on the list of Invasive Alien Species of Union Concern but is already considered invasive in most EU countries [50]. *R. pseudoacacia* is pioneer, fast-growing species that tolerates a diverse range of soil and climate conditions [51, 52]. The flowering period occurs in late spring with fragrant white to yellow flowers. These flowers contain fruit nectar which attracts bee pollinators, from which they then produce a honey [53]. *R. pseudoacacia* honey is one of the most highly prized types of honey for taste and flavour. The liquid honey is transparent, and the aroma is fruity, light and refreshing [54]. Because this honey contains a higher ratio of fructose than glucose sugar, it slowly crystallises and can remain as a liquid for several months. This helps bees to survive all winter [55].

Impatiens glandulifera Royle or Himalayan balsam is a perfect example of a species used as an ornamental plant that "escaped" from its native habitat [56]. Originally from North-West Pakistan to northern India, it has naturalised and invaded most countries of the EU, part of North America and New Zealand [57]. A large population has been recorded in the UK, Germany, Sweden, Austria and throughout the Baltic [56, 58, 59]. *I. glandulifera* is listed on the list of Invasive Alien Species of Union concern; within 18 months from the listing, the member states have an obligation to establish effective management measures [33]. It grows mainly in riparian zones, disturbed areas, river banks and forest edges. On the other hand, *I. glandulifera* flowers have the highest sugar nectar production per flower than any native European plant species, which attracts bumblebees, honeybees and moths [60, 61]. Flowering starts in August and thereby fills the gap between the end of the summer and the autumnal crop season [62]. In the future, this plant may serve as a significant seasonal pollen and nectar resource for honeybees and other insects.

4.5. Land reclamation

Nowadays we are increasingly faced with rapid land degradation due to anthropogenic intervention, pollution and pesticide use, deforestation, natural disasters and climate change. Land and soil reclamation is a slow process that often takes several years and greatly depends on conditions in the natural environment.

Some invasive species can be used to control erosion on slopes or along edges of traffic lanes, for reclamation of landfill sites and mine spoils, the establishment of protective forest shelterbelts and the conversion of disturbed land back to its original state [63, 64]. *A. altissima* is known for its ability to grow in barren, inhospitable and highly disturbed sites. It is also suitable for afforestation of the arid sites, as its root system contributes to soil drainage, slowing water run-off. Due to its resistant but soft and easy wood, it contributes to soil stabilisation because it generates lower pressure on the soil [19, 63]. *Casuarina equisetifolia* L. is an evergreen conifer-like tree native to Malaysia, Vietnam, Australia and French Polynesia. It was introduced in Florida, USA, in 1898 by the US Department of Agriculture plant explorer for coastal landscaping and erosion control [65]. Today it is one of the most invasive species in South Florida, self-seeding in disturbed areas [66]. *C. equisetifolia* colonises sandy habitats near shores and barrier islands, ruderal habitats and vacant lots and is extremely resistant to salt spray [67, 68]. Salt resistance and desiccation avoidance in countries such as Egypt, China and India turned out to be a benefit for the reforestation of coastlines [69, 70]. Thus, *C. equisetifolia* controls the movements of sand dunes, reduces wind erosion and finally starts the process of land reclamation. Florida is often affected by hurricanes and heavy storms which erode sands offshore. Native species usually are not able to colonise the beach as rapidly after such natural disasters [71]. In the future, invasive species such as *C. equisetifolia* can potentially help in this initial colonisation of new coastal plant communities.

Introduced species may in some occasions act like ecosystem engineers and help with the reestablishment of a new habitat [15]. *Crassostrea gigas* Thunberg or the Pacific oyster is an oyster native to Asia that settles on rocky coastlines in dense aggregations. Since the eighteenth century in the European Wadden Sea, oyster fisheries overexploited the native oyster *Ostrea edulis*. *C. gigas* was introduced in Europe and Australia for the aquaculture industry but today has become highly invasive in Scandinavian coastal waters, North America and Australia [72]. This oyster is known for its high rates of growth and reproduction. It acts as an ecosystem engineer by colonising un-vegetated mudflats, generating new solid reefs [73]. Consequently, new reefs are increasing densities of native invertebrate species relative to native oyster beds [74].

Recently in Puerto Rico, a large area of the native forest was destroyed by farming. In attempts to nurture back this degraded land, native trees do not have pioneering potential as soil and climate conditions are often poor and inhospitable. On the other hand, *Spathodea campanulata* P. Beauv., also known as the African tulip tree, has colonised the area instead [75]. *S. campanulata* is native to tropical forests in sub-Saharan Africa and was introduced in Puerto Rico in the 1920s. Soon it became the prevailing tree on abandoned farmlands, but studies have shown that *S. campanulata* forests provide new habitat to native species [76]. Several native forest fauna populations have recovered, such as the endangered frog *Peltophryne lemur* Cope and parrot *Amazona vittata* Boddaert [77, 78]. The leaf litter in *S. campanulata* forests can bring back forest invertebrates to deforested sites and other animals like bats and reptiles [76]. According to past experiences, these new forests remain dominated by alien trees for the first three or four decades. After 60–80 years of growth, Puerto Rican forests will become mixtures of both alien and native trees [15].

4.6. Fibre sources

Wood fibres are extracted from trees and used to make materials including paper. Different plant species or species' blends are best suited to provide the desirable sheet characteristics. Among different tree species, some non-native and also invasive species have the potential to be used as a fibre source. *Ailanthus altissima* has potential as a raw material for papermaking [19]. It produces paper with properties similar to those of *Eucalyptus globulus*, the most common species used for this purpose in temperate regions [18]. This tree species has several desirable properties (tolerance of poor soil, drought and pollution) for use in degraded environments and so can be used simultaneously for paper production and aid in conservation issues.

Paulownia tomentosa (Thunb.) Steud. is also thought to have potential for paper production, especially considering its extremely rapid growth rates [39].

4.7. Medicinal use

Plants used in herbal medicine have been discovered and used in traditional practices since historic times. For example, since 1968, in Africa, weeds and exotic plants have been used as medicines by specialist and non-specialist healers [79], a practice which has been conducted for centuries.

Some invasive alien plants are used by local inhabitants as a substitute for scarce indigenous plants. A study conducted in the Waterberg District investigated medicinal usage of several invasive plants in the South African Republic. It revealed that *Schinus molle L., Catharanthus roseus L., Datura stramonium L., Opuntia stricta* Haw., *Opuntia ficus-indica, Sambucus canadensis L., Ricinus communis L., Melia azedarach L., Argemone ochroleuca* and *Eriobotrya japónica* species are used for treatment of various diseases such as chest complaints, blood purification, asthma, hypertension and infertility. These plants inhabit poor land sites and are adaptable to different environments and climate conditions. Due to its high regenerative capacity, they are difficult to eradicate. Therefore, these invasive alien plants can be utilised by communities to combat various diseases in humans, thereby reducing pressure on heavily harvested indigenous plants [80].

Ailanthus altissima, a plant known for its useful ecosystem services, can also be used for medicinal purposes. A. altissima, known as the Tree of Heaven, is a deciduous wood native to central China that was introduced to Europe and America in the mid-eighteenth century. It was planted as an ornamental tree throughout cities because of its resistance to pollution, fast growth and ability to thrive in nutrient-poor conditions [81]. Due to its rapid growth and prolific seed production, it quickly escaped cultivation and soon became one of the most invasive species in the world [82]. Ailanthus altissima produces toxins in its roots, bark and leaves which inhibit the growth of other nearby plants. Chemical analysis revealed the presence of alkaloids, terpenoids and aliphatic bioactive compounds as major constituents of the plant [83]. From plant extracts, scientists isolated quassinoids, ailanthone and 6-aplha-tigloyloxychaparrinone, which have shown strong activity against strains of Plasmodium falciparum in vitro [84]. The major quassinoid constituent, ailanthone, has potent anti-amoebic activity against Entamoeba histolytica both in vitro and in vivo [85]. On the other hand, fresh plant parts can also have active medicinal usages, like fresh stem bark for the threat of diarrhoea and dysentery; root bark for heat ailments, epilepsy and asthma; fruits to threat ophthalmic diseases; and leaves used in lotions for seborrhoea and scabies treatments [86]. In Asia, extracts of A. altissima bark and fruits are used as an antimicrobial, anthelmintic and amoebicide [85].

4.8. Pharmaceutical use in agriculture

Some invasive plants have, due to their chemical composition, herbicidal properties. Their high invasive potential is determined by many properties, such as tolerance for a wide span of ecological conditions and pollution; high reproduction, growth and regeneration rates; and a production of secondary metabolites with herbicidal and insecticidal activities. For example, the main component responsible for a herbicidal effect in *A. altissima* is shown to be ailan-

thone, a chemical in the group of quassinoids [9] mainly present in the Simaroubaceae family. Several studies have shown that ailanthone is toxic for many plant species, including weeds, crops and trees [9, 87]. It is believed that, by producing and releasing ailanthone through its tissues largely through the roots, *A. altissima* has an allelopathic effect on nearby plant species, slowing their growth and outcompeting them [9]. Considering its high phytotoxicity, ailanthone shows potential as a possible future natural product herbicide, although its nonselectivity observed in multiple studies would present an obstacle if not resolved in some way. In addition, its rapid biodegradability could be a positive feature from the conservational aspect as it has a short, lasting effect in the environment but a negative one if possible applications as a herbicidal compound would be taken into account [88].

4.9. Ornamental

Many non-native species have been introduced for intentional ornamental and horticultural purposes (e.g. *Ailanthus altissima* and *Paulownia tomentosa*) [31, 48, 81]. Such species, due to their reproductive potential and regenerative capacity, soon increase in density. After some years of their uncontrolled spread, the cultivation loses importance; thus legal introduction and commerce are stopped.

5. Conclusion

IAS management must take into account all impacts of new species in a certain ecosystem. Natural resource management bodies should base their management plans on the real effects of a particular species in an ecosystem and not on traditionally repeated claims of non-selective negative effects of alien species. All species have some useful potential in an ecosystem, and many have easily defined services. Although some non-native species can cause serious problems that should be taken into account, a wider perspective on the role of each species in an ecosystem is needed. Their role is also mixed with new challenges arising from other environmental changes such as climate changes and human interventions. Land managers must focus more on the function of a species in an ecosystem than on their origin. As our understanding of biological invasions is growing, our capability to describe the ecological and economic consequences is more precise enabling the environmental managers to make objective decisions about IAS management.

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Conflict of interest

The authors declare no conflict of interest related to the present paper.

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Ecosystem Services Provided by Benthic Macroinvertebrate Assemblages in Marine Coastal Zones

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Additional information is available at the end of the chapter

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Abstract

Ecosystem services provided by marine inter- and sub-tidal benthic macroinvertebrate assemblages are often overlooked given their benthic location that is not evident to most observers. The macro-flora and macro-fauna that are the basis for these assemblages are impacted by changes in physical, chemical, and hydrological short and long-term alterations to their habitats. Globally, benthic macroinvertebrate assemblages can be categorized to examine ecosystems services provided by these highly productive coastal areas and the significance of the biodiversity of these assemblages should not be taken for granted. Ecosystem services provided can be categorized just as other global ecosystem services. The ecosystem services provided by marine coastal zones thus include Provisional, Supporting, Regulating, and Cultural Services. Significant environmental impacts to all of these types of ecosystem services have ensued from both natural and human events during the last decade. In addition to ongoing coastal human activity related threats to these areas, the disturbances to these assemblages immediately after a natural disaster event are currently a focus of research. Quantifying the impacts across the subunit of macroinvertebrate benthos is a focus of much current research. The current knowledge base and predicted recovery timeframes, in addition to the need for further investigation of long-term environmental societal factors are important globally.

Keywords: macroinvertebrate assemblages, coastal zone ecosystem services, benthic macroinvertebrates, environmental perturbation

1. Introduction

Natural changes over time or environmental perturbations as the result of geological changes such impact the ecosystem services provided by macroinvertebrate assemblages

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in the marine coastal zones. Events such as seismic activities (like tsunamis or earthquakes) or large scale meteorological events (hurricane/cyclone, mudslides, or volcanic events) can trigger toxic land run off, changes in the hydrology, alteration to the topography, and increased sedimentation that have an immediate and devastating negative impact on the coastal macro-benthos that inhabit near shore marine waters. Human development and related environmental changes can locally affect the larger biotic system to produce the same negative impacts.

Global coastal zones are the most productive and highly used regions and support fisheries and myriad other human activities and impacts after major perturbation events are only beginning to be a focus of attention by the scientific community from multi-disciplinary research [1, 2].

The loss of ecosystem services provided by the macro-flora and macro-fauna in the marine coastal zones are significant concerns. Natural and human impacts that are the basis for environmental changes often negatively impact the biota of near shore marine waters that provide them. The near shore biotas provide both the structural diversity and trophic base for these ecosystem services, and the macroinvertebrates communities that are a key part of these assemblages in many cases are the foundation for these services.

The macro-biota that provide the trophic base for macroinvertebrate assemblages may be intertidal or sub-tidal, tropic or temperate, and have either a direct source of primary producers or subsist on suspended or settled organic materials [3]. In depth Coastal and Marine Ecological Classification Standards (CMECS) [4] can be used to categorize biotopes based upon water column, geoform, substrate and biotic components in near-shore waters of the Atlantic Coasts [5, 6] but are also being applied globally outside of North American Atlantic waters [7].

Macroinvertebrate assemblages that make up the near shore biota occur across coastal habitat types, and assemblages in major biotopes can be categorized into five major categories based on a CMECS systems identified for US marine coastal zones. These major categories are: (1) vascular plant dominated (VP), (2) macroalgae/protista dominated (MA), (3) unconsolidated substrate dominated (US), (4) hard substrate dominated (HB), and (5) reef species dominated (RS) indicated in **Table 1**.

The overall components (CMECS) are organized into four perspectives that make it possible to record and define the attributes of marine coastal environmental units and biota within each ecosystem setting. The four identified components are: the Water Column Component (WC), the Geoform Component (GC), the Substrate Component (SC), and the Biotic Component (BC). Each component is a stand-alone construct that can be used on its own or in combination with other components or settings. For the purposes of ecosystem services provided by the macroinvertebrate biota here, only the BC and SC units are a focus. Given the proximity to shorelines and providing direct impacts on ecosystem services in general, the benthic and biotic assemblages are the most wide scale identifiable ecosystem units. **Table 2** identifies the major biotic groups that are dominated by macroinvertebrates and their contribution to global

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Habitat type	Intertidal/subtidal	Temperate/temporal	Nutrient base
Sea grass bed (VP)	Subtidal	Temperate to tropical	Primary productivity
Salt marsh (VP)	Intertidal	Temperate	Primary productivity
Tidal mangrove (VP)	Intertidal	Tropical	Primary productivity
Kelp forest (MA)	Subtidal	Temperate	Primary productivity
Calcareous algae bed (MA)	Intertidal	Tropical	Primary productivity
Mud flat (US)	Intertidal/subtidal	Temperate/tropical	Suspended organics and infauna
Sandy bottom (US)	Intertidal/subtidal	Temperate/tropical	Suspended organics and infauna
Cobble/boulder (HS)	Intertidal/subtidal	Temperate/tropical	Suspended organics and infauna and epifauna
Rocky shoreline (HS)	Intertidal	Temperate/tropical	Suspended organics and epifauna
Human created (HS)	Intertidal/subtidal	Temperate/tropical	Suspended organics and epifauna
Coral reef (RS)	Subtidal	Tropical	Primary productivity, suspended organics and infauna and epifauna

Table 1. Categories of habitats that support coastal marine benthic macroinvertebrate assemblages (and thus ecosystem services) and their location in the marine coastal zone, dominate climate zone, and nutrient base (after Rife [2]).

ecosystem services are indicated in **Table 3**. The units within the BC and SC are organized into traditional hierarchical frameworks, and thus lend themselves to being connected directly to research available for the coastal zone macroinvertebrate assemblages from a global perceptive. The two designations identified that best identify the category of these assemblages are the Biogeographic Setting (BS) and the Aquatic Setting (AS).

The BS identifies ecological units based on species aggregations and features influencing the distribution of organisms. Coastal and marine waters are organized into regional hierarchies composed of realms (largest), provinces and ecoregions (smallest). CMECS adopts the approach described in Marine Ecosystems of the World (MEOW) to characterize Biogeographic Settings occurring in the Estuarine System and in the Marine Near-shore and Marine Offshore Subsystems [31]. MEOW is worldwide in coverage and identifies five realms, eight provinces, and 24 ecoregions in U.S. waters.

The Aquatic Setting (AS) identified in the CMECS divides the coastal and marine environment into three Systems: Marine, Estuarine, and Lacustrine. These align with those described in the Classification of Wetlands and Deep-water Habitats in the United States. This classification is a key aid in the discussion of ecosystem services as they define the areas as a whole geographically and biologically. Secondary and tertiary layers of the Aquatic Setting describe Subsystems (e.g., Near-shore, Offshore, and Oceanic within the Marine System) and Tidal Zones within the Estuarine System and Marine Near-shore Subsystem. The subsystems additionally aid in the identification of key macro-flora and macro-faunal components allowing ecosystem services to be examined.

Habitat type and global location	Geo-morphological features	Hydrological features Photic quality modifier (PQM) and energy intensity modifier (EIM)	Climatic environmental factors Temperature range modifier (TRM) and salinity regime modifier (SRM)	Geographical aspects and key factors
Vascular plant dominated habitat (VP) subset: sea grass bed Globally VP assemblages are located in Shallow salty and brackish waters in many parts of the world, from the tropics to the Arctic Circle	Tidal aquatic vegetation beds dominated by any number of seagrass or eelgrass species	PQM—photic or seasonally photic EMI—moderate current energy	TRM—cold to hot SRM—mesohaline, lower polyhaline, upper polyhaline, euhaline	Lacustrine, Estuarine, and/or Marine Temperate to Tropical with occasional polar littoral zones
Vascular plant dominated habitat (VP) subset: tidal salt marsh	Emergent tidal marsh communities dominated by emergent, halophytic, herbaceous vegetation and aquatic brackish marshes	PQM—photic or seasonally photic EIM—moderate current energy	TRM—cold to hot SRM—oligohaline, Mesohaline, lower polyhaline, upper polyhaline, euhaline, hyperhaline	Lacustrine and Estuarine coastal zones Temperate to tropical coastal zones
Vascular plant dominated habitat (VP) subset: mangels	Tidally influenced shore zone dominated by true halophytic mangroves (and associates)	PQM—photic or seasonally photic EIM—moderate current energy	TRM—warm to very warm SRM—oligohaline, mesohaline, lower polyhaline, upper polyhaline, euhaline, hyperhaline	Estuarine, and/or marine Tropical or subtropical shoreline zone
Macroalgae dominated habitat (MA) Globally MA assemblages are located at all depths within the photic zone, on diverse substrates, and across a range of energy and water chemistry regimes	Aquatic beds dominated by macroalgae attached to the substrate, such as kelp, intertidal fucoids, and calcareous algae	PQM—photic and seasonally photic EMI—very low current energy to moderate current energy	TRM—very cold to hot SRM—oligohaline, mesohaline, lower polyhaline, upper polyhaline, euhaline	Lacustrine, Estuarine and/or marine Circumglobal subtidal
Unconsolidated sediment dominated habitat (US) Globally US assemblages are located in the subtidal zones of the nearshore and offshore marine subsystems	Fine unconsolidated substrates (sand, mud) and that are dominated in percent cover or in estimated biomass by infauna, sessile epifauna and other macroinvertebrates	PQM—aphotic EIM—very low current to moderate current energy	TRM—very cold to hot SRM—oligohaline, mesohaline, lower polyhaline, upper polyhaline, euhaline hyperhaline	Lacustrine, Estuarine, and/or marine Circumglobal subtidal

Habitat type and global location	Geo-morphological features	Hydrological features	Climatic environmental	Geographical aspects and key
		Photic quality modifier (PQM) and energy intensity modifier (EIM)	Temperature range modifier (TRM) and salinity regime modifier (SRM)	14(1015
Hard substrate	Nearshore rocky reefs that	PQM-aphotic	TRM-very cold to	Lacustrine,
dominated (HB)	have rich algal, invertebrate,	Dysphotic	very hot	Estuarine, and/or
Global HB assemblages are located in all depths	mammal communities	Photic and seasonally photic	SRM—oligohaline, mesohaline, lower polyhaline, upper polyhaline, euhaline, hyperhaline	Circumglobal
substrate occur on the ocean bottom including boulder and cobble, and any areas where hard, persistent material has been placed either purposely or accidentally by humans		EIM—very low current energy high current energy		
Coral reef dominated habitat (CS)	Shallow/mesophotic coral reef biota	PQM-photic	TRM—warm to very warm	Marine
Globally CS assemblages are located in shallow tropical and subtropical area in the photic zone of the Western Pacific, Indian, and Atlantic Oceans	Areas with ample light that are dominated by hermatypic (reef-building) hard corals or nonhermatypic reef colonizers	EIM — very low current energy to low current energy (occasionally moderate if shallow reef)	SRM—euhaline	subtropical and subtropical subtidal in optimal depth for light penetration

Table 2. Macroinvertebrate assemblage with CMECS descriptors for geo-morphological, hydrological, climatic, and geographical aspects of the global habitat (after Rife [2] and CMECS [4]).

Category of macrobenthic community	Examples of sub- units identified by CMECS	Ecosystem services provided	Direct/ indirect	Supporting literature	
Vascular Plant	Seagrass bed	Provisioning services	Direct	[8-16]	
dominated (VP)	Tidal mangrove	Provides building materials and indii Areas for fisheries and associated industries			
(vr)	Brackish				
	Tidal aquatic vegetation	Supporting services			
		Soil formation, primary productivity, and nutrient cycling			
		Nursery areas for the young stages of fishes and invertebrates			
		Regulating services			
		Capturing and filtering sediments and organic			

wastes in transit from inland regions to the ocean

Category of macrobenthic community	Examples of sub- units identified by CMECS	Ecosystem services provided	Direct/ indirect	Supporting literature
Macro-algae	Kelp forest	Provisioning services	Indirect	[17]
dominated (MA)	Calcareous algal bed Canopy-forming	Pharmaceutical compounds derived from marine algae and invertebrates		
	algal bed	Regulating services		
	Coralline/crustose algal bed	Capturing and filtering sediments and organic wastes in transit from inland regions to the ocean		
Unconsolidated	Tunneling megafauna	Provisioning services	Indirect	[18]
dominated	Burrowing anemones Bivalve bed	Pharmaceutical compounds derived from marine algae and invertebrates		
(03)	Other non-molluscan	Regulating services		
	invertebrate bed	Capturing and filtering sediments and organic wastes in transit from inland regions to the ocean		
		Sediment stabilization		
		Primary production of benthic algae, high levels of secondary production and great diversity in benthic animals, provide forage for crabs, finfish and shorebirds		
Hard substrate	Mineral/wood boring fauna Diverse colonizers	Provisioning services	Indirect	[19–21]
dominated (HS)		Pharmaceutical compounds derived from marine algae and invertebrates		
	Attached tube-	Regulating services		
	building fauna Mobile crustaceans and gastropods on hard or mixed substrates Sessile/attached molluscs and/ or non-molluscan	Capturing and filtering sediments and organic wastes in transit from inland regions to the ocean		
		Hard substrate for attached animals, provides finfish, crustacean and shorebird forage		
		Filters suspended material from the water for improved water quality.		
		Sediment Stabilization erosion control via wave reduction.		
	communites	High levels of secondary production and great diversity in benthic animals, forage for crabs, finfish and shorebirds		
Reef species	Branching/columnar/	Provisioning services	Direct	[22–30]
dominated	foliose/plate/table	Provides building materials	and indiract	
(10)	Encrusting coral reef	Fisheries and associated industries	maneet	
	Massive coral reef	Pharmaceutical compounds derived from marine algae and invertebrates		
	Shallow molluscan	Supporting services		
	Mesophotic reef	Soil formation, photosynthesis and nutrient cycling		
	Mesophotic reef	Cultural services		
		Scuba diving and other nature-based tourism		

Table 3. Marine coastal macro-biotic assemblages that comprise the benthic component for CMECS standards and ecosystems services provided [2, 4, 5].

The sub-ecosystems of the biotic and substrate biotopes are described in terms of macrobiota for the identified biotopes, with the majority being named by the dominant macroinvertebrate faunal species. Identifying key components of these assemblages is facilitated by CMECS descriptors that allow for comparison across global biotic assemblages [4].

The biogeographic and aquatic setting for these coastal habitats, as defined this framework, is crucial for continued global comparisons of macroinvertebrate assemblages. Defining these lesser known assemblages in this way will allow discussion of how to manage these areas in terms of economic valuation, prediction of recovery times, and quantification of losses resulting from an environmentally perturbing event based on the coastal marine biotopes that are impacted by human or natural environmental perturbations.

2. Ecosystem services provided

Ecosystem services provided by coastal macroinvertebrates assemblages include both direct and indirect benefits (**Table 3**). Marine ecosystem services provided by these groups of macrofauna and flora that directly provide benefit encompass the services that provide food, medicine, recreation, support of fisheries, and storm protection. Other ecosystem services are less tangible, and so more difficult to documents, such as the habitat's role in absorbing carbon from the atmosphere—a positive effect on our global climate. In addition to the economic supports coastal areas provide, human attitudes, beliefs, behaviors, customs, and traditions are often associated with the surrounding nature and environmental quality. These cultural ecosystem services are often neglected but are a significant feature of the services that could be lost if the biodiversity of these assemblages becomes threatened.

Ecosystem services provided by marine coastal zones are classified by four categories (as they are for most identified ecosystem services). The four categories identified are Provisional, Supporting, Regulating, and Cultural Services. Provisioning services include food, water, and products such as building materials from mangrove and coral reef, and pharmaceutical compounds derived from marine algae and invertebrates. Supporting services include soil formation, primary productivity, and nutrient cycling; coastal habitats such as seagrass beds and mangroves are important nursery areas for the young stages of fishes and invertebrates that support coastal communities and commercial and recreational fisheries. Regulating services include regulation of climate; natural hazards such as floods, disease, wastes, and water quality, coastal wetlands play an important role in water quality regulation by capturing and filtering sediments and organic wastes in transit from inland regions to the ocean. On a global scale, fixation of atmospheric carbon by oceanic algae and its eventual deposition in deep water represents an important part of the global carbon cycle and thus influences climate trends. Cultural services include recreational, esthetic, and spiritual benefits derived from nature. Coastal tourism is the fastest-growing sector of the global tourism industry [9], and is a major part of the economies of many small island-developing nations. Moreover, the cultures and traditions of many coastal peoples are intimately tied to the marine ecosystems on which they depend.

Coastal marine ecosystem services are also provided directly, through human use or experience of the service or indirectly, via impacts of supporting and regulating services on other services and environments. Cultural ecosystems services of a variety provided by macroinvertebrate communities near the coasts include those tied to the culture and traditions of coastal peoples in many developing nations by supporting local small scale fisheries, recreational and esthetic services across the globe as a source of natural interest and exploration for people of all ages, scientific and sociological endeavors, and ecotourism opportunities like scuba diving and sport fishing.

Macroinvertebrate assemblages form the basis for the majority of the coastal marine services as illustrated by the biotopes that are defined by the species that characterize the biotic components.

Changes in the local coastal marine environments following perturbations are myriad and occur in both the short term and long term spatial and temporal realms [10–16]. Changes to these environments, either by a natural or human induced physical change can impact the resident macro-fauna assemblages and the ecosystem services they provide in a numerous of ways. The majority of the threats identified to these communities is heightened after an environmentally perturbing event that is of a large scale, and as documented are altered long-term for certain near shore biotopes (see **Table 3**).

Delineating the impacts of large scale events on coastal marine benthic invertebrate assemblages are identified in literature from natural hazards such as hurricane and earthquake events [17–19].

To examine the global effects that result in terms of the macro-benthic assemblages, one needs to characterize each major habitat type and synthesize current findings with related environmental disturbance known impacts. Based on the CMECS, major macroinvertebrate assemblages can be categorized as follows to examine the ecosystem services provided and possible impacts after a major change (see **Table 1**).

2.1. Vascular plant dominated habitat (VP)

Three subsets make up the VP biota (see **Table 4**). Sea grass beds, tidal marshes, and mangels globally provide significant ecosystem services but also experience the greatest threats from human activity. Seagrass beds, are a lesser known area for many, given their submergence and often hidden location for most observers. Rooted flowering aquatic grasses dominate this assemblage of biota. These sea grasses are significant refugia for the macroinvertebrate assemblages that depend on their bioprocessed and are dominated by turtle grass species in the tropical zones (Thalassia spp., Halodule spp., Syringodium spp., etc.), and Posidonia spp., Ruppia spp., and Zostera spp. in the more temperate waters [20]. These habitats stabilize and protect the shorelines, but additionally support a diverse array of macroinvertebrates. These various community members in tern support the higher order consumers and thus, support fisheries in both adult and juvenile stages. A significant feature of these (VP) areas is that they provide a complex structural habitat that serves as a nursery area for many commercially important species that might not depend on these areas beyond the nursery stages. An often overlooked global ecosystem service provided by these VP assemblages are the carbon stored in sediments from these coastal ecosystems and is known as "blue carbon" because it is stored in the marine environs.

Vascular plant dominated habitat (VP)	Important species of the assemblage	Assemblage biotic structure	Key biodiversity aspects of assemblage
CMECS biotic group: sea grass bed	The approximately 72 species of sea grasses are commonly divided into four main groups: Zosteraceae, Hydrocharitaceae, Posidoniaceae and Cymodoceaceae. The major sea grasses include Cymocedea sp., Halodule sp., Thalassia sp., Halophilla sp., Vallisnera sp., Ruppia sp., Phyllospadix sp., and Zostera sp.	Seagrass beds are complex structural habitats that provide refuge and foraging opportunities for abundant and diverse faunal communities. Slow moving mollusks, larger crustaceans, sponges and echinoderms are all commonly found associated with these areas	There are six seagrass bioregions according to Short et al. [2, 32] which is the current standard used by the international seagrass research community. These six bioregions are Temperate North Atlantic (I), Tropical Atlantic (II), Mediterranean (III), Temperate North Pacific (IV), Tropical Indo-Pacific (V), and Temperate Southern Ocean (VI), and are based on assemblages of taxonomic groups of seagrasses in temperate and tropical areas and the physical separation of the world's oceans
CMECS biotic subclass: emergent tidal marsh and biotic group: brackish marsh	Salt bushes and grasses are the dominant plants, with Sparina sp., Juncus sp. and Salicornia sp. common in the plant Communities. The plants are dominated by emergent, halophytic, herbaceous vegetation (with occasional woody forbs or shrubs) along low-wave-energy, intertidal areas of estuaries and rivers. Also brackish marshes dominated by species with a wide range of salinity tolerance	Fish and shrimp come into salt marshes looking for food or for a place to lay their eggs. Larger decapods and oysters are also key species that depend on the tidal marshes	Marine and freshwater species occur in the intertidal zone of coastal estuaries. These areas and are usually intermixed with intertidal mudflats that are rich with invertebrates and seaweeds. These transitional zones are key nursery areas for many commercial species
CMECS biotic group: tidal mangrove forest and tidal mangrove shrubland biotic group. Mangrove forests	Mangroves are not a taxonomic group but identified by their salt tolerance. Several tree and shrub species are the structural basis for these tropical vegetation that supports many diverse invertebrate species as juveniles	The list of common species supported by mangels is line and includes: barnacles, oysters, mussels, sponges, worms, snails and small fish live around the roots. Mangroves water contain crabs, jellyfish and are a nursery to many juvenile fish	Tidally influenced, dense, tropical or subtropical forest with a shore zone dominated by true mangroves (and associates) that generally are 6 m or taller. Dwarf shrub and short mangroves are placed in the tidal mangrove shrubland biotic group. Mangrove forests occur along the sheltered coasts of tropical latitudes of the Earth, and are commonly found on the intertidal mud flats along the shores of estuaries, usually in the region between the salt marshes and seagrass beds and may extend inland along river courses where tidal amplitude is high. Also, mangrove cays may occur within the lagoon complex of barrier reefs

This VP category of biota include these groups—biotic group: seagrass bed—tidal aquatic vegetation beds dominated by any number of seagrass or eelgrass species; biotic subclass: emergent tidal marsh—communities dominated by emergent, halophytic, herbaceous vegetation; and biotic group: tidal mangrove forest—tidally influenced, dense, tropical or subtropical forest with a shore zone dominated by true mangroves (and associates) that generally are 6 m or taller [4].

Table 4. Vascular plant dominated habitat (VP) CMECS definition and important species and dominancy relations in these ecosystems.

Perturbations to sea grass beads, and impacts of large-scale weather events (such as tsunamis for example) have indicated that seagrass beds are resilient to perturbations. The findings regarding the macroinvertebrate diversity of major taxonomic groups is less positive as it is most likely that the biota that are part of these VP areas are tied to density of vegetation [33, 34].

Another category of VP are the salt marshes of the temperate and tropic areas. These prominent vegetated coastal habitats and their proximal coastal areas are well known to of high value as a nursery grounds. Their value as land run off filters is significant. Lesser recognized for the importance of these areas is the high diversity of macroinvertebrate species. As a nursery grounds these areas are significant to both commercial and sport fishing activities. Perturbing events that shift the sediments and inundate the area with fresher water draining of streams or highly saline off shore water, can load toxic land run off, scour vegetative areas, and/or deposit debris that compromises the health of these habitats and thus the macroinvertebrate assemblages [22]. The transitional nature of these areas between land and ocean make them particularly subject to physical changes such as those often seen by development.

Mangels, also known as mangrove habitats, are a group of coastal tropical halophytes that provide structural complexity and protect the shoreline by stabilizing sediments. Because the halophytes that form the basis of these assemblages are from various taxonomic groups, different environmental factors (beyond salinity) can impact their viability. Development of these areas often occurs given the tropical climate and attractiveness for tourism, the development of these shorelines destroys these areas. Tsunami impacts have been examined for some habitats, and it appears mangroves may never fully recover from events that result in the extirpation of these halophytes [23, 35]. Loss of the mangroves mean loss of the ecosystem services they provide in addition to losing the associated macroinvertebrate fauna. As with the salt marshes of the temperate zones, mangels are a significant nursery for many fish, both sport and commercially important fisheries can be impacted by their loss.

2.2. Macroalgae dominated habitat (MA)

Table 5 offers an overview of the macroalgae dominated habitat. Kelp forests are temperate near-shore habitats that support diverse macro-invertebrate assemblages. There are other MA assemblages but the kelp forest are the most dominant example from a global perspective and also provide significant ecosystems services. Both the primary productivity and the structural complexity of their fronds are key factors in support of the whole ecosystem. Kelp, in particular the brown kelps, are well adapted to be resilient against strong currents, they are tolerant to storm surges. Interestingly, they appear to be prone to concentration radioactive material, after the tsunami of the Indian Ocean in 2010 radioactive were found in the kelp off the California coast in the weeks after the tsunami event in Japan. The materials did not remain in the kelp for a long period of time. This suggests they are able to be expelled into the biotope, but as a result presumably to be taken up by other organisms [24, 25].

2.3. Unconsolidated sediment dominated habitat (US)

Perhaps one of the most overlooked macro-faunal assemblages are mud flats and other fine sediment habitats (**Table 6**). Although not at all evident to most, these areas support infaunal

Macroalgae dominated habitat (MA)	Important species of the assemblage	Assemblage biotic structure	Key biodiversity aspects of assemblage
CMECS biotic subclass: benthic macroalgae	Aquatic beds dominated by macroalgae attached to the substrate, such as kelp (<i>Fucus</i> sp., <i>Macrocystis</i> sp.), intertidal fucoids, and other calcareous algae	Kelp forests provide both primary productivity and a structural base for many species. The holdfasts as well as the surface mats of kelp fronds support thousands of invertebrate individuals, including polychaetes, amphipods, decapods, and ophiuroids. Larger vertebrates frequent these areas	Many macroalgal types and communities have low temporal persistence and can bloom and die-back within short periods. This aspect of macroalgae impact the nature of the ecosystem services at an given time

Macroalgal communities can exist at all depths within the photic zone, on diverse substrates, and across a range of energy and water chemistry regimes [4].

Table 5. MA biotic subclass: benthic macroalgae – aquatic beds dominated by macroalgae attached to the substrate, such as kelp, intertidal fucoids, and calcareous algae.

Unconsolidated sediment dominated habitat (US)	Important species of the assemblage	Assemblage biotic structure	Key biodiversity aspects of assemblage
CMECS soft sediment fauna	Often dominated in percent cover or in estimated biomass by infauna, sessile epifauna, mobile epifauna, mobile fauna that create semi- permanent burrows as homes, or by structures or evidence associated with these fauna	Species tunnel freely within the sediment or embed themselves wholly or partially in the sediment (e.g., tilefish burrows, lobster burrows). Other organisms such as crustaceans, echinoderms and mollusks may be locally abundant	Subtidal soft bottom habitats are diverse based on distinct organism assemblages that are influenced by differences in substrate type (sand vs. mud), organic content and bottom depth. Most of these fauna possess specialized organs for burrowing, digging, embedding, tube-building, anchoring, or locomotory activities in soft substrates

Table 6. Biotic class: soft sediment fauna—areas that are characterized by fine unconsolidated substrates (sand, mud) and that are dominated in percent cover or in estimated biomass by infauna, sessile epifauna, mobile epifauna, mobile fauna that create semi-permanent burrows as homes, or by structures or evidence associated with these fauna [4].

macrobenthos that provides key services. These small and relatively overlooked groups of invertebrates turn the sediments and process organics. These fine soils and the high degree of organics and detritus associated can be harmed by strong surges and deposited elsewhere smothering other areas with hypoxic sludge [26]. These US areas are frequently dredged to replenish shorelines and considered to be unattractive. Overlooking the services they provide would be an error.

Sand habitats are teeming with diversity despite the common assumption that they do not, the macro-invertebrates present in these tidal zones show resilience to storm events and recover quickly after a Tsunami event [27]. The recovery of the macro-invertebrates in these assemblages can be quick if recruitment areas adjacent are not impacted. The planktonic nature of the larvae of most invertebrates living in these areas allows for quick recruitment and recovery after a large environmental change like the shifting of sediments from a beach restoration or large-scale weather event.

2.4. Hard substrate dominated biotopes (HB)

This category includes artificial reefs (human places). Macroinvertebrates that colonize hard substrates are generally in competition for space to attach to in the larval stages (**Table 7**). After a large weather event with strong currents or storm surges, boulders and cobble are scattered, and rocky shores could be scoured by these water movements or also by thermal pollution. New human created habitat can also occur in the form of unintentional deposition of sediments of large size and intentional artificial reef type habitat (many recreational charter captains create and maintain their own reefs by submerging solid structures as a base such as old chicken coops or shopping carts to create a reef that they can locate to support their businesses). Little is known about the specific effects on these types of macroinvertebrate assemblages that populate the HB areas. The high larval settling needs and competition for hard places for larvae to settle, these coastal assemblages may be the first to recover after a storm event [28, 29].

2.5. Coral reef dominated habitat (CS)

The highest biodiversity in the list of coastal macro-invertebrate assemblages is not surprising to be the coral reefs and related invertebrate reef macroinvertebrate assemblages (**Table 8**). As identified by CMECS "The Shallow/Mesophotic Coral Reef Biota are largely based on the growth form of the dominant corals that (a) reflect differences in environmental conditions and (b) provide varied habitat circumstances (such as increased cover) for associated fish and invertebrate species. The same coral species can present different growth forms under different environmental circumstances. For example, *Acropora* sp. can have both branching and table growth forms, depending on the environment. To reflect the differences in the physical and biological environments, the same species may be used to define communities in more than one coral group the interaction between ecological processes responsible for the growth of

Hard substrate dominated (HB)	Important species of the assemblage	Assemblage biotic structure	Key biodiversity aspects of assemblage
CMECS biotic subclass: attached fauna/ anthropogenic origin hard substrates	Dominated by fauna which maintain contact with the substrate surface, including firmly attached, crawling, resting, interstitial, or clinging fauna. Fauna may be found on, between, or under rocks or other hard substrates or substrate mixes	Depending on water depth, light penetration, wave energy, and other physical and biological processes, algae and macroalgae can provide extensive or sporadic cover and food for other species in the nearshore subsystem. Many attached fauna are suspension feeders and feed from the water column. Other attached fauna are benthic feeders, including herbivores, predators, detritivores, deposit feeders, and omnivores	Rocky subtidal habitat includes all hard substrate areas of the ocean bottom. Anthropogenic reefs include any areas where hard, persistent material has been placed either purposely or accidentally by humans. Examples include rock jetties at the entrance to many bays, shipwrecks, anchoring systems for renewable energy projects, and unburied portions of underwater cables or pipelines

Table 7. Biotic subclass: attached fauna – areas characterized by rock substrates, gravel substrates, other hard substrates, or mixed substrates that are dominated by fauna which maintain contact with the substrate surface, including firmly attached, crawling, resting, interstitial, or clinging fauna [4].

Coral reef dominated habitat (CS)	Important species of the assemblage	Assemblage biotic structure	Key biodiversity aspects of assemblage
CMECS biotic subclass: shallow/mesophotic coral reef biota	Stony (scleractinian) corals and crustose coralline red algae	Macroinvertebrates from all taxonomic groups comprise the assemblages	Nearly 25% of all known marine species are associated with coral reefs the rich biodiversity covers most taxonomic groups and has many complex interactions with adjacent fauna as well

In order to be classified as reef biota, colonizing organisms must be judged to be sufficiently abundant to construct identifiable biogenic substrates. When not present in densities sufficient to construct reef substrate [4].

Table 8. Biotic class: reef biota areas dominated by reef-building fauna, including living corals, mollusks, polychaetes or glass sponges.

coral and other carbonate producers and physical processes such as waves and currents that modulate ecological processes and redistribute carbonate material within reef systems." [4]. These areas are well known as the most diverse and likely also provide the most significant oceanic ecosystems services as a result. These areas additionally provide the most varied in terms of type of services as they provide more esthetic and ecotourism support to a greater degree than any other macroinvertebrate assemblages. Yet these significant areas are also some of the most delicate and threatened habitats. Coral bleaching can occur as the result of numerous stressors and large-scale weather events can devastate large regions from both abiotic and biotic stressors [27, 30, 36, 37]. Of all the marine coastal biotopes, literature suggests it is the coral dependent fauna that can be devastated from large-scale changes such as those that occur after a tsunami event, but more investigation is needed to determine if recovery is possible.

Although much more study is needed to determine specific impacts in local areas, globally speaking, macroinvertebrate assemblages do recover after severe natural environmental perturbing events in general, but do so differentially. Anthropogenic perturbations that destroy the physical support of the biotic assemblages are less likely to recover, generally due to development of the shoreline and drainage of these areas. More work is needed to verify the longer term impacts that natural events have from habitat perturbation to ecosystem service losses, anthropogenic impacts have yet to be documented to a great degree from a global perspective. Human impacts are more often permanent, so prevention of further threats are the main reason more knowledge and awareness of the ecosystem services is crucial [32, 38–49].

In general, vascular plant dominated biotopes (VP) seem resilient (except for mangroves) after an environmentally perturbing events with recovery well underway in one annual cycle. Macroalgae/protista dominated biotopes (MA) may be impacted even at great distance from source of perturbations or related contamination little is known about the effects on the fauna they support. Both unconsolidated substrate dominated (US) and hard substrate dominated biotopes (HB) are noted to have recovery times close to that identified for sea grass areas. Reef species dominated areas (CS) are subject to many environmental stressors, the physical and chemical changes that result from an environmental perturbing event impact the corals species negatively but the fauna that rely on the physical structural components may shift in diversity but do persist. Defining recovery in terms of the macro invertebrate assemblage would seem

to suggest that recovery occurs relatively quickly, with mangroves being the exception as it is suggested that they may never fully recover once the integrity of the habitat is destroyed.

There are many environmentally perturbing threats both natural and human that can limit the ecosystem services provided by marine coastal zone assemblages (**Table 9**). There are new research areas that focus on different regions and habitats, and more large scale methods are beginning to allow a picture of ecosystem services and the complex ways these macroinvertebrate assemblages provide them [21, 42, 44, 46–51].

Identified threats to coastal marine macro-invertebrate communities	Mechanisms of impact	Potentially heightened by an environmentally perturbing event
Toxic substances	Organochlorine compounds, heavy metals, organic tin compounds, organophosphates, polycyclic aromatic hydrocarbons, synthetic detergents, and surfactants	Yes—reach the oceans either directly (because the pollutants originate in coastal area), or indirectly through river systems or the atmosphere. In some cases they are released as a result of ocean dumping
Organic pollution	Excessive input of organic water and/or nutrients, or to a deterioration in the natural cleansing power	Yes—more pronounced in bays and other enclosed or semi-enclosed waters
Introduction of debris	Either direct dumping or indirect introduction of waste materials	Yes—more significant adjacent to urban areas
Nutrient depletion	Over development and urbanization which results in depletion of key nutrients and the indirect impact to decreased productivity and/or fertility	Yes—often as the result of loading and blooms and die offs as the result of agriculture or development
Radioactive contamination	Above-ground nuclear tests conducted in years past constitute the principal source of such pollutants. Nuclear-powered ships, discharges by land-based nuclear facilities, and ocean dumping (including illegal dumping) are major sources of marine radioactive contamination	Yes—particularly in the case of facilities begin breached by earthquake activity
Depletion of resources vital to preservation	Land reclamation operations, embankment reinforcement projects, and other physical alterations to shallow-water environments have directly as well as indirectly contributed to the loss of seaweed beds, tidal marshes, coral reefs, mangrove forests	Yes—marine nutrient imbalances as well as degeneration of the natural resilience or cleansing ability of marine ecosystems
Public awareness	Lack of understanding of the aquatic habitats and biotic interaction and their role is goods and services such as assuring human populations opportunities for closer contact with the natural world	Yes—but perhaps in a positive manner if the event increases awareness and understanding
Biotic disruptions	Many non-native wildlife species have penetrated marine ecosystems simply because they were attached to ship hulls or concealed in ship ballast water	Yes—a potential for introduction of previously un established species that have the potential to effect the biotic balance
Thermal pollution	Heat energy discharged by power plants or factory cooling water, or by urban wastewater effluent (warm wastewater)	Yes—but localized

Identified threats to coastal marine macro-invertebrate communities	Mechanisms of impact	Potentially heightened by an environmentally perturbing event
Oil pollution	Human activities, including the flushing of ocean vessel bilges, leakage from undersea oil wells, and runoff or discharges from land-based facilities	Yes—significant for breached coastal nuclear and industrial facilities
Declining fishery resources	Marine environmental change and the fishery industry effects on environmental disruption	Yes—death assemblages and large numbers of eggs or fry of certain fish species

Table 9. Threats and potential for heightened effects to macro invertebrate near shore communities after an environmentally (human impacts or natural) perturbing event.

3. Conclusions

Limiting the human environmental changes to the coastlines from the decision-making perspective are one significant way that the ecosystem services of the marine coastal zone macroinvertebrate and associated macro-flora can be sustained. The macroinvertebrate biodiversity of these areas is resilient overall but the basis for the ecological assemblages, either the physical aspects or the biotic bases, must be able to provide the structure needs for refuge or attachment to support them. Additional challenges in considering the ecosystem services provided by macroinvertebrate assemblages in marine coastal zones resides in the policy makers, the planning decisions, coastal development, and most importantly of building consensus around ecosystem services in a locality. Research is needed that explores the application of a consensus approach across different land and seascape units. Assessment of the coastal zone biota still requires much research and practical work; finding ways to incorporate ecosystem services and its myriad values into the work of planners and policy makers in the marine and coastal environment is as important as it is challenging (**Table 9**) [8].

Further scientific and societal endeavors are needed to identify ecosystem services in a locality and to then identify effects to ecosystem services provided by the macroinvertebrate assemblages specifically. Globally a picture of services and negative impacts on the services provided are identified in general. Specific impacts for categories of macroinvertebrate assemblages are lesser known, even as the body of research grows (**Table 3**). To maintain the ecosystem services provided by marine coastal zones macroinvertebrate assemblages (Provisioning, Supporting, Regulating, and those relating to Cultural Services) will `require an understanding and collaborative approach among researchers, planners, and those that ultimately rely on these services. Ultimately, more research is needed to identify which actions can be taken to lessen the loss and speed the recovery of these communities after large-scale events originating from both natural and human impacts to restore these important human related ecosystem services. The most significant gains could be made in determining further what recovery after an event is possible can be made in the different biotic assemblages, and what methods to safeguard against human impact can be possible.

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Ecosystem Services across US Watersheds: A Meta-Analysis of Studies 2000–2014

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Abstract

Despite increasing awareness on the importance of rivers in maintaining human wellbeing, there has not been a comprehensive inventory of watershed-scale ecosystem services across the USA. Here, we analyze and summarize the scientific literature within the context of the supply and demand for ecosystem services across 18 major watersheds of the continental US. We reviewed 305 articles and found that 68 provided information on both the biophysical delivery (supply) and the sociocultural and economic values (demand) of ecosystem services. Maintaining populations and habitats, water filtration, and nutrient sequestration/storage were the most extensively assessed services, while educational and aesthetic values were the least frequently studied. Biophysical assessments were the most frequent valuation followed by economic approaches. The majority of the studies were conducted in the eastern US, while the region least studied was the southwest. In addition to identifying the knowledge gaps in watershed-scale ecosystem services, we highlight the need for a common framework for assessing ecosystem services that includes both the assessment of the supply and demand of ecosystem services provided by US watersheds. There is an urgent need to incorporate the role that cultural services and values can play in water resources management and planning in the USA.

1. Introduction

Preserving freshwater resources is a critical global issue [1, 2]. Water resources are vital for maintaining the welfare of humans and wildlife; however, humans have often prioritized freshwater for economic development at the expense of ecosystem health [3, 4]. There is

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concern in the USA about how to maintain future water supplies because of rapid growing human populations and climate change [5, 6]. Tradeoffs between securing water for human needs and ecosystem health will only become more challenging in the future with increasing human demand for freshwater coupled with impending shifts in the duration and frequency of extreme climatic events. This challenge is already being realized with increasing interstate water disputes across the nation [7]. Thus, there is an urgent need to implement new frameworks that consider the interdependent social, economic, and biophysical dynamics of water resources [8, 9].

Ecosystem services are the benefits that humans derive from ecosystems [10]. Examples of ecosystem services provided by freshwater ecosystems include (1) provisioning services obtained directly from the ecosystem such as drinking water and irrigation; (2) regulating services such as water regulation and quality, habitat, and air quality; and (3) cultural services, which are nonmaterial benefits that people obtain from ecosystems through spiritual enrichment, cognitive development, education, recreation, and esthetic experiences [10, 11]. The ecosystem service framework is useful in natural resource management [12] because it enables focusing on human-environment interlinkages by translating ecosystem properties into human needs [4, 13]. However, watershed management in the USA has traditionally maximized the production of one ecosystem service (e.g., energy or agriculture production), resulting in declines in other services (e.g., water quantity and quality) and producing human conflicts [14]. Therefore, understanding the different tradeoffs among ecosystem services associated with different watershed management strategies is key to maintain ecosystem services and decrease conflict. Such analyses should include an assessment of both the supply and societal demand of ecosystem services [15–17].

Despite the increasing number of publications that present innovative ideas and complementary insights from various perspectives, there is growing uncertainty with respect to the appropriate methodologies for quantifying ecosystem services. A common challenge in implementing the ecosystem services framework for watershed management is to quantify the capacity of watershed to provide services (supply side) as well as characterizing the social demand for those services (demand side) [16, 18]. The supply-demand framework highlights that the status of an ecosystem service is influenced not only by the ecosystem's properties but also by societal needs [16]. Here, we define the supply side as the capacity of a particular watershed to provide a specific bundle of ecosystem services within a given time period [15, 18] and the demand side as the sum of all ecosystem services currently consumed, used, or valued in a particular area over a given time period [3, 4].

This chapter provides a meta-analysis of the scientific knowledge related to ecosystem services across the major continental US watersheds. First, we present the data structure followed in this analysis. Several classifications and analytical frameworks have been proposed to assess ecosystem services. Based on our exploration of the scientific literature, we structure the results of this review based on the biophysical supply and social demand of ecosystem services [8, 15, 18]. Second, we describe and analyze the published articles and case studies under multiple perspectives (e.g., type of approach, geographical distribution, main focus, services valued). Then, we present the current knowledge across US watersheds related to



Figure 1. Ecosystem services framework used in reviewing the biophysical supply and the societal demand of services.

ecosystem services by differentiating between studies focused on the quantification of their biophysical supply and social demand. Finally, we identify the major knowledge gaps, both geographically and conceptually (**Figure 1**).

2. Methodology

2.1. Review criteria and selection

We reviewed scientific publications including journal articles and book chapters, from Web of Science (www.webofknowledge.com/) covering studies conducted at the watershed scale in the USA [19]. The systematic review follows the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) statement (**Figure 2**) [20]. The revision included terms related to the object of valuation (e.g., ecosystem services or environmental goods), the level of assessment (e.g., watershed or basin), and the location of the case study (e.g., U.S. or United States). See Appendix.1 for more detailed information. Eligibility criteria included manuscripts published between January 2000 and March 2014. Articles were screened to



Figure 2. Flow diagram of the methodology and selection process of the systematic review following the Preferred Reporting Items for Systematic Reviews (PRISMA).

determine relevant articles for this study. Overall, 305 articles were selected. Gray literature was omitted from this review. Our search was focused on articles that had framed their work explicitly in the ecosystem service concept (i.e., measuring the supply and demand of ecosystem services) across US watersheds [21].

A total of 305 articles were screened to determine relevant articles for this study (**Figure 2**) [20]. In addition, articles were excluded if they used the concept of ecosystem service to justify or explain the study, but did not actually assess ecosystem services. Overall, 150 were selected after excluding duplicates. Then, only articles that carried out assessments of ecosystem services from supply and demand perspective were considered (n = 99 studies). In this second selection process, the exclusion criteria included factors related to the type of valuation methods based on the multidimensional assessment of ecosystem services [8]. After this final selection, 68 articles were kept for the quantitative review (**Figure 2**) [20].

2.2. Data collection and structure

We classified all studies using the supply-demand framework of ecosystem services [16, 18] and grouped them by major watersheds (hydrologic unit code, level 2; HUC-2). Data collection was organized based on the general characteristics of this chapter, and the variables and methods

used to estimate both the biophysical supply and demand of ecosystem services (**Figure 2**). Appendix.2 shows a description of the variables collected in the review including the characteristics of the articles and study area, the type of ecosystem services valuation methods used, the classes of ecosystem services following the Common International Classification of Ecosystem Services (CICES), the type of biophysical quantification, the type of value, and the type of stake-holders involved. All the information was summarized and organized to facilitate its use by researchers and practitioners wanting maps of both the supply and demand of ecosystem services across the major US watersheds. Finally, we explored the current state of knowledge on the ecosystem service valuation through a general descriptive analysis of the studies. We analyzed the temporal evolution, methods, and type of analysis used, and spatial distributions of ecosystem services and publications across the major US watersheds.

3. Results

3.1. Analysis of published articles

The number of articles assessing ecosystem services from supply and demand perspectives in the USA increased exponentially after 2010 (**Figure 3A**), with only six articles published before 2004. From 2001 to 2010, the average rate of publication was around two articles per year. Thereafter, the publication rate rose to 11 articles per year. Most of the selected articles (60 articles) had a biophysical or an environmental perspective followed by economic (28 articles), interdisciplinary assessments (24 articles), and sociocultural assessments (14 articles) (**Figure 3B**). Only a few studies actually produced maps of ecosystem services. Almost half of the studies (45 articles) used empirical data for quantifying ecosystem services (**Figure 3C**). Over a third of studies performed modeling data analysis, and only 16 articles conducted theoretical approaches. From all the selected articles, 38 articles were carried out at a local scale, followed by 25 articles at a regional scale, and seven at a national scale (**Figure 3D**). Local scale was defined when the study covered just one US state, regional scale when for two US states, and national when it covered more than two US states.

3.2. Ecosystem services values and frameworks employed

Results show that over 78% of all studies did not use or mention any ecosystem services framework to structure goals, 21% used the [10] framework, and only 1% used the supply and demand frameworks (**Figure 4A**). Overall, considering the [10] classification of ecosystem services, we found that regulating services was the class most commonly quantified or valued (82%), followed by provisioning (41%) and cultural ecosystem services (21%) (**Figure 4B**). However, over half of the studies (52%) included more than one ecosystem service type in the analysis.

Using the Common International Classification of Ecosystem Services (CICES, <u>www.cices.eu</u>), we found that the regulating services were the most frequently studied category; however, the number of articles including cultural services in their assessments was higher than those studying provisioning services (**Figure 5**). Overall, the review identified a total of 308 ecosystem services studied. Among the regulating services, filtration, sequestration, storage and accumulation by ecosystems,



Figure 3. (A) Number of publications 2001–2014 that quantified ecosystem services across U.S. watersheds; (B) number of publications by authors' discipline(s); (C) number of articles by type of analysis, and (D) number of articles by spatial scale.



Figure 4. (A) Number of articles using different ecosystem services frameworks; (B) percentage of articles based on ecosystem service categories. Each article can be represented in multiple categories.

habitat maintenance, and chemical conditions of freshwaters were the services most studied, while disease control, pest control, and storm protection were the least studied (**Figure 5**). There were no studies that addressed pollination or seed dispersal. Regarding provisioning services, filtration and sequestration by biota, water for non-drinking purposes, and raw material were the most studied while groundwater for drinking purposes and physical and experimental use of plants and animals were the least studied. Genetic pools and raw medicines were not studied. Finally, in terms of cultural services, we found that recreation, existence value, and esthetic values were the most studied while educational and cultural heritage were the least studied (**Figure 5**).



Figure 5. Number of articles assessing ecosystem services based on the Common International Classification of Ecosystem Services (CICES).

3.3. Ecosystem services across US watersheds

The 68 studies evaluated in our dataset covered 18 of the 21 HUC-2 US watersheds (**Figure 6**). The assessments predominantly focused on ecosystem services delivered by watersheds located in the eastern half of the USA, with the three most studied watersheds being the South Atlantic-Gulf (HUC 03, N = 15, the Mid-Atlantic (HUC 02, N = 8), and the Upper Mississippi (HUC 07, N = 17)). By contrast, the US watersheds with no studies were located in northern and western regions, respectively, the Souris-Red-Rainy (HUC 09, N = 0) and the Upper Colorado (HUC 14, N = 5) (**Figure 6**). Watershed regions including the Pacific Northwest (HUC 17), the Missouri (HUC 10), the Arkansas-White-Red (HUC 11), the Texas-Gulf HUC 12), and the Lower Mississippi (HUC 08) were well represented with 10–12 articles per watershed (**Figure 6**).

We found differences across US watersheds in relation to the number of studies implementing the assessment of the supply and demand side of ecosystem services (**Figure 7**). Results show that 47 articles performed studies of the supply of ecosystem services and 19 articles implemented assessment of the social demand of ecosystem services. From the supply perspective,



Figure 6. Number of articles evaluating ecosystem services across major U.S. watersheds. Only 18 of the 21 HUC-2 U.S. watersheds showed results. Legend: New England (HUC 01), Mid-Atlantic (HUC 2), South Atlantic-Gulf (HUC 3), Great Lakes (HUC 4), Ohio (HUC 5), Tennessee (HUC 6), Upper Mississippi (HUC 7), Lower Mississippi (HUC 8), Souris-Red-Rainy (HUC 9), Missouri (HUC 10), Arkansas-White-Red (HUC 11), Texas-Gulf (HUC 12), Rio Grande (HUC 13), Upper Colorado (HUC 14), Lower Colorado (HUC 15), Great Basin (HUC 16), Pacific Northwest (HUC 17), California (HUC 18).

using either modeling techniques or proxies, a total of 137 ecosystem services were assessed: 60 regulating, 42 provisioning, and 35 cultural services. From the social demand perspective, using either sociocultural or economic valuation techniques, a total of 60 ecosystem services were assessed: 26 regulating, 16 provisioning, and 22 cultural ecosystem services.

The major US watersheds with the greatest number of studies implementing biophysical assessment of the ecosystem services supply were located in southeastern and midwestern regions (**Figure 7A**). Overall, all watershed regions included supply assessment of the three classes of services, that is, regulating, provision, and cultural, with the exception of the Ohio and Tennessee regions that only included provisioning and regulating services. The watershed regions that were most studied from the supply perspective included the Upper Mississippi (HUC 07), the Missouri (HUC 10), and the South Atlantic-Gulf (HUC 03). The Souris-Red-Rainy (HUC 09) and the Upper Colorado (HUC 14) were the regions that were least studied using the supply dimension.

Studies that assessed the social demand of ecosystem services (i.e., implementing sociocultural or economic valuation) were concentrated in the eastern half of the country (**Figure 7B**). Overall, all watershed regions included assessment of the three classes of services, that is, regulating, provision, and cultural, with the exception of the Texas-Gulf region that only included cultural services. The most-studied major watersheds from the social demand perspective included the Upper Mississippi (HUC 07), the South-Atlantic (HUC 03), and the Mid-Atlantic (HUC 02). The remaining watersheds, with the exception of the Pacific Northwest (HUC 17), the Great Lakes (HUC 04), and the Lower Mississippi (HUC 08), had less than six studies on the social demand of ecosystem services.

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Figure 7. Number of studies evaluating the biophysical supply (A) and social demand (B) of ecosystem services across major U.S. watersheds. Only 18 of the 21 HUC-2 U.S. watersheds showed results. Legend: New England (HUC 01), Mid-Atlantic (HUC 2), South Atlantic-Gulf (HUC 3), Great Lakes (HUC 4), Ohio (HUC 5), Tennessee (HUC 6), Upper Mississippi (HUC 7), Lower Mississippi (HUC 8), Souris-Red-Rainy (HUC 9), Missouri (HUC 10), Arkansas-White-Red (HUC 11), Texas-Gulf (HUC 12), Rio Grande (HUC 13), Upper Colorado (HUC 14), Lower Colorado (HUC 15), Great Basin (HUC 16), Pacific Northwest (HUC 17), California (HUC 18).

4. Discussion

Water resources management and planning in the USA face the challenge of not only ensuring the needs for humans but also preserving ecosystem health, which has a direct connection to human well-being through ecosystem services [4, 6]. This meta-analysis provides a comprehensive inventory of watershed-scale ecosystem services knowledge across major US watersheds. More specifically, our analysis summarizes the scientific literature since 2000 within the context of the number of studies investigating the biophysical supply and social demand for ecosystem services. We found a temporal trend in the number of publications similar to that found from international studies following the global development trend in this research area [3, 22]. Our results emphasize the urgent need to implement interdisciplinary frameworks that take into account the interdependent social, economic, and biophysical dynamics of shared water resources and the need for using integrative approaches to capture different value domains [18, 23].

Overall, our results showed that the number of studies investigating regulating and provisioning services was higher relative to those investigating cultural services. This finding is consistent with similar studies across the globe, where research on the supply and demand of ecosystem services has focused mainly on provisioning and regulating services [24, 25]. In the Mediterranean region, for example, [21] showed that provisioning services attracted much more scientific attention, which is also consistent with most of the findings related to the assessment of ecosystem services in European landscapes [13, 23]. Furthermore, using the CICES classification, we found that from a total of 308 ecosystem services studied across all US watersheds, regulating services (e.g., filtration, sequestration, storage and accumulation by ecosystems, habitat maintenance, and chemical conditions of freshwaters) were most commonly studied, while cultural services (e.g., educational and cultural heritage) were the least studied. As recently highlighted by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), there is an urgent need for global efforts by governments, academia, and society to promote knowledge of earth's biodiversity and ecosystems, with the aim of informing sustainable policy and management of natural resources [26, 27]. One of the key components of the IPBES approach is the notion of nature's contributions to people, which recognizes the critical role that culture plays in defining all links between humans and ecosystems. We therefore argue that there is also a need to recognize the important role that cultural services and values can play in water resources management in the USA and the need to operationalize the role of indigenous and local knowledge in understanding watershed's contribution to people [26, 28].

Different disciplines have traditionally assessed ecosystem services separately [18, 24], which has led to the conclusion that ecosystem services values are multidimensional, and thus their evaluation must be conducted from the ecological, social, and economic perspective [23, 28, 29]. Although we found a small percentage of studies that used this multidisciplinary approach in their assessments, our results showed that most of the studies conducted across US watersheds implemented a biophysical approach, which points out the gap of integrating different approaches into ecosystem service research [30, 31]. We believe that this gap is due to the absence of a shared theoretical framework, as we found that over 78% of all studies in the USA did not use a standard ecosystem services framework. In a recent article, [32] concluded that integrated valuation of ecosystem service supply and demand still faces challenges in understanding the tradeoffs among ecosystem services. With regard to ecosystem service demand, it is necessary to use systematic methods for different stakeholders (beneficiaries, impairers, and managers) because of their different knowledge types, capabilities, demographics, rights, and value systems [32, 33]. We also identified methodological limitations in current ecosystem services research conducted across major US watersheds. Most of the studies were focused on a single ecosystem service without investigating the potential implications that trade-offs between multiple ecosystem services may have in watershed management [3, 4]. Many recent investigations have showed that investigations on single ecosystem services may result in producing a knowledge gap that can only be solved by integrative and holistic approaches for the assessment of multiple ecosystem services [22, 34, 35]. Understanding the different tradeoffs among ecosystem services should include assessments of both the supply and societal demand of ecosystem services [15–17]. Thus, we need to integrate multiple indicators, data sources, and methods in order to assess the suite of ecosystem services from supply to social demand across different spatial and temporal and stakeholder scales [32, 33].

5. Conclusions

Overall, we found that the use of the supply and demand framework of ecosystem services for watershed-scale studies in the USA has been extremely limited. The majority of the watershed case studies were found in the eastern half of US, with very few in the Southwest. Studies implementing biophysical assessment of the ecosystem services supply were located in the Southeast and Midwest, while studies investigating the social demand of ecosystem services were concentrated along the east coast of the USA. In addition to identifying the gaps in our knowledge of watershed-scale ecosystem services across the USA, we call attention to the scale issue in ecosystem services research, which describes the mismatch between the scale at which ecosystem services are provided and the scale at which those services are used, valued, or managed [16]. Future studies should not only address multiple spatial and temporal scales; they should also assess different stakeholder scales, from the individual to the community to the municipality to the state, and beyond.

Understanding and quantifying tradeoffs between ecosystem services, considering their ecological, cultural, and economic value, is a key challenge for water resources management and planning in the USA [36] and beyond [37]. Our study demonstrates the knowledge gap across US watersheds in terms of integrating biophysical, sociocultural, and economic dimensions to assess the biophysical supply and social demand for services, which is key for increasing public awareness of the importance of river systems in maintaining human well-being [3, 38]. Moving forward, we would like to see more comprehensive ecosystem service studies at watershed scales using integrative (yet standard) approaches to assess tradeoffs at multiple spatiotemporal and stakeholder scales.

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Appendix 1. Keywords used in the review based on the goal of the study, location and the level of assessment. Searcher = Web of Science

Category	Keywords
Localization	"US" or
	"USA" or
	"Unites States" or
	"United states of America"
Level of assessment	"Watershed" or "basin "or "catchment"
Goal: ecosystem services	"ecosystem serv*" or "environmental servic*" or "ecological services"

Appendix 2. Description of the variables collected in the analysis matrix for further analysis

Variables	Туре	Description
Related with the type of article		
Number of authors	Ordinal	Number of authors in the paper
First author occupation (e.g., academia vs. government vs. private)	Qualitative	Academia versus government versus private
Field of expertise of the first author		
Economics	Binary	1 = If it belongs to economics; 0 = If it does not belong to economics
Natural sciences	Binary	1 = If it belongs to <i>Natural sciences</i> ; 0 = If it does not belong to <i>Natural sciences</i>
Sociocultural sciences	Binary	1 = If it belongs to <i>Sociocultural</i> ; 0 = If it does not belong to <i>Sociocultural field</i>
Interdisciplinary group	Binary	1 = If it belongs to an interdisciplinary group; 0 = If it does not belong to an interdisciplinary group
Social-ecological system (SES) framework	Binary	1 = If it uses the SES framework; 0 = If it does use the SES framework
Year of the publication	Continuous	Year of publication
Journal	Qualitative	Name of the Journal
Field of expertise	Qualitative	Area(s) where the paper is classified

Variables	Туре	Description
Approach of the study		
Type of study (case-study vs. comparative study vs. meta-analysis vs. review vs. conceptual vs. commentary)	Qualitative	Description of the study: case-study versus comparative study versus meta-analysis versus review versus conceptual versus commentary
Analytic or empirical	Binary	1 = If it is an <i>analytic or empirical</i> study; 0 = If it is not an <i>analytic or empirical</i> study
Modeled	Binary	1 = If it is a modeled study; 0 = If it is not a modeled study
Theoretical	Binary	1 = If it is an <i>Theoretical</i> study; 0 = If it is not a <i>Theoretical</i>
Source of data		
Primary	Binary	1 = If the study used primary data, 0 = any study using primary data
Secondary	Binary	1 = If the study used secondary data, 0 = any study used secondary data
Length of study period		
Punctual	Binary	1 = If the study period is considered <i>Punctual</i> ; 0 = If the study period is not considered <i>Punctual</i>
Time series	Binary	1 = If the study period considers a <i>time series</i> 0 = If the study period does not consider a <i>time series</i>
Related with the study area		
Watershed	Qualitative	Name of the watershed
Geographical coordinate	Continuous	Description of geographical coordinates
Major US watershed	Qualitative	Name of the US watershed (see map)
Major LCC Landscape Conservation cooperative	Qualitative	Name of major LCC (see map)
River	Qualitative	Name of the river
WATERSHED OR BASIN SCALE		
Local	Binary	1 = If the study is defined as local scale, 0 = If the study is not considered local scale.
Regional	Binary	1 = If the study is defined as regional scale, 0 = If the study is not considered regional scale.
National	Binary	1 = If the study is defined as <i>national</i> scale, 0 = If the study is not considered as national scale.
State	Binary	Name of the state
Watershed surface occupied (entire or part of the watershed)	Qualitative	Description of the watershed (entire vs. part of)
Surface of the study area	Continuous	Description of surface occupied
MAJOR BIOMES (see map)		
Desert and dry shrubs	Binary	1 = If the study focuses on desert and dry shrubs, 0 = If the study does not focus on desert and dry shrubs

Variables	Туре	Description
Flooded grassland	Binary	1 = If the study focuses on flooded grassland, 0 = If the study does not focus on flooded grassland
Mediterranean Shrubs	Binary	1 = If the study focuses on Mediterranean Shrubs, 0 = If the study does not focus on Mediterranean Shrubs
Temperate Broadleaf forest	Binary	1 = If the study focuses on <i>Temperate Broadleaf forest</i> , 0 = If the study does not focus on Temperate Broadleaf forest
Temperate coniferous forest	Binary	1 = If the study focuses on Temperate coniferous forest, 0 = If the study does not focus on Temperate coniferous forest
Temperate grassland	Binary	1 = If the study focuses on Temperate grassland, 0 = If the study does not focus on Temperate grassland
Tropical Coniferous forest	Binary	1 = If the study focuses on Tropical Coniferous forest, 0 = If the study does not focus on Tropical Coniferous forest
Level of protection		
Protected	Binary	1 = If the study area is protected, 0 = If the study is not protected
Federal level of protection	Binary	1 = If there is a federal protection, 0 = If there is not a federal protection
Sate level of protection	Binary	1 = If there is a state protection, 0 = If there is not a state protection
Local level of protection	Binary	1 = If there is a local protection, 0 = If there is not a local protection
Related with valuation methods		
Mapping values (both biophysical, social, or economic)	Binary	1 = If it maps values; 0 = If it does not map values
Valuation arguments	Qualitative	Arguments of the authors to perform the assessment.
Dimension of assessment		
Biophysical technique	Binary	1 = If the study uses a biophysical technique, 0 = If the study does not use a biophysical technique
Biophysical indicator	Binary	1 = If the study uses a biophysical indicator, 0 = If the study does not make a biophysical indicator
Sociocultural technique	Binary	1 = If the study uses a sociocultural technique, 0 = If the study does not uses a sociocultural technique
Sociocultural indicator	Binary	1 = If the study uses a sociocultural indicator, 0 = If the study does not uses a sociocultural indicator
Monetary or economic technique	Binary	1 = If the study uses a economic technique, 0 = If the study does not uses a economic technique
Monetary or economic indicator	Binary	1 = If the study uses a economic indicator, 0 = If the study does not uses a economic indicator
Methods used		

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Variables	Туре	Description
Market valuation	Binary	1 = If the study uses market techniques; 0 = If the study does not use market techniques.
Revealed preferences	Binary	1 = If the study uses revealed preference techniques, 0 = any study uses revealed preference techniques.
Stated preferences	Binary	1 = If the study uses stated preference techniques, 0 = any study using stated preference techniques.
Biophysical quantification	Binary	1 = If the study uses a biophysical model to quantify the delivery, 0 = If the study does not use a biophysical model to quantify the delivery
Ecosystem services (CICES ES-classes)		
ES classification used (MEA, TEEB, IPBES, CICES)	Qualitative	Name of the classification used in the paper
Number of ES	Continuous	Number of ecosystem services valued by the study.
PROVISIONING		
Biomass from animals or plants	Binary	1 = If the study values food, 0 = If the study does not value food
Ground Water for drinking	Binary	1 = If the study values <i>Ground Water</i> , 0 = If the study does not value <i>Ground Water</i>
Surface Water for drinking	Binary	1 = If the study values <i>Surface Water</i> , 0 = If the study does not value <i>Surface Water</i>
Water for non drinking purposes	Binary	1 = If the study values <i>Water for non drinking purposes</i> , 0 = If the study does not value <i>Water for non drinking</i> <i>purposes</i>
Raw material	Binary	1 = If the study values <i>Raw material</i> , 0 = If the study does not value <i>Raw material</i>
Mechanical energy	Binary	1 = If the study values <i>Mechanical energy</i> , 0 = If the study does not value <i>Mechanical energy</i>
Biomass-based energy sources	Binary	1 = If the study values <i>Biomass based energy sources</i> , 0 = If the study does not value <i>Biomass based energy sources</i>
Natural medicines	Binary	1 = If the study values <i>Natural medicines</i> , 0 = If the study does not value <i>Natural medicines</i>
Genetic pool	Binary	1 = If the study values <i>Genetic pool</i> , 0 = If the study does not value <i>Genetic pool</i>
Regulating		
Bio-remediation by biota	Binary	1 = If the study values <i>Bio-remediation by biota</i> , 0 = If the study does not value <i>Bio-remediation by biota</i>
Filtration, sequestration, storage, accumulation by biota	Binary	1 = If the study values <i>Filtration, sequestration, storage,</i> accumulation by biota, 0 = If the study does not value <i>Filtration, sequestration, storage, accumulation by biota</i>
Bio-remediation by ecosystems	Binary	1 = If the study values <i>Bio-remediation by ecosystems</i> , 0 = If the study does not value <i>Bio-remediation by ecosystems</i>
Filtration, sequestration, storage, accumulation by ecosystems	Binary	1 = If the study values <i>Filtration, sequestration, storage,</i> <i>accumulation by ecosystems,</i> 0 = If the study does not value <i>Filtration, sequestration, storage, accumulation by</i> <i>ecosystems</i>

Variables	Туре	Description
Control of erosion	Binary	1 = If the study values <i>Control of erosion</i> , 0 = If the study does not value <i>Control of erosion</i>
Buffering and attenuation of mass flow	Binary	1 = If the study values <i>Buffering and attenuation of mass flow</i> , 0 = If the study does not <i>Buffering and attenuation of mass flow</i>
Hydrological cycle and water flow maintenance	Binary	1 = If the study values <i>Hydrological cycle</i> , 0 = If the study does not value <i>Hydrological cycle</i>
Flood protection	Binary	1 = If the study values <i>Flood protection</i>
		, 0 = If the study does not value $Flood$ protection
Storm protection	Binary	1 = If the study values <i>Storm protection</i> , 0 = If the study does not value <i>Storm protection</i>
Pollination and seed dispersal	Binary	1 = If the study values <i>Pollination</i> , 0 = If the study does not value <i>Pollination</i>
Maintaining populations and habitats	Binary	1 = If the study values <i>Habitat for species</i> , 0 = If the study does not value <i>Habitat for species</i>
Pest control	Binary	1 = If the study values <i>Pest control</i> , 0 = If the study does not value <i>Pest control</i>
Disease control	Binary	1 = If the study values <i>Disease control</i> , 0 = If the study does not value <i>Disease control</i>
Decomposition and fixing soil processes	Binary	1 = If the study values <i>soil processes</i> , 0 = If the study does not value <i>soil processes</i>
Chemical condition of freshwaters	Binary	1 = If the study values <i>Chemical condition of freshwaters</i>,0 = If the study does not value <i>Chemical condition of</i> <i>freshwaters</i>
Atmospheric composition and climate regulation	Binary	1 = If the study values <i>climate regulation</i> , 0 = If the study does not value <i>climate regulation</i>
Cultural		
Physical and experiential use of plants, animals, or landscapes	Binary	1 = If the study values <i>experiential use</i> , 0 = If the study does not value <i>experiential use</i>
Educational		1 = If the study values <i>Educational</i> , 0 = If the study does not value <i>Educational</i>
Heritage, cultural		1 = If the study values <i>Heritage, cultural,</i> 0 = If the study does not value <i>Heritage, cultural</i>
Entertainment or recreation		1 = If the study values <i>Recreation</i> , 0 = If the study does not value <i>Recreation</i>
Esthetic		1 = If the study values <i>Esthetic</i> , 0 = If the study does not value <i>Esthetic</i>
Scientific	Binary	1 = If the study values <i>Scientific</i> , 0 = If the study does not value <i>Scientific</i>
Existence value	Binary	1 = If the study values <i>Existence value</i> , 0 = If the study does not value <i>Existence value</i>
Bequest value	Binary	1 = If the study values <i>Bequest value</i> , 0 = If the study does not value <i>Bequest value</i>
Variables	Туре	Description
------------------------------------	-------------	--
Several categories of services	Binary	1 = uses several categories of ecosystem services, 0 = use a single category of services ecosystem services
Type of biophysical quantification		
Mapping delivery	Binary	1 = If the study map the delivery, 0 = If the study does not map the delivery
Use of proxy to quantify ES	Binary	1 = If the study uses a proxy, 0 = If the study does not use a proxy
Biophysical units used	Qualitative	Description of the unit used
Biophysical model used	Qualitative	Name of the model
Trade-Offs analysis	Binary	1 = If the study estimates Trade-offs analysis, 0 = If the study does not estimate Trade-offs analysis
Multiple ecosystem services	Binary	1 = If the study estimates multiples services, 0 = If the study does not estimate multiples services
Types of value		
Use value		
Direct	Binary	1 = If the study assesses direct use value 0 = If the study does not direct use value.
Indirect	Binary	1 = If the study assesses indirect use value 0 = If the study does not indirect use value.
Option value	Binary	1 = If the study assesses <i>Option value</i> 0 = If the study does not value <i>Option value</i>
Non-use value		
Existence value	Binary	1 = If the study assesses <i>Existence value</i> 0 = If the study does not <i>Existence value</i>
Bequest value	Binary	1 = If the study assesses <i>Bequest value</i> 0 = If the study does not <i>Bequest value</i>
Types of stakeholder group		
Beneficiaries involved	Binary	1 = If the study involves beneficiaries; 0 = If the study does not involve the beneficiaries.
Locals	Binary	1 = If the study involves locals; 0 = If the study does not involve locals
Professionals or experts	Binary	1 = If the study involves professionals; 0 = If the study does not involve professionals
Tourists	Binary	1 = If the study involves tourist; 0 = If the study does not involve tourists
Mixed	Binary	1 = If the study involves mixed stakeholders; 0 = If the study does not involve mixed stakeholders
Impact on beneficiaries	Binary	1 = If the study involves impact on beneficiaries; 0 = If the study involves no impact on beneficiaries.
Type of beneficiaries	Qualitative	Description the types of beneficiaries

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Laticifers and Secretory Ducts: Similarities and Differences

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Abstract

During the evolution of terrestrial plants, many protective strategies have emerged, guaranteeing the survival of plants in the most varied environments. Among these strategies, we highlight the chemical defense of plants given by secretory structures, such as laticifers and secretory ducts. These glands are responsible for the production of viscous exudates that can be toxic, deterrent or repellent to herbivores, in addition to acting against microorganisms and sealing wounds. The similarities between latex and resin produced by certain ducts led several researchers to misinterpret their characteristics and generated a great number of divergences in the literature. This chapter aims to review the similarities and differences between laticifers and ducts and to demonstrate the structure, secretory activity and chemical composition of the secretion of each one, as well as the evolutionary and ecological aspects that can be associated with the high rate of survival and diversification of the plants that contain laticifers and/or ducts.

Keywords: evolution, latex, resin, tubular secretory systems, protection

1. Introduction

The huge biological diversity is responsible for relations between different species of plants, animals and microorganisms, with emphasis on the correlation between plants and insects. The interrelationships between these two groups of organisms are already well established in the evolutionary history of both. In addition, they may account for more than 75% of the current biodiversity [1] in both beneficial associations, such as pollination, and adverse relationships, such as herbivory [2–4].



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Herbivory has important implications for the evolutionary processes of the plant community. Its analysis reveals a continuous evolutionary adaptation [5] in which the plants developed physical and chemical defense mechanisms, just as the insects co-evolutionarily improved molecular, physiological and behavioral components in response to these mechanisms [2, 4, 6–10].

Herbivory generates a negative impact on the plant and minimizes its growth, reproduction and its adaptability to the environment [11, 12]. Therefore, several defensive strategies are observed in different groups of plants that protect them against herbivores and pathogens. These strategies may be (1) physical defenses, like trichomes, calcium oxalate crystals and sclerenchyma, which provide greater hardness to plant tissue and prevent it from penetration and degradation [13–15] and (2) chemical defenses, through the production of secondary metabolites by secretory cells [3, 6, 16–21]. The secondary metabolites found in the different secretions (or natural products) include a great diversity of alkaloids, terpenoids, cyanogenic glycosides and phenolic compounds that are toxic and play a selective role in relation to the enemies, mainly against herbivory [10, 17, 19, 22, 23], thus enhancing the plant adaptive success in many environments [10, 18, 24].

2. Defensive secretory structures

Secretions are present in all groups of vascular plants and may be composed of a high diversity of secondary and/or primary metabolites [16, 19, 21, 25, 26] and have a well-defined ecological role. Although a single metabolite may predominate within a taxon, especially in the case of some alkaloids [19], when we consider the totality of compounds produced by plant secretory structures (or glands), they usually vary even within a species due to genotypic variations and abiotic conditions [25].

Different secretions are produced by specialized cells and can be directly released to the environment or stored in the plant in intracellular or intercellular sites [16, 21]. Secretory structures vary enormously in relation to their structural complexity, and may be composed of a single cell (e.g., idioblasts and some laticifers) or many cells, as in the case of more complex structures such as trichomes, colleters, nectaries, osmophores, secretory cavities and ducts, among others [2, 16, 20, 21, 27–29]. Some of these secreted compounds can be profoundly affected, with their production being increased or reduced when the plant is subjected to some form of stress, such as wounds, infections or variations of climatic or edaphic factors [19, 25, 30].

Among the defensive glands, we highlight the tubular secretory systems that can form an anastomosed and branched network throughout the plant, a similarity that has generated numerous errors of identification between laticifers and resin ducts due to the production of similar secretions [6, 17, 25, 29, 31]. What are the similarities and differences between these two secretory structures?

3. Laticifer and resin duct

Laticifers and ducts can occur as single structures that often anastomose forming an interconnected network through all organs of the plant, whose viscous and mostly terpenic secretion is only released to the outside by the rupture of the secretory system. However, these are the only similarities. Misidentifications are mainly due to the observation of the appearance and color of the secretion in the field, since latex and resin possess predominantly the same classes of chemical compounds. On the other hand, laticifers and ducts are very different in terms of structure and secretory activity.

3.1. Laticifer

A laticifer is a single cell or a row of specialized cells that contain latex [16] (Figure 1A). When the laticifer is composed of a single cell, it is classified as non-articulated; when it is formed by a row of cells (Figure 1B), it is classified as articulated [32]. Although their classification and morphological variations are very subtle, the identification of the laticifer must be made in the light of an ontogenetic study of the structure, since some articulated laticifers observed in Apocynaceae and Euphorbiaceae can differentiate rapidly next to the promeristem (Figure 1C). In these cases, few cell layers away from the promeristem, the laticifer cells completely dissolve their terminal walls, becoming a continuous tube without border remains between the different cells that compose it (Figure 1D). Thus, this type of articulated laticifer resembles a single cell at maturity, which may or may not be branched (Figure 1E). This has generated numerous divergences in the literature over time, and more detailed studies of the apical portion of the laticifer have tried to unravel its mode of growth among the meristems.

Apparently, the non-articulated laticifer has a more complex development. Several researchers have reported a predetermined number of laticifer initials present in the embryo, which theoretically develop and branch through the entire body of the plant, regardless of its size [8, 33]. This unlimited elongation would result from an intrusive autonomous growth of the laticifer tip between meristematic cells. This way, this type of laticifer would present cell division without the occurrence of cytokinesis, forming a long multinucleated, coenocytic tube [9, 33–36] (**Figure 1F**). Although this type of growth has also been recorded for a few articulated laticifers [35, 37], several studies have demonstrated the impossibility of its occurrence due to the absence of a subcellular apparatus capable of constantly producing cell wall at the laticifer tip [38], besides the lack of records of karyokinesis within laticifers in the main families of latescent plants [7, 39, 40]. Thus, the possible unlimited growth of the laticifer needs to be reviewed, and the record of articulated and non-articulated laticifers in the same genus and even in the same species should be re-evaluated ontogenetically [7, 33, 35, 39–41], since the current data point to the absence of non-articulated laticifers in all the families in which they were described.

Latex is the laticifer's protoplast itself, which has most of the metabolites stored inside a large, central vacuole [7] (**Figure 1G** and **H**). This highly heterogeneous content forms a suspension or emulsion of many small particles in a fluid [16], whose typical color is milky white; however, depending on the latex composition, it may be red, orange, yellow, green and even colorless [7, 9, 10, 23, 30, 33, 34, 39, 42].

Although latex is a mixture of many distinct compounds, there is always a predominance of terpenoids in its composition [10, 40, 43] (**Figure 2A–C**). In general, these terpenoids are triterpenes or tetraterpenes, but rubber tree has up to 45% polyisoprenes (rubber) in its latex composition [30, 43, 44]. In addition, fatty acids, phytosterols, alkaloids, phenolic compounds, proteins, cardenolides, starch grains, among other compounds, have already been identified in the latex of many species [7–10, 30, 39, 42] (**Figure 2**).



Figure 1. Laticifers. A, E–G. *Euphorbia milii* (Euphorbiaceae). B, H. *Musa paradisiaca* (Musaceae). C, D. *Thevetia peruviana* (Apocynaceae). A. Latex within the laticifer. B. Articulated laticifer. C. Laticifer ontogeny near the promeristem. D. Laticifer network. E. Branched laticifers. F. Multinucleated laticifer. G, H. Latex metabolites within the vacuole and peripheral nucleus. Arrow, terminal wall; arrowhead, nucleus.



Figure 2. Histochemistry of the laticifers of *Hura crepitans* (Euphorbiaceae). A. Detection of lipids with Sudan black B. B. Resins identified within the laticifer using NADI reagent. C. Globules of essential oils and resins in the latex. NADI reagent. D. Detection of phenolic compounds with ferric chloride. E. Mucilage identified using ruthenium red. F. Polysaccharides within laticifers detected by PAS reaction. G. Proteins in the latex identified with coomassie blue.

The function of such compounds is, either individually or synergistically, to protect plants against herbivory and penetration of pathogens; further, they have the ability to seal wounds, since latex polymerizes when in contact with the air [6, 7, 10, 23, 25, 30, 33, 39, 40, 45, 46].

The protective function of the latex is reflected in the time of laticifer differentiation, since all the secretory defense structures originate early in the organogenesis. Laticifers are present from the younger portions of the plant and are widely distributed in almost all tissues (**Figure 1**), but there is a higher frequency of laticifers associated with vascular tissues, especially with the phloem [40, 41] (**Figure 1H**). This proximity allows a direct transference of the transported nutrients to the laticifer, supplying the intense biosynthetic demand of this cell. This fact becomes even more relevant when it is considered that a single laticiferous cell can produce all the major classes of secondary metabolites [10]. These compounds, which can be extremely toxic, are isolated from the rest of the plant tissues remaining inside the laticifer and will only be released to the environment if there is a rupture of the secretory system [8, 23, 38].

3.2. Resin duct

Ducts are glands formed by a secretory tissue called epithelium that delimits an intercellular space, the lumen, where the secretion is stored (**Figure 3A**). The ducts are always elongated (**Figure 3B**) and can remain individualized or anastomose laterally (**Figure 3C**) forming a



Figure 3. Resin ducts. A–D. General view. A, D–J. Transverse sections. B, C. Longitudinal sections. A, B, E, H. *Schinus terebinthifolius* (Anacardiaceae). C, D, F, I, J. *Clusia* sp. (Clusiaceae). G. *Protium heptaphyllum* (Burseraceae). E–J. Histochemistry. E. Lipids stained with Sudan black B. F. Resins identified using NAD1 reagent. G, H. Phenolic compounds detected by toluidine blue (G) and ferric chloride (H). I. Polysaccharides identified with PAS reaction. J. Proteins stained using coomassie blue. Arrow, duct initials rosette; Ep, epithelium; Lu, lumen.

complex network of ducts throughout the plant [9, 23, 25]. Although this branched duct system may superficially resemble some types of laticifers, ducts are never composed of a single cell or a single row of cells. Actually, the epithelium of some ducts may have dozens of cell rows lining the lumen.

In addition, ducts differ from laticifers in relation to the origin and the mode of secretion storage. The main event in duct morphogenesis is the process of lumen formation. Initially, we observe a set of meristematic cells called rosette (**Figure 3D**), which may form an intercellular space by means of three processes: (1) schizogeny, in which a space is formed by separation of the rosette initials through an active movement of the cells; (2) lysigeny, in which a space is formed by programmed cell death of one or more central cells of the rosette; and (3) schizolysigeny, where the lumen is initially formed by programmed cell death and then spread apart cells enlarging the intercellular space [9, 23, 25, 34, 47, 48].

After the formation of the lumen and concomitant differentiation of the epithelium, the secretory process is initiated by means of which the produced secretion will be stored extracellularly in the lumen [17, 25, 34, 49] (**Figure 3A** and **B**). This secretion's composition varies depending on the group and may be constituted of mucilage, gum or resin.

Despite all the differences between laticifers and secretory ducts, many divergences are found in the literature of some families for which some authors described the secretory structure as ducts, laticifers or latex ducts (=laticiferous canals). This confusion occurs exclusively in relation to the resin ducts, since the resin of some families may be white, especially in species of Anacardiaceae, Burseraceae, Cactaceae, Calophyllaceae and Clusiaceae [42, 47, 50–58].

Although resins are usually associated with the amber coloration, they may also be colorless [52, 59] or white. In the same way that latex varies in color, resins vary in color depending on their composition. By definition, resins are composed of phenolic compounds, terpenoids or a mixture of both [60] but what is observed in those five families is that the resin is composed of several classes of compounds [21, 59], although its constitution is mostly terpenic (**Figure 3E** and **F**), such as the resin of the gymnosperms and almost all angiosperms [60]. This fact led some authors to propose mixed terms, such as gum-resin to indicate the heterogeneity of the secretion. However, this term is not comprehensive enough, as this resin may have other compounds, such as phenolic compounds, alcohols, aldehydes, esters, gums, mucilage, proteins and alkaloids [16, 21, 23, 25, 48, 59, 61, 62] (**Figure 3G–J**).

The high chemical complexity of some resins confers functions similar to those of the latex, acting against herbivory and microorganisms, besides sealing wounds by the polymerization of their compounds when in contact with the air [6, 63]. The secretion is stored in the lumen and does not come into contact with any surrounding tissue. Its release to the environment occurs only by rupture of the secretory system. Ducts have an early formation during plant organogenesis but due to its more complex structure in relation to the laticifers, they are found in mature stage at a little longer distance from the promeristem than laticifers (**Figure 4A**). Ducts also occur preferentially in the vascular system (**Figure 4B**) or in the surrounding area (**Figure 4C**).

In our study, we have analyzed the five families that have disagreements regarding the presence of resin or latex. In Anacardiaceae, Venning [64] reported the presence of ducts in *Schinus* as laticifers with schizogenous origin, and Fahn and Evert [47] attributed the milky white color of *Rhus* resin to the fact that the secretion contains carbohydrates in its constitution.

The tribe Protieae (Burseraceae) is recognized for presenting resinous latex or latex [50–52]. *Mammillaria* is a genus of Cactaceae described as latescent due to the presence of a milky



Figure 4. Resin ducts. A, B. Schinus terebinthifolius (Anacardiaceae). C. Clusia sp. (Clusiaceae). D. Protium heptaphi/llum (Burseraceae). E, F. Mammillaria sp. (Cactaceae). G, H. Kielmeyera appariciana (Calophyllaceae). A, F, H. Longitudinal sections. B–E, G. Transverse sections.

white exudate [42, 53–57], and Mauseth [65] states that the *Mammillaria* laticifers would have evolved independently of all other latescent families, since their mode of formation is completely different. In addition, *Kielmeyera* (Calophyllaceae) and *Clusia* (Clusiaceae) are registered as latescent [42, 66, 67] due to the production of a white to yellowish exudate [58].

Our analyses showed that the genera of these five families, in which some authors suggested the presence of latex, actually have resin ducts (**Figures 3** and **4**). The white color of the secretion is due to the high heterogeneity of its composition, which is formed by several types of lipids, mainly terpenoids, phenolic compounds, polysaccharides and proteins (**Figure 3E–J**).

3.3. Occurrence of laticifers and resin ducts in plant taxa and their distribution according to the environment

The plant ability to produce latex or resin is not related to growth habit and seems to be related to a phylogenetic conserved trait or to a key evolutionary innovation that arose in a particular group, influenced directly or indirectly by the environment in which it lives.

Laticifers occur in about 10% of the angiosperm families and the resin ducts in other 10% of them. As they usually do not occur in the same groups, both together are found in about 20% of the flowering families (**Table 1**), being very common defensive secretory structures. Moreover, this number may be underestimated, and laticifers have been identified in several genera of Sapindaceae described as non-latescent due to the inconspicuous latex released when the plant is ruptured [68]. We have noticed that the amount of latex, as well as resin, depends on the gland density in the organ, the degree of anastomosis of the secretory system, climatic and edaphic conditions and even the injuries caused by microorganisms or environmental factors.

According to our updated survey, laticifers are found in Marsileaceae (fern), Gnetaceae (gymnosperm) and 38 families belonging to almost all major lineages of angiosperms. Similarly, resin ducts occur in seven families of gymnosperms, belonging to Ginkgoales and Pinales, and are widespread within angiosperms in which they are present in 40 families (**Table 1**). Both in terms of absolute and proportional estimates, latescent and resinous families predominate in tropical regions [42, 60] (**Table 1**). It is estimated that 14% of the tropical species produce latex compared to 6% of the species in temperate regions [42]. In addition, the largest number of resin-producing families which have numerous genera that produce copious resins occur in tropical areas [60].

The comparative analysis shows that 17 orders have both laticifers and resin ducts but generally in different families. The occurrence of both secretory structures in the same family was recorded only for Araceae, Salicaceae, Fabaceae, Cannabaceae, Moraceae, Cornaceae and Asteraceae, which are tropical families or have a wide distribution in tropical regions (**Table 1**).

3.4. Evolution of laticifers and resin ducts and ecological implications

The production of latex or resin is a highly convergent trait that has evolved independently multiple times (**Figure 5**). Despite the co-occurrence of laticifers and resin ducts being found in only 50% of the angiosperm orders which have these secretory structures (**Table 1**), the possible presence of laticifers or resin ducts in the ancestor of the same major lineages is noticeable (**Figure 5**). This fact may indicate the emergence of an ancestral metabolic capability to synthesize higher molecular weight terpenoids, which resulted in similar possibilities to

Groups	Order and families	Laticifer	Resin duct	Distribution
Ferns	Salviniales			Regnellidium, Southern Brazil and
	Marsileaceae	+	-	Argentina
Gymnosperms	Ginkgoales			China
	Ginkgoaceae	-	+	
	Pinales			Southern S. America, Malesia to Australia
	Araucariaceae	-	+	and New Zealand
	Cupressaceae	-	+	Northern and southern hemispheres
	Pinaceae	-	+	Northern hemisphere
	Podocarpaceae	-	+	Tropics and subtropics
	Sciadopityaceae	-	+	Japan
	Taxaceae	-	+	Northern hemisphere, scattered in south temperate regions
	Gnetales			Tropics
	Gnetaceae	+	-	
Angiosperms	Nymphaeales			World-wide, rather scattered
	Cabombaceae	+	-	
	Nymphaeaceae	+	-	World-wide
Magnoliids	Piperales			Tropics
	Piperaceae	-	+	
Monocots	Alismatales			Pantropical, also temperate
	Alismataceae	+	-	
	Aponogetonaceae	+	-	Old world tropics
	Araceae	+	+	American tropics, W. Indies
	Pandanales		_	<i>Cyclanthus,</i> Central and tropical South America
	Cyclanthaceae	+		
	Liliales			North Temperate
	Liliaceae	+	-	
	Asparagales			World-wide
	Amaryllidaceae	+	-	
	Asparagaceae	-	+	World-wide
	Asphodelaceae	-	+	Xanthorrhoeoideae; Australia
Commelinids	Arecales			Indomalesia, esp. W. Malesia
	Arecaceae	-	+	
	Zingiberales			Africa, South Asia, Philippines and
	Musaceae	+	-	N. Australia

Groups	Order and families	Laticifer	Resin duct	Distribution
Eudicots	Ranunculales			East Asia, E. North America and South
	Berberidaceae	-	+	America
	Lardizabalaceae	+	-	South East Asia and Chile
	Papaveraceae	+	-	N. Temperate, S. Africa and South America
	Proteales			Temperate, E. North America and E. Asia
	Nelumbonaceae	+	-	
	Platanaceae	-	+	North Temperate, S.E. Asia
Superrosids	Saxifragales			Indomalesia, E. Mediterranean, E Asia,
	Altingiaceae	-	+	S.E. North America, Central America
	Peridiscaceae	+	-	S. America, tropical W. Africa
Fabids	Zygophyllales			Dry and warm temperate, also tropical
	Zygophyllaceae	-	+	
	Celastrales			World-wide
	Celastraceae	+	-	
	Malpighiales			Tropics
	Calophyllaceae	-	+	
	Clusiaceae	-	+	Tropics
	Euphorbiaceae	+	-	Pantropical
	Humiriaceae	-	+	Tropical America, W. Africa
	Malpighiaceae	+	-	Tropics and subtropics
	Salicaceae	+	+	Pantropical, temperate to Arctic
	Fabales			Tropics
	Fabaceae	+	+	
	Rosales			Central Asia, N. temperate zone
	Cannabaceae	+	+	
	Moraceae	+	+	Tropical to warm temperate
	Rhamnaceae	-	+	N. hemisphere to Brazil, S. Africa
	Rosaceae	-	+	Temperate zones and tropical mountains
	Urticaceae	+	_	World-wide, esp. tropical
	Fagales			North Temperate to Andes and S.F. Asia
	Betulaceae	_	+	rrr

Groups	Order and families	Laticifer	Resin duct	Distribution
Malvids	Myrtales			Worldwide, esp. tropical-warm
	Myrtaceae	+	-	temperate
	Sapindales			Tropical, also temperate
	Anacardiaceae	-	+	
	Burseraceae	-	+	Tropics
	Rutaceae	-	+	Largely tropical
	Sapindaceae	+	-	Tropics and subtropics, Australia
	Simaroubaceae	-	+	Largely tropical; a few temperate
	Malvales			Pantropical
	Bixaceae	+	-	
	Cistaceae	_	+	Mediterranean region, N. Africa, N. America, S. South America
	Dipterocarpaceae	-	+	Tropical, esp. Malesia
	Thymelaeaceae	-	+	World-wide, tropical Africa and Australia
	Brassicales			Tropical America and Africa
	Caricaceae	+	-	
	Gyrostemonaceae	-	+	Australia, Tasmania
Superasterids	Santalales			Tropics
	Loranthaceae	+	-	
	Olacaceae	+	-	Pantropical
	Caryophyllales			Mammilaria, America
	Cactaceae	-	+	
	Plumbaginaceae	-	+	Tropical, warm regions
Asterids	Cornales			N. temperate zone, S. America,
	Cornaceae	+	+	Indomalesia
	Nyssaceae	+	-	East Asia, Indo-Malesia and E. North America
	Ericales			Pantropical
	Sapotaceae	+	-	
	Styracaceae	-	+	Warm N. temperate to tropical
Campanulids	Aquifoliales			World-wide
	Aquifoliaceae	+	-	
	Cardiopteridaceae	+	-	Tropics
	Asterales			World-wide
	Asteraceae	+	+	
	Campanulaceae	+	-	World-wide
	Goodeniaceae	-		Australia
	Apiales			World-wide, esp. N. temperate
	Apiaceae	-	+	
	Araliaceae	-	+	Largely tropical, few temperate

Groups	Order and families	Laticifer	Resin duct	Distribution
Lamiids	Gentianales			Largely tropical to warm temperate
	Apocynaceae	+	-	
	Rubiaceae	-	+	World-wide, esp. Madagascar and the Andes
	Solanales			World-wide
	Convolvulaceae	+	-	
	Solanaceae	-	+	World-wide, esp. tropical America
	Boraginales			Largely north (warm) temperate, some
	Boraginaceae	-	+	on mountains in the tropics
	Lamiales			Epithemateae, tropics
	Gesneriaceae	-	+	
	Scrophulariaceae	-	+	World-wide
	Garryales			Central China
	Eucommiaceae	+	-	
	Icacinales			Pantropical
	Icacinaceae	+	-	

Note: + = present; - = absent. The occurrence of laticifers or ducts in only one infra-familial group was highlighted with the taxon in bold. . Survey based on Metcalfe [41], Lewinsohn [42], Langenheim [60], Montes [68] and personal observation. (Occurrence not confirmed was not included. Classification *sensu* APG IV [69].)

Table 1. Occurrence of laticifers and resin ducts in vascular plants according to plant taxa and their distribution.

the evolution of laticifers and resin ducts. This hypothesis is strengthened by the correlation between the evolution of resin ducts and a remarkable chemical diversification of terpenoids [70]. However, this issue is not so simple. Many resinous families do not have resin ducts in all their members, and latescent families rarely possess all their representatives with laticifers. Apocynaceae stand up as an exception in which laticifers are ubiquitous [7, 40] but laticifers have apparently evolved multiple times within other families, such as Sapindaceae [68].

The multiple evolutions of these defensive secretory structures may be associated with a sharp increase in insect herbivory during Paleocene–Eocene [1]. In this epoch, angiosperms became the predominant plant group and coevolved with the insects that fed on these plants and pollinated them [71]. Although the first fossil records of plants with resin ducts were found in pteridosperms from the Carboniferous period of the Paleozoic era [71–74], laticifers were apparently first seen over 250 million years later in the beginning of Cenozoic era [71], when abrupt global warming seems to be related to an increase of both insect diversity and population density [1].

The emergence of laticifers and resin ducts during evolutionary history of vascular plants represents key innovations that have spurred adaptive radiation in plants. Farrell et al. [6] showed that plants that have laticifers or secretory ducts have more advantages in the environment in which they live in relation to those that do not have them or in which these secretory structures



Figure 5. Comparative evolutionary analysis of the distribution of laticifers and resin ducts in vascular plants. All orders containing one latescent or resinous species, at least, were labeled. The data were obtained from the surveys of Metcalfe [41], Lewinsohn [42], Langenheim [60], Montes [68] and personal observation optimized on the current phylogeny [69] using parsimoney analysis.

are reduced, promoting a greater diversity in both the reproductive capacity and individual fitness [7, 39]. This can be observed in the higher occurrence of resin and latescent species in tropical regions, where the herbivory rate is higher [40, 42, 60]. If, on the one hand, tropical environments provide better conditions for plant metabolism in terms of photosynthesis and water availability, on the other hand, they also favor a greater diversity of phytophagous insects and pathogenic fungi [6, 61, 75].

Although specialist insects can feed on some plants that produce latex or resin, generalist ones are highly affected by the properties of these secretions, which are either toxic or deterrent [2, 5, 23]. Strategies to reduce the intake of toxic plant secretions have appeared in multiple insect lineages, allowing to verify the convergent evolution of similar behaviors in several latescent or resinous plants, regardless of the plant morphology or phylogenetic relationships [3, 5, 6, 17, 23, 25, 26, 30, 76–79].

These specialized insects' ability to avoid the ingestion of toxic compounds involves leaf veintrenching, vein-cutting, girdling and leaf clipping strategies, among others, reducing by up to 90% the ingestion of the exudate [17, 23, 30, 79, 80]. It is noteworthy that some specialist insects have developed chemical defenses – such as digestive proteases – against latex compounds [81] and also sequester toxic components from the exudate to reuse them later in their own defense against predators [77].

4. Conclusions

Laticifers and resin ducts have similarities in relation to the secretion, which is mostly terpenic, function as protection against herbivory, present high viscosity and polymerize in contact with the air, and the resin, at times, is white. However, laticifers and ducts are structurally very distinct and have different origins and mode of secretion storage. It is also important to highlight that, since latex is the own protoplast of the laticifer, when it extrudes, there is not only metabolites in the exudate but also membranes, organelles and nuclei. As the resin is an extracellular secretion, these cellular remnants are not present, and when they are found in its composition, it is due to a completely different process related to a holocrine release of the secretion to the lumen.

Since the secretions are confused only when they are white, it should be noted that, although latex is typically white, and resin is typically amber, both secretions may have different colors and may even be colorless or change their color when in contact with the air. The concept of latex is linked to that of the laticifer and to its complex composition, rather than to its color. Thus, if a white secretion is produced by a duct, it must not be considered latex, and the structure cannot be a laticifer. We propose that the term resin be used in a broad sense for the secretions mainly composed of terpenoids (or phenolics in few cases) which are produced by secretory ducts, regardless of their color, as well as the term latex is used for all secretions produced by laticifers, even when it is not milky white.

The evolutionary analysis of both structures shows that they emerge multiple times in the phylogeny, often in the same order, although they are not usually present in the same plants. Our analyses indicate that the appearance of the higher molecular weight terpenoid metabolic route in the ancestral of some major lineages, associated with events of increased herbivory, leads to the emergence of either laticifers or resin ducts in distinct families. In some cases, the presence of both latex and resin within certain families, such as Fabaceae and Asteraceae, certainly conferred greater adaptive success in several environments.

5. Future perspectives

Much remains to be studied about laticifers and ducts. Although their structures have been known for more than a century, and we have clear and objective definitions of them, discrepancies in the descriptions still remain. Divergences about the origin, mode of growth and the lack of information about the chemical composition of latex and resin of several groups still prevent a series of evolutionary analyses that may clarify the factors that determined the emergence of these structures in different groups, especially considering that both appeared multiple times throughout the evolution of plants.

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Conflict of interest

The authors declare no conflict of interest.

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Social and Humanecological Aspects of Ecosystem Services

Ecosystem Service Mapping: A Management-Oriented Approach to Support Environmental Planning Process

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Additional information is available at the end of the chapter

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Abstract

Effective integration of ecosystem services (ESs) into spatial planning and decision-making processes has been advocated as an opportunity to improve current practices and to promote sustainable development. However, the actual uptake of ecosystem services is still challenging, in part due to the complexity of ES studies, data scarcity, and ES compartmentalization, and so on. This chapter presents a case of mapping and characterizing coastal ecosystem services in a way that deals with these issues in order to facilitate its integration in the decision-making and planning process. It gives an insight into which ESs are currently provided in Ria de Aveiro coastal region (Portugal), how are they distributed in space, and identifies multifunctional areas. We argue that the use of existing and available data, as well as tools and approaches that are similar to those used in spatial planning, notwithstanding its limitations, has the potential for bridging science and decision-making spheres. ES-related information could be thus gradually incorporated in the design of local strategies towards sustainable and transparent planning and management processes.

Keywords: social-ecological system, coastal lagoon, mapping, multifunctional areas, multiple ecosystem services, Ria de Aveiro, strategic planning

1. Introduction

Coastal and transitional regions are complex social-ecological systems in the interface of marine, terrestrial, and freshwater environments. They are characterized by providing numerous ecosystem services that contribute to the economic growth and human well-being [1–3] and, consequently, are regions where human presence and activity is especially intense

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[4, 5]. Society's demands and development priorities are constantly shaping ecosystems as well as the services they provide [6]. Climate change, coastal erosion, overfishing, land use/ land cover changes, and point and non-point source pollution are among the pressures that threaten these interface and highly productive systems [5–8].

Even though there is not always agreement in the direction marine and coastal management should take, the need for improvement of convectional management practices is clear and consensual, specifically through the better acknowledge and incorporation of biodiversity, trade-offs, complexity of social-ecological systems, and stakeholders' concerns and expectations [9–11]. Any strategy designed to address these issues and to follow an ecosystem-based management approach requires the understanding of social and ecological processes and their relationships [12, 13].

The ecosystem services (ESs) concept offers a framework for revealing and better understanding the links between ecosystems and human well-being [1, 14, 15], helping to assess how ecosystems benefit humanity and how human actions impact ecosystems and the services they provide [10]. It is argued that together with spatially explicit mapping, ES information has the potential to inform sectoral policies and to enable decision-makers to develop more effective and integrated strategies [16–20].

The assessment of ecosystems and their services is increasingly being undertaken worldwide at a variety of scales: (1) regional and global assessments (e.g. biodiversity and ES assessments carried out by Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)); (2) European (e.g. pilot studies carried out by mapping and assessment of ecosystems and their services (MAES) working group to support the implementation of the EU Biodiversity Strategy to 2020, action 5); (3) national, for example, [21, 22]; and (4) subnational, for example, [14, 23, 24].

Despite the growing body of work, mapping and assessment of marine ecosystems is less advanced than for terrestrial ecosystems. The main reasons pointed out are the lack of high-resolution spatially explicit information for marine ecosystems and incomplete understanding of ecosystem processes and functions in a highly dynamic three-dimensional fluid environment [2, 25, 26]. Moreover, ES studies tend to focus on a small set of ES rather than having a comprehensive overview of social-ecological systems [27]. For instance, regarding coastal and marine ecosystems, food provision (fisheries), water purification, coastal protection, life-cycle maintenance, and climate regulation are the ES most commonly studied [2]. Considering that decisions are frequently interdisciplinary and involve multiple services, a compartmentalized approach might not be enough to inform decision-makers [7, 28]. These aspects, together with the complexity involving ES studies and assessment tools, are among the reasons why ES integration into planning and decision-making processes is still limited, despite the broadly recognized potential for contributing to environmental management [27–29].

This chapter provides a comprehensive analysis and mapping of the multiple ESs currently provided by Ria de Aveiro coastal region (**Figure 1**). The used approach allows overcoming some of the challenges identified earlier and aims to bridge the spheres of ES research and environmental planning. Moreover, it discusses how ES-related information can be further used by planners in the design of local strategies.

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Figure 1. Location of the case study-Ria de Aveiro coastal region-and surrounding municipalities.

The Ria de Aveiro coastal region, located in the northwest coast of Portugal, is used as a case study. It encompasses 19,058 ha of land and 43,527 ha of water, of which 71% are coastal waters. Its landscape is characterized by the presence of the coastal lagoon, plain and open territories, with few vertical elements, extensive areas of agriculture (both open fields and smallholdings), dunes, and pine forests fixing the dunes along the extensive coastline that separates the lagoon from the ocean [30].

2. Which ES are currently provided and where are they delivered?

The approach used to identify and map the ESs provided by Ria de Aveiro coastal region is described in [31]. It uses a set of qualitative indicators as well as various sources and types of information (including data on administrative processes and legal instruments) that indicate the presence of ESs. This approach allows to map a high number of ESs that otherwise would not be possible and contributes to achieving more accurate maps consistent with the case study's reality. Common International Classification of Ecosystem Services (CICES) was the adopted classification system. It follows a hierarchical structure and organizes the ESs in three main categories called 'Sections': provisioning, regulating and maintenance, and cultural services, which are then divided into 'Divisions', 'Groups', and 'Classes'. Even though

CICES V4.3 no longer includes abiotic materials and renewable abiotic energy, abiotic outputs were considered in this study (see [31] for a relation between CICES and the ESs provided by the Ria de Aveiro coastal region).

A total of 11 thematic maps, presented in the following subsections, were produced for Ria de Aveiro coastal region. Depending on the complexity and amount of overlapping ESs classes, each thematic map displays the ESs classes under each CICES's division or group (including abiotic outputs). The aim is to present clear and visually attractive maps, easily understandable by technicians, planners, and other stakeholder groups [31].

2.1. Provisioning services

2.1.1. Nutrition

Regarding nutrition (Figure 2a), over 23% of the study area land is used for crop production, of which 28% is also used for grazing. A large part of this area is called Baixo Vouga Lagunar (BVL) and is characterized by its alluvial plain/soils and three main landscape units such as open fields, wetlands, and *bocage* (a characteristic man-shaped landscape of BVL consisting of smallholdings divided by living hedges and draining ditches, providing shelter for cattle and crops) [32]. Here, the main crop production is soy, beans, corn, wheat, rice, and forage, and there is only an indigenous cattle species: the certified marinhoa breed [32, 33]. Over half of the entire case study area (59%) is used for fisheries. A wide range of fish and shellfish populations of commercial interest are harvested in the coastal lagoon, in the Vouga, Agueda, and Levira rivers, and in the coastal waters. Fishery is a relevant sector for the region in terms of employment, wealth creation, and sociocultural identity [34]. With smaller expressions in terms of covered area but not less important are the marine fish and shellfish production in aquaculture farms and the salt production [35, 36]. The harvesting of wild plants such as common samphire (Salicornia) to be sold as a gourmet product is an emerging activity as well as the production of marine macroalgae (Gracilaria verrucosa, Chondrus crispus, Ulva lactuca, Porphyra spp., Codium tomentosum) in aquaculture for human consumption [37].

2.1.2. Materials

Concerning the materials division (**Figure 2b**), woodland is estimated to cover approximately 5,397 ha, which represents 17% of the land area. During low tide, the solitary tube worm (*Diopatra neapolitana*), the ragworm (*Hediste diversicolor*), and the catworm (*Nephtys hombergii*) are collected in intertidal mudflats to be used as bait for fishing [38–40]. The harvesting of plant material for direct use, processing, or agricultural use was once an important activity in the lagoon: rush marshes were used as animal bedding and afterwards as fertilizer; it was also used as raw materials for mats and for protecting salt mounds from wind and rain; seagrasses and macroalgae were used as fertilizers in agriculture; and reeds were used for traditional products/handcraft such as mats. Currently, the use of seagrasses, reeds, and rush marshes is done in a small scale, mostly for handicraft. Also, a small amount of macroalgae is collected for in situ macroalgae farming. Concerning genetic materials, *marinhoa* cattle, registered as Protected Designation of Origin, is bred in Central region of Portugal,

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Figure 2. Spatial distribution of provisioning services in Ria de Aveiro coastal region. (a. Nutrition; b. Materials; c. Energy).

particularly in the BVL. Surface water is abstracted from the coastal lagoon, lakes, rivers, and ditches for aquaculture and salt production, crops irrigation, livestock consumption, forest-fire control, and industrial use (e.g. pulp and paper industry). Groundwater is abstracted for public supply. Regarding abiotic materials, approximately 54% of the marine area is composed of sand and gravel which can be exploited for artificial beach nourishment [41].

Ria provides the ideal conditions for exploring in situ aquaculture farms of marine fish (e.g. gilthead seabream, *Sparus aurata*; seabass, *Dicentrarchus labrax*; and turbot, *Psetta maxima*) and shellfish (Japanese oyster, *Crassostrea gigas* and clams, *Ruditapes decussatus*) [34, 38].

2.1.3. Energy

Regarding the energy division (**Figure 2c**), the use of *marinhoa* cattle in the agriculture was identified in the case study as animal-based energy.

2.2. Regulation and maintenance services

2.2.1. Mediation of waste, toxics and other nuisances

The microorganisms, algae, plants, and animals that live in Ria de Aveiro and the ecosystem itself have the ability to purify the water and regulate air quality through biochemical and physicochemical processes (e.g. filtration, absorption, decomposition, dilution). These services are grouped in the CICES' division 'mediation of waste, toxics and other nuisances', which covers 97% of the study area (**Figure 3a**). For instance, macrophytes, filter organisms (e.g. oysters, clams, and mussels), and microorganisms have the ability to reduce the availability of nutrients and potentially toxic elements (e.g. metals, organic pollutants) in the sediment and water column through storage/accumulation, biological filtration, and decomposition; salt marshes and seagrass meadows have the ability to promote the retention of pollutants; riparian areas maintain water quality by capturing and filtering water through their soils before it gets to the streams. Rivers, lakes, transitional waters, and the ocean have the capacity to dilute gases, wastewater, and solid waste through bio-physicochemical processes. *Bocage* landscape helps minimize the visual impact and the odor from the pulp mill industry.

2.2.2. Mediation of flows

Of the 'mediation of flows' division, 'buffering and attenuation of mass flows' together with 'mass stabilization and erosion control rates', and 'flood protection' are the most representative ESs classes in terms of the covered area. Overall, vegetation cover helps to stabilize the terrestrial ecosystems and control erosion rates. This service covers approximately 46% of the land (or 23% of the study area) and is mostly provided by vegetated dunes, crucial for its formation and for coastline stabilization; by riparian areas, essential for riverbanks' stabilization; and also by forests and natural grassland. Moreover, dunes, salt marshes, and seagrass meadows help to maintain the lagoon's integrity. In addition, seagrass meadows and salt marshes reduce sediment re-suspension and turbidity in the water column, contributing to increase the light availability in the water column; rivers, lakes, transitional waters, and coastal waters have the ability to transport and store sediment (**Figure 3b**). Concerning the 'mediation of
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Figure 3. Spatial distribution of regulating and maintenance services in Ria de Aveiro coastal region under the divisions 'Mediation of waste, toxics and other nuisances'. (a 'Mediation of flows'; b. Mass flows; c. Liquid flows; d. Gaseous/ air flows).

liquid flows' group (**Figure 3c**), functional geographical units such as salt marshes, sand dunes, *bocage*, riparian, and alluvial forests provide resilience to extreme weather events, act as physical buffering of climate change, and provide protection from floods. For instance, salt marsh vegetation attenuates wave energy; sand dunes provide direct coastal protection; sand beaches dissipate wave energy by absorbing it; and riparian areas and *bocage* have the ability to slow/reduce the water flow. The class 'hydrological cycle and water flow maintenance' was considered to be present/relevant in the areas where evapotranspiration is higher (see [42])—which in this case coincides with *bocage*, woodland, and salt marshes—and in riparian areas, which have the capacity to store water for its future use, maintaining the water flow. Regarding 'mediation of gaseous/air flows' group (**Figure 3d**), the only ES class identified was air ventilation and evapotranspiration enabled by living hedges of *bocage*.

2.2.3. Lifecycle maintenance, habitat, and gene pool protection

The study area provides a wide variety of habitats (**Figure 4a**), some of them classified under Habitats Directive (92/43/CEE). From the diversity of habitats, we highlight the extensive areas of salt marshes (habitats 1310 pt1, 1320, and 1330), intertidal flats (habitats 1140 pt1 and 1140 pt2), estuaries (habitat 1130), salt pans, coastal dunes (habitats 2120, 2130, and 2170), forests (including habitats 91E0pt1, 91E0pt3, and 91F0), *bocage* landscape, rush marshes, reed marshes, rivers, and freshwater lakes ([35, 43], RCM no. 1125-A/2008 of July 21st]. The most representative benthic habitats present in the marine area of the case study are infralittoral fine sand (EUNIS A5.23) and circalittoral fine sand (EUNIS A5.25), which cover 55% and 44% of the total area, respectively [44]. The habitats present in the coastal lagoon and in the BVL are important feeding and breeding areas for a variety of bird species (approximately 175 species), particularly aquatic and migratory bird species ([43], RCM no. 1125-A/2008 of July 21st). Vouga, Levira, and Águeda rivers are important spawning grounds for anadromous migratory species (as *Petromyzon marinus* Linnaeus, *Alosa alosa*, and *Alosa fallax*) and *Lampetra planeri*. Infralittoral and circalittoral fine sand provide feeding and nursery grounds for several commercially exploited species [43].

Hedgerows, within *bocage* landscape, and woodlands along agricultural fields, support a wide range of pollinators. Therefore, its spatial distribution was used as an indicator of the presence of pollination and seed dispersal services.

2.2.4. Soil formation and composition

Soil composition (**Figure 4b**) is maintained by intertidal mudflats, seagrass meadows, and saltmarshes that play an important role in the nitrogen cycling (nitrogen fixing, denitrification, decomposition) and by terrestrial ecosystems such as woodlands, natural grasslands and some crops (e.g. corn, rice) that contribute to the maintenance of bio-geochemical conditions of soils by decomposition/mineralization of dead organic material, nitrification, and denitrification.

Weathering processes have less expression, being present where fluvisols and woodlands or floodplains overlap.

2.2.5. Atmospheric composition and regulation

Atmospheric carbon is sequestrated by, and stored in, ocean through oceanic algae, woodlands, and macrophytes (e.g. salt marshes, seagrass meadows). These habitats contribute to the global climate regulation by reducing greenhouse gas concentration (**Figure 4c**). Micro and regional climate is regulated not only by green infrastructures but also by blue infrastructures (through abiotic processes), which contribute to the control of atmospheric conditions. For



Figure 4. Spatial distribution of regulating and maintenance services in Ria de Aveiro coastal region under the division 'Maintenance of physical, chemical, biological conditions'. (a. Lifecycle maintenance, habitat and gene pool protection; b. Soil formation and composition; c. Atmospheric composition and regulation).

instance, *bocage* constitutes a barrier to the wind; freshwater ecosystems can moderate extreme temperature; and wetlands, due to higher evaporation, can increase relative humidity [45].

2.3. Cultural services

2.3.1. Physical and intellectual interactions

Cultural services provided by the region of Ria de Aveiro are extensive from both physical and intellectual points of view (Figure 5). For instance, natural and semi-natural beaches, salt pans, quays, public gardens along rivers and lakes, city channels, Ria's islands, São Jacinto dunes Nature Reserve, and BVL are some places favored for landscape appreciation and birdwatching. Maritime and fluvial beaches are ideal for swimming; pathways along lagoon's margins, lakes, rivers, and ditches are used for walking and cycling; watercourses are used for sailing, canoeing, rowing, surfing, kitesurfing, paddling, and also for angling. The marine and coastal area, the Ria de Aveiro and the Vouga river basin, are subject matter for scientific research as well as a source for education through environmental interpretative centers and museums. Areas such as archeological sites (e.g. shipwrecks, ship hull); traditional fisherman and salt workers neighborhoods (e.g. Beira-Mar); traditional architecture (e.g. Palheiros in Costa Nova); and the traditional activities related with the lagoon and the sea (e.g. Arte Xávega—an ancient fishing gear; salt production; seagrass, and rush collecting) have significant cultural and heritage value. The ecosystems and biodiversity are also enjoyed/appreciated ex situ through festivals (e.g. gastronomic fairs, Vagueira surf festival, Ria de Aveiro Weekend, ObservaRia-Birdwatching fair, moliceiro festival, N.ª S.ª dos Navegantes religious festival); provide artistic inspiration for writers and painters; and provide sense of place and identity.

2.4. Multifunctional areas

In order to gain an understanding of the multifunctional areas, that is, areas that have the ability to provide more than a single ES, the spatial results from individual ES classes were analyzed together. In the ArcGIS 10.0, a sequence of geoprocessing tools was performed in order to overlay the individual ES classes from the thematic maps and count the overlapping polygons, lines, and/or points. This resulted in: (1) three-section maps (one map for each CICES' section) representing the multifunctional areas with different overlapping degrees (**Figure 6a–c**) and (2) a synthesis map combining the ES classes from all CICES' sections (**Figure 6d**).

Regarding provisioning services (**Figure 6a**), 12 of 16 ES CICES' classes and 2 of 6 abiotic outputs were identified and mapped. *Bocage* landscape has the higher number of multiple provisioning services, combining four ES classes such as cultivated crops, reared animals and their outputs, genetic materials from all biota, and animal-based energy.

From the 21 ES CICES' classes plus 3 abiotic outputs under the regulating and maintenance section, 20 were identified and 16 (including one abiotic output) were mapped (**Figure 6b**). The number of overlaying ES classes ranged from a minimum of 2 to a maximum of 11. The results show that *bocage* landscape, riparian forests, *Zostera noltei* beds, salt marshes, forests and alluvial forests, coastal waters, transitional waters, forested dunes, and freshwater habitats are associated with a high number of regulating and maintenance classes (over six ES classes).

Concerning cultural services, 9 of the 11 ES CICES' classes were identified and 7 were mapped (**Figure 6c**). The higher number of cultural services is mostly present in the water courses, walking, and cycling pathways in the BVL as well as in the Aveiro city's channels.



Figure 5. Spatial distribution of cultural services in Ria de Aveiro coastal region.

The synthesis map (**Figure 6d**) reveals that a significant part of the case study (approximately 80%) has the ability to provide a high number of ES (seven or more ES classes identified and mapped). *Bocage, Zostera noltei* beds, riparian areas, salt marshes, coastal waters, and freshwater lakes are among the ecosystems present in the case study that provide the higher number of ES, namely maintaining good water quality, reducing patterns of erosion, flood protection,



Figure 6. Multifunctional areas by ES section: (a) provisioning, (b) regulating and maintenance, (c) cultural; and a synthesis map combining all the ES classes (d).

maintaining nursery populations and habitats, landscape and scenic quality, recreation, education, and research.

3. Discussion

In this research, an effort was made to bridge science and decision-making, more specifically ES research and environmental planning processes. Therefore, it used existing and available data, as well as mainstream software with the aim of enabling the uptake of the produced information, as well as the approach itself, by spatial planners and technicians. Additionally, it provided:

- an integrated and comprehensive view of the ecosystems services present in the case study, that is, acknowledged the diversity of ecosystems, uses, and activities, and sought to identify and map a wide range of ESs and abiotic outputs rather than focusing on a single or a small set of ESs;
- spatially explicit information relevant to the spatial scale at which decisions regarding the management of social-ecological systems are made;
- an approach that deals with the lack of quantitative and systematic data, particularly at the land use/land cover level.

Being an interface system, Ria de Aveiro coastal region holds a diversity of ecosystems: from marine to seagrass meadows, saltmarshes, freshwater, extensive areas of agriculture, and so on. This brought out the differences in quality, scale, and accuracy of the available data. Marine and coastal lagoon ecosystems, and related uses and activities, have considerably less public and available information, with lower spatial detail than terrestrial ones. Availability of quantitative and systematic data at the ecosystem or land use/cover level rather than administrative is scarce, posing a constraint in the assessment of certain ESs at this scale of analysis.

We argue that ES characterization and mapping, as well as the identification of multifunctional areas, is only the beginning of the integration of ES in the environmental planning process. The analysis and diagnosis of a social-ecological system—which most often correspond to the first stages of any spatial planning process—should incorporate other layers of information, for instance, identify the main pressures resulting from human activities, management options, and/or climate change threatening multifunctional areas and identify their impacts on ecosystems and on their ability to provide ESs, as well as the effects on human well-being. This type of analysis is considered valuable to inform the design of local strategies to adapt communities to current and future challenges; to minimize the impact of pressures on the ecosystems; to identify priority areas for intervention; and to guide public investment. The incorporation of stakeholders' perceptions on significant ESs and concerns regarding the main pressures is also seen as an opportunity to improve the degree of policy and social relevance of the analysis, as it helps meeting the real needs of local population and potentially improving the acceptability of future decisions by communities.

4. Conclusion

The process of identifying multiple services delivered by coastal ecosystems together with their spatial representation, even without any subsequent valuation, is crucial for informing environmental planning process and decision-making. Notwithstanding its limitations, the applied framework proved to be valuable in providing relevant information on ES provision and spatial distribution. We consider that the use of tools and approaches that are familiar to planners or similar to those habitually used is an opportunity for bridging these two spheres and promoting ES integration in planning and decision processes. This must be an adaptive process so it can assimilate new information as methods become standardized or technical capacity is developed.

The authors argue that ES maps and characterization should be used as a foundation—along with other layers of information typically analyzed in the first stages of the spatial planning process—in the design of strategies for socioeconomic development and nature conservation, either at terrestrial or marine ecosystems. Moreover, the combined analysis of ES distribution (including multifunctional areas) and the most vulnerable areas to certain pressures has the potential to better inform planners in the design of local strategies, promoting a more transparent decision, and planning processes.

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Conflict of interest

The authors declare no competing financial interests.

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The Role of Ecosystem Services in Community Well-Being

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Abstract

Natural ecosystems provide services to humans that make life possible. Life, as well as the economy, is dependent upon these ecosystem goods and services (EGS). These services also contribute to a "good" or "quality life" by influencing the well-being of individuals and communities. Understanding the relationships among EGS that contribute to and shape well-being is an important task for researchers, decision makers and policy makers. In the past, these relationships were almost completely dependent upon income and consumption of goods. Today, the relationships are based on a more holistic perception including environmental and social attributes. The importance of ecosystem services to community well-being and their interactions are described through examples of communities' perceptions of the importance of various attributes of well-being and the role of ecosystem services in defining public health.

Keywords: ecosystem services, human well-being, indicators, community

1. Introduction

Natural ecosystems provide innumerable services which make human civilization possible. Unfortunately, many, if not most, people believe these services are provided for free and are, therefore, valueless and have no direct traditional economic value [1–3]. We, as a community, may not pay directly for these ecosystem services but we do pay significantly for their loss through infrastructure and policy costs (e.g., construction and operation of wastewater treatment facilities, increased illness, losses in soil fertility and reductions in basic human wellbeing). Everyday decisions made by communities and their constituents have some effect on

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the amount and quality of these services. We, as a scientific community and members of larger governance communities, must emphasize the interrelated aspects of human well-being and the functioning of ecosystems (i.e., natural and human-altered) [1].

Life, as well as the economy, is dependent upon goods and services provided by natural ecosystems [2]. One of society's greatest challenges is to maintain natural ecosystems while promoting economic growth and the quality of life [3]. Ecosystem services like cleansing, renewal and recycling coupled with ecosystem goods like food and fiber, timber, and esthetics have significant tangible and intangible value. Yet, in the name of economic growth, humans stress the environment by disrupting its natural functioning and provision of these basic services in oceans and fisheries [4], wetland resources [5], habitat loss and trophic collapse [6], pollinator declines [7], soil quality and agricultural production [8]. We have changed ecosystems massively in the last several decades [2] in order to meet growing demands for freshwater, food, and fuel (to name but a few commodities). While these changes have clearly supported the needs of billions of people, the changes have caused irreparable losses in ecosystem structure and function (e.g., diversity loss, ecosystem capacity for service generation) as well as our perceptions of place, comfort and well-being [9–11].

Over the decades described above, well-being research has received increased attention as a contributor to "good" or "quality life" [12–20]. Unfortunately, researchers' determinations of what constitutes well-being have largely been ignored by decision makers and governments [21]. While well-being indices are often linked to social and economic policies (with the intent of progress), environmental drivers, particularly ecosystem services, are not included in these human well-being measures despite the proven role that the environment and ecosystem services play in the quality of well-being [22–25]. Examining ecosystem goods and services in relation to sustainability and their contributions to social, economic and environmental well-being [11]. In short, regardless of economic utility theory [26, 27] ecosystem goods and services can only be partially "monetized" and a consideration of well-being is necessary to determine a full valuation.

There is no single definition of human well-being but, at a generalized level, it is useful to distinguish between the dimensions of subjective and objective well-being. Broadly, objective well-being includes basic social, economic and environmental needs and can be directly measured [28, 29], while subjective well-being encompasses often what humans feel and think [30]. Well-being, whether individual or group (community), must be treated as a multidimensional aspect focusing on circumstances that can be both objectively and subjectively assessed [31]. This approach requires that elements of emotions, engagement, and satisfaction as well as economics, environmental and social issues be incorporated into our vision of well-being.

The interaction of ecosystem services and community well-being includes the relationship of these topics to global issues as well. Alterations in climate (on large and small temporal scales), biodiversity and general sustainability affect both services and well-being. Community resilience to acute meteorological events [32] represents a major issue involving ecological services, overall well-being and community sustainability. Natural disasters, as well as investments in natural disaster protection, impose significant and long-lasting stress on financial, social and ecological systems that drive human well-being. From hurricanes to tornadoes to wildfires, no corner of the globe is immune from the threat of a devastating climate-event. Across the globe, there is a recognition that the benefits of creating and supporting environments (built and natural) resilient to adverse climate events helps promote and sustain community well-being over time. The challenge for communities is in finding ways to balance the need to preserve the socio-ecological systems on which they depend in the face of constantly changing natural hazard threats. The Climate Resilience Screening Index (CRSI) [32, 33] is an endpoint for characterizing resilience outcomes that are based on risk profiles and responsive to changes in governance, societal, built and natural system characteristics. The Climate Resilience Screening Index (CRSI) framework serves as a conceptual roadmap showing how acute climate events impact resilience after factoring in the community characteristics. By evaluating the factors that influence vulnerability and recoverability, an estimation of resilience can quantify how changes in these characteristics will impact resilience given specific hazard profiles. Ultimately, this knowledge will help communities identify potential areas to target for increasing resilience to acute climate events and enhancing their sustainability. Other services, such as green infrastructure, can similarly contribute to climate adaptation at a variety of spatial scales [34].

Changes in biodiversity can also affect community well-being by altering the complexity and resilience of natural ecosystems and changing their long-term sustainability. Sustainable development equally includes environmental protection including biodiversity, economic growth and social equity, both within and between generations [35–37]. Reductions in biodiversity and habitat fragmentation decrease gene flow, increase genetic drift and the potential for inbreeding and increase the probability of patch extinction [38]. Unfortunately, the relationship between ecosystem services and biodiversity is often confusing resulting in damaged efforts to create coherent policy formulation [38]. Biodiversity has key roles as a regulator of ecosystem processes, as a major ecosystem service and as an ecosystem good that could be subject to valuation (economic or otherwise). As a result of this potential for valuation in policy formulation, this service can easily impact planning for sustainable community well-being.

2. Characterizing well-being in the context of service flows

Understanding the relationships among ecosystem goods and services that contribute to and shape well-being is a core task for both researchers and policy makers. Our understanding of this relationship has evolved over the last several decades from being synonymous with income and consumption of marketed goods [39, 40] to a broader view incorporating non-economic issues like gender [41, 42], sustainability [43–45], and the environment [44, 46]. Given this evolution of thought, it is amazing that many still view the most reliable measure of human well-being to be income [47]. Yet, the importance of ecosystem services as a driver for well-being has been well established in the Millennium Ecosystem Assessment [23]. The World Economic Forum's [48] environmental sustainability index, Wackernagel's et al.'s [49] national estimates of ecological footprints, and the New Economics Foundation report [50]

all emphasize the importance of the role of environmental factors (e.g., ecosystem goods and services) in the establishment of well-being.

Much of the drive to include ecological information in the estimation of well-being derived from ongoing discussions of whether humans are a part of an ecosystem rather than simply a stressor on ecosystems [51]. This approach termed Ecosophy T is a view of the central role of ecosystems and states that every being, whether human, animal or plant has an equal right to live and prosper [51]. This holistic emphasis requires that the self-realized Ecological Self should not act without understanding how that action will affect other living beings. An understanding of the unintended consequences of actions is the equivalent of the liberal harm principle [52, 53]. To go from an understanding of unintended environmental consequences (i.e., humans as stressors) to an inclusion of ecosystems and ecological understanding in well-being (i.e., humans as part of ecosystems) is a logical and fairly straightforward thought process.

The HWBI framework illustrates the relationship between service flows provided through social, economic and environmental sectors and the domains of HWBI (**Figure 1**). Collectively, the components of HWBI are similar to Maslow's pyramid of self-actualization [54] where basic human needs represent physiological and safety needs; economic needs represent employment, education, wealth, infrastructure, growth and trade; environmental needs represent clean air and water, and low risks of contamination; and, subjective happiness needs represent life satisfaction, freedom, solastalgia [55], topophilia [56], and biophilia [57]. The Human Well-being Index (HWBI) is intended to be used as an endpoint measure responsive to changes in service flows from natural, human and built capital [18].

HWBI was developed as a composite measure based on eight dimensions of well-being (domains) characterized by 20 multi-metric indicators reflecting both objective and subjective measures [18, 58]. The HWBI domains are sub-indices that serve as proxy measures representing various aspects of human well-being (**Table 1**) which are aggregated into the composite index. In a nutshell, The HWBI calculation follows these four steps as summarized by Harwell et al. [59]:

- Indicator scores are calculated as population weighted averages of related standardized metric values.
- Domain scores are obtained by averaging indicator scores related to a specific domain.
- Relative importance values (RIVs) are optional factors that may be included in HWBI calculations to represent stakeholder priorities associated with well-being domains.
- The HWBI is calculated as the geometric mean of equally or unequally weighted domain scores.

Substitutions at the metric level in the HWBI allow for the index to be adapted to include data that more closely reflect characteristics in specific use case applications (e.g., geographical locations or population groups) while maintaining the integrity of the index at the indicator level [59–61].

The HWBI framework is designed to reflect stakeholder viewpoints regarding the relative importance of each of the eight domains. Since the domains are relevant to characterizing

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Figure 1. Conceptual model of the human well-being index (from [19, 20]). Model links goods and services (ecosystems, social, and economic) with the eight domains of well-being through relationship functions.

human well-being, regardless of time, space and culture [18], communities can easily "relate" to these well-being dimensions, making prioritization a fairly straight-forward exercise in developing relative importance values (RIVs) as weighting factors to customize HWBI. Applications of stakeholder RIVs utilized in a real community case studies are presented in Fulford et al. [62]. The foundational research in the development of HWBI [11, 25, 63, 64] has also been used to inform community-based landscape planning via the valuation ecosystem services [64].

Domain	Description				
Connection to nature	Describes how people feel about nature. It is measured by people's perception of nature and how it affects them.				
Cultural fulfillment	Describes people's cultural involvement. Measures include how often people participate in the arts and spiritual activities.				
Education	Covers basic skills in reading, math and science. Measures of student safety and health are also included.				
Health	Characterizes people's involvement in healthy behaviors, prevalence of illness, access to healthcare, mortality and life expectancy.				
Leisure time	Describes how time is spent including: employment, care for seniors and activities that people partake in for personal enjoyment. Measures represent work-life balance.				
Living standards	Contains information about lifestyles. It includes measures of basic necessities, wealth and income.				
Safety and security	Covers information about perceived safety, actual safety and potential for danger.				
Social cohesion	Describes people's connection to each other and their community through measures of involvement in family, civic engagement, and the community as a whole.				

Table 1. Description of domains used in the HWBI.

Additionally, ecosystem services have been linked to community well-being priorities based on HWBI domains for the purpose of setting conservation targets for coastal ecosystems to deliver ecosystem and human benefits [65].

3. Linking services to well-being

The HWBI framework demonstrates that ecosystem, economic and social services can be linked to the domains of well-being by relationship functions (**Figure 1**). Summers et al. [66] demonstrated that relationship functions can be derived between services information and well-being domain information at the county level. Similarly, relationships exist among indicators and metrics of well-being domains that were used to develop the ecosystem, economic and social services/well-being relationships (**Table 2**). Achieving balanced decisions requires techniques to examine the potential consequences (both intended and unintended; both positive and negative) on well-being associated with changing services. Summers et al. [66] used an approach for forecasting that employs (1) models derived from ecological, social and economic production functions (e.g., [67, 68]) and (2) models examining how communities feel about decision outcomes [69, 70]. Such models require a framework for linking changes in service production to changes in well-being.

The functional equations for each well-being domain were determined through the use of bidirectional step-wise regression [71]. This process identified main effects and primary pairwise interactions of service indicators and identified predictive variables based on adjusted R^2 and sequenced F-tests [72]. The forecasts for each year in all counties of all states were

Types of capital	Community goods and services	Domains of well-being
Social	Re-distribution (Ec)	Connection to nature
Natural	Production (Ec)	Cultural fulfillment
Human	Innovation (Ec)	Social cohesion
Built	Finance (Ec)	Safety and security
	Employment (Ec)	Living standards
	Consumption (Ec)	Education
	Capital investment (Ec)	Health
	Air quality (E)	Leisure time
	Food, fiber and fuel provisioning (E)	
	Greenspace (E)	
	Water quality (E)	
	Water quality (E)	
	Public works (S)	
	Labor (S)	
	Justice (S)	
	Healthcare (S)	
	Family services (S)	
	Emergency preparedness (S)	
	Education (S)	
	Community and faith-based initiatives (S)	
	Communication (S)	
	Activism (S)	

Table 2. Types of capital, community good and services, and well-being domains used to construct forecasting models [66].

compared to actual data for model fit and construction (7 of 10 available years) with 3 years of data withheld for validation. In addition, simple Pearson product-moment correlation coefficients were determined among the eight well-being domains to address likely co-occurrences of changes in multiple domains.

The results of these evaluations are documented in Summers et al. [66] regarding forecast inclusion of service indicators, model fit and validation, and scenario building using the forecasting tools. Overall examples of the forecasting applications are depicted in **Figure 2** where observed and predicted are shown for the 3 years of withheld data for all 50 states (3 years of data not used in construction). Similarly, the strong inter-correlations among well-being domains are shown in **Table 3**. The use of the forecasting regressions in concert with the



Figure 2. Comparison of observed and predicted values from forecast models for well-being based on ecosystem. Economic and social services (from [66]).

	D1	D2	D3	D4	D5	D6	D7	D8
D1	-	-0.581*	-0.616*	-0.392*	0.075	-0.438*	-0.499*	-0.703*
D2		-	0.415*	0.407*	-0.088	0.334*	0.326*	0.346*
D3			-	0.642*	0.004	0.120	0.605*	0.407*
D4				-	0.157	0.202	0.680*	0.159
D5					-	-0.199*	-0.017	-0.206
D6						-	0.355*	0.104
D7							-	0.387*
D8								-

D1 = Connection to nature; D2 = Cultural fulfillment; D3 = Education; D4 = Health; D5 = Leisure time; D6 = Living standards; D7 = Safety and security; D8 = Social cohesion.

Table 3. Correlations (Pearson product moment) among human well-being domains (* = p < 0.0001; N = 561) (from [66]).

inter-domain correlation permits the evaluation of intended and unintended consequences of specific decisions to augment services or potentially improve well-being domains and overall well-being.

4. Differences in well-being by respondent or community type

Effective measures of human well-being can be useful to decision making at the community level. Community decision-making is based on a shared commitment to achieving realizable improvements in family, child and neighborhood conditions in order to build accountability and capacity to achieve those results. This type of decision-making achieves the best results when it:

- Uses timely, relevant and reliable data
- Authentically involves community stakeholders
- Assists communities in establishing and monitoring progress toward objectives
- Develop a community agenda for investment
- Assesses accurately community resources and assets
- Accurately reflect community priorities
- Engages multiple networks to support well-being
- Reports regularly to stakeholders.

These attributes can be accomplished through effective engagement with community stakeholders. Stakeholder engagement is a necessary process of evaluation because effective use of the HWBI as an assessment tool requires information on the relative importance of the domains of HWBI for any given community (i.e., their community value structure), as well as the baseline value of well-being against which we can measure change.

Using the Relative Valuation of Multiple Ecosystem Services method (RESVI), Jordan et al. [3] queried three respondent groups to determine their overall value judgments related to various ecosystem services. The RESVI method uses an assessment where respondents are (1) briefed about policy questions to be examined with regard to the extent and nature of the ecosystem(s) and services involved, (2) asked to assign relative values to a list of ecosystem services in terms of what proportional dollar value for one service versus another, (3) application of a dollar value based on literature or research for each service type, and (4) creation of an index for all services using reference and relative values determined by the respondents.

The RESVI was used with three respondent groups – programmatic regulators, research scientists, and community stakeholders. The results compared the relative values of eight ecosystem services (**Figure 3**) – habitat functions, water quality regulation, water supply, recreation, flood control, esthetics, biodiversity and climate regulation. The test groups valued



Figure 3. Overall mean relative values for three respondent groups using to RESVI to ascertain relative values of ecosystem services (from [3]).

habitat functions and water quality regulation more than the other ecosystem services by a wide margin. However, some differences were observed among the respondent types with regard to their valuation systems. Regulators tended to more heavily value regulatory services while researchers tended to place higher values on ecosystems functions. Finally, general community stakeholders tended to value services that impacted landscapes.

Similarly, Fulford et al. [62] found that different community types could reflect different attitudes with regard to the relative importance of domains of well-being and the services that drive that well-being. There is an increasing understanding that decisions made by local communities can have significant impacts on community well-being and require a degree of understanding regarding local impact as well as cumulative impact across multiple communities [73–76]. All communities have unique characteristics resulting in the potential for varying views regarding the importance of different ecosystem services as well as the components of well-being. Similarly, different communities can have beliefs and value systems in common. Using a community typology approach, Fulford et al. [62] developed a system to inform decision makers about sustainable decision outcomes based on the similarities and differences of communities' priorities, belief systems, and values. Communities can be divided into one of

eight types, which differ both in their baseline HWBI scores and in the relative importance of the different domains of HWBI (**Figure 4**). The developed approach aids communities by defining meaningful changes in well-being across similar communities through the establishment of reference points that can provide information regarding investment in activities like conservation, restoration of natural capital and mitigation [77–79].

The holistic suite of indicators used in the Human Well-Being Index (HWBI) represent a synergistic measure of the outcome of ecosystem good and services production and delivery [11, 19, 25]. However, measures of well-being and their constituents (e.g., civic engagement, social cohesion, connection to nature) are not always easily understood and are not a direct measure of the delivery of services. The key at a community level is linking these broader well-being measures to community-specific desires and values. Fulford et al. [62] took a comparative approach toward well-being points of references based on an ecosystem goods and servicesbased community topology and Bayesian model-based cluster analysis [80] The HWBI was compared among community cluster groups to detect patterns in well-being as a function of the ecosystem goods and services community types (Figure 4). The key differences among community groups were population density and composition, economic dependence on local resources (e.g., forestry, fishing, agriculture), and to some extent geography. Differences among coastal county groupings indicated both strong and weak similarities resulting in three major clusters among the eight topological types (Figure 5). Fulford et al. [62] determined that community decision makers could use the classification system to identify well-being values from which to gauge impact of decisions that could shift well-being.



Figure 4. Analytical comparison of human well-being among categorical groups of U.S. coastal counties based on a multivariate community topology (dashed arrows = data dependency; solid arrows = outcomes) (adapted from [62]).



Figure 5. Map showing example of Gulf of Mexico coastal counties separated into eight classification types and bar chart indicating differences in unweighted HWBI composite scores average (SE) by classification group. See [62] for more information on HWBI calculations and group delineations. Community types are represented by 1 = Urban/Suburban, 2 = Rural manufacturing, 3 = Rural farms, 4 = Rural high ethnic diversity, 5 = Rural balance of natural resource dependence and manufacturing, 6 = Rural dependence on natural resources, 7 = Older suburban, 8 = Suburban industrial.

Similarly, Fulford et al. [81] used a keyword-based approach to determine common terminology used by 97 counties in three regions of the U.S. (Gulf of Mexico, western Great Lakes and Northwest) to refer to community fundamental objectives closely aligned with the domains of HWBI. They analyzed strategic planning documents using the eight domains of human wellbeing described by Summers et al. [19] and listed in **Table 2**. Living Standards and Safety and Security were the most common well-being domains referred to in community strategic plans. Health and Cultural Fulfillment were the least commonly addressed domains in these documents. Major community type (same typology as used in Fulford et al. [62] differences were largely between urban and rural areas with urban community types focusing on Living Standards and Education while rural communities tended toward Leisure Time and Social Cohesion.

5. Examples of linking ecosystem services to well-being and public health

Ecosystem goods and services (EGS) are the result of processes that can contribute to social welfare [82]. Social welfare can easily be translated into elements of human well-being as defined by Summers et al. [19, 20]; particularly, health, social cohesion and cultural fulfillment. Over 50 recent reviews relating human health and ecosystem services [83] showcase the focus of connecting ecosystem goods and services (EGS) with this aspect of well-being. However, fewer studies exist directly linking physical or mental health to natural systems via ecosystem goods and services, tracing the full pathways from ecosystem structure and function to EGS to health [83]. One recent review uses causal criteria analysis (CCA) to link health and EGS [1, 84].

Causal criteria analysis was developed in epidemiology to support health decision making often based on weak but independent information [85, 86]. One study [84] conducted a CCA focusing on the effects of EGS provided by greenspaces on human disease (Figure 6). Green spaces included any vegetation with an environment dominated by humans [87] - urban trees, wetlands, and green roofs. The health endpoints included gastro-intestinal disease, respiratory illness, cardiovascular disease, and heat morbidity. Simply put, green spaces can abate floods and storm surge hazards by reducing runoff through natural percolation or physically limiting the influence of waves and storm surge [88]. This type of mitigation can lower human exposure to contaminated flood waters potentially reducing gastrointestinal diseases and reducing conditions that can lead to asthma through mold growth [89]. Green spaces potentially remove toxicants, reduce the prevalence of gastrointestinal disease, trap contaminants and mitigate extreme temperatures [90–94]. CCA results showed sufficient evidence for causality for all tested greenspace-EGS pairings (heat hazard mitigation, clean air, water hazard mitigation and clean water), three of six EGS-health pairings (heat hazard-heat morbidities, water hazard mitigation-gastrointestinal disease and clean water-gastrointestinal disease) and two of four direct greenspace-health pairings (heat morbidities and cardiovascular disease). This work indicates that most current literature supports intermediate pathway connections between ecosystems and ecosystem goods and services as well as ecosystem goods and services and health. However, very few studies support a direct connection between the presence of ecosystems and health outcomes. Of those studies that exist, few simultaneously measure the mediation by ecosystem goods and services (Figure 6).

As a specific example, ongoing studies in the San Juan Bay Estuary, Puerto Rico are evaluating the role of wetlands on Dengue fever by means of ecosystem services (e.g., biological control, clean water, and heat hazard mitigation) [95] (**Figure 7**). Ecosystem goods and services associated with heat hazard mitigation may help reduce mosquito biting, oviposition rate, and viral load. Clean surface water provides habitat for wildlife and healthier ecosystems, favoring bio-control of mosquitoes [96–99]. Preliminary findings suggest that wetlands and wetland services are negatively associated with Dengue cases even after controlling for potentially confounding variables (**Figure 8**). Wetlands and wetland services were also found to help reduce temperature which is an environmental driver of Dengue transmission [98]. These findings help support a connection between an important ecosystem in the San Juan Bay area,



Figure 6. Proposed linkages between green spaces, the ecosystem services provided by green spaces and human health conditions (from [84]). EGS = Ecosystem goods and services, CVD = Cardiovascular disease, GI = Gastrointestinal, A = Intermediate steps linking green space and EGS, B = Evidence linking green space directly to human health outcomes.



Figure 7. Hypothesized conceptual model of wetlands and Dengue fever occurrence through wetland ecosystem services (adapted from [95]).



Figure 8. Predicted relationship between two wetland types ((A) grassy and (B) woody) and dengue cases in San Juan, Puerto Rico (Figure adapted from [95]).

and an ecosystem service that directly influences human health. In the future, this and other eco-health research may help inform predictive models to estimate changes in health benefits under different decision scenarios.

6. Conclusions

Many obstacles exist in developing useful and informative relationships between ecosystem services and community well-being including cultural differences in the perception of ecosystem services and well-being, lack of consistently available data to demonstrate a causal connection between services and well-being. This is often the case when combining natural sciences and social sciences data, approaches and interpretations. Even within these disciplines, the integration of data representing indicators to create indices or demonstrate connections is highly contentious. Some policy makers suggest that summary tools (e.g., models, indices, statistical assessments) lack meaningful interpretation and have little value in the real world [100, 101]. Others argue that the time is ripe for pushing these concepts into public policy – that the real world is a complex interaction of social, economic, and environmental activities where focus on

single issues is insufficient to represent reality [102–104]. No matter who we are, or where we live, our well-being depends on the way ecosystems function. Defining, classifying and integrating ecosystem services into community decision making [105, 106] and, hence, community well-being is necessary for a holistic policy view that minimizes unintended consequences [66].

The research described in this chapter provides a management roadmap for linking ecosystem services to human wellbeing, but significant work still needs to be accomplished. The complexity of the relationship between ecosystem services and community well-being signifies an urgent need to develop further the transdisciplinary science of ecosystem management bringing together ecologists, biologists, resource economists, social scientists, and holistic systems specialists. A primary goal of this transdisciplinary research is the development of a valuation system potentially based on well-being and well-being improvement through the provision of goods and service A focus on the underpinning processes is necessary to understand where there are trade-offs and synergies and how these outcomes change with environmental variation. All members of the transdisciplinary team described above need to build a stronger science for stocks and flows, link this work to natural capital studies and create a stronger socio-ecological science that reflects the fact that ecosystems are coupled human-environmental systems.

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Urban and Industrial Habitats: How Important They Are for Ecosystem Services

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Abstract

The sustainable management of natural resources can make human survival possible. Sustainable management is based on a deep understanding of the complex mechanisms of the Earth's natural ecosystems and of how those resources can be managed without compromising future benefits and availability. The sustainable management of natural resources becomes much more complicated when there is severe and constant anthropogenic impact, and therefore, an interdisciplinary approach has to be undertaken to improve the understanding, assessment, and maintenance of the natural capital, and the related ecosystem services, in urban-industrial areas. In ecological restoration, the biggest challenge is to find a general consensus of suitable biodiversity indicators and economically viable measures, which will produce multiple socially and ecologically guided environmental benefits. There is difficulty in reaching such consensus because of the complexity, and differing understanding, of the biodiversity concept. In an effort to restore sites disturbed by industrial (mining) activities, restoration projects should involve ecologically based methods and approaches, which will be able to fulfill many stakeholders' expectations for sustainable development and human well-being. The integrated natural and human models for sustainable management can used to understand the dynamics of ecosystems, including biodiversity and trophic levels (including midtrophic consumer influences), in order to simulate and evaluate different management scenarios in relation to biodiversity and ecosystem services. There is still a need for the increasing understanding of the role of biodiversity and ecosystem service identification as important factors influencing the dynamics of ecosystem and sustainable management scenarios.

Keywords: biodiversity, ecosystem functioning, natural capital, urban-industrial areas, ecosystem services, interdisciplinary approach, sustainable management scenarios

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1. Introduction

Human existence is dependent on nature [1]. The sustainable management of natural resources, based on a deep understanding of the complex mechanisms of the Earth's natural ecosystems, can make human survival possible [2]. These mechanisms become much more complicated when there is severe and constant anthropogenic impact, and therefore, an interdisciplinary approach has to be undertaken to improve the understanding, assessment, and maintenance of ecosystem services in urban-industrial areas.

In the twentieth century, it is argued that the Earth has entered the Anthropocene epoch [3]. It is in this epoch that human influence has become the dominant driver of changes to the global Earth systems [3]. The main characteristic of the Anthropocene epoch is that human influences are shifting the natural conditions beyond their limits, and beyond the natural conditions, humans need for their own existence [4]. Everard [5] states that we have to co-create a symbiotic future of natural forces (soil, water, air, and living organisms) with human forces (innovations, development, and human well-being) [6].

When discussing ecosystem services, it is important to consider natural capital as the key provider of natural assets from which ecosystem services are derived. Often the terminology regarding natural capital and ecosystem services is used interchangeably, and this complicates the understanding of this complex subject [7]. Natural capital can be considered as the stock, or natural assets, within an ecosystem or an area. The natural assets can include the biotic elements, such as the ecological communities and the soils (with living organisms and soil organic matter, etc.), and the abiotic elements, such as land, minerals, water, and air. The natural capital can then provide or generate ecosystem services through environmental production and processes over time [7].

The natural capital of any one area or ecosystem can vary according to different parameters, for example [8]:

- the amount of an area covered by vegetation;
- the physical and chemical composition of the environment and biological diversity of the habitats;
- the variety, in space and time, of the mosaic of suitable habitats to provide conditions for the development for species, communities, or functional groups aiding the fulfillment of their roles in the ecosystem (ecosystem service);
- the establishment of the combination of particular species and/or functional groups;
- the abiotic factors that interact with the biotic factors in the above groups.

Ecosystem services that are derived from natural capital through environmental processes and functions can also differ depending on the area or ecosystem involved [8]. It is the processes and functional relationships between natural capital and ecosystem services that directly or indirectly influence human life, which produces human benefit [9–12]. Therefore, the variety of the Earth's ecosystems, including the environmental properties (EvP) and the environmental functioning (EvF), can provide that which is necessary for human existence and human well-being. The natural capital element alone is of value, but the most important is the proper interaction and relationships between the elements that provide the ecosystem services [13, 14]. To some extent, human activity is able to enrich these relationships, particularly in the highly populated urban and industrial areas. However, conversely, habitat degradation and the disturbance of resources associated with natural capital cause the decrease of ecosystem services in some places [15, 16].

As ecosystem services are defined as "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life" [17], this concept is shaping human-environmental interactions [18] within the environmental and sustainable context and reveals an understanding of the concept of urban populations' dependence on elements of [19–21].

The global increase in human population is leading to the increasing range of land-use activities, including the conversion of natural landscapes for human use or by changing the system of management practices on land that is already human-dominated. For example, large areas of the Earth's land surface have been transformed through intensive agriculture, natural resource excavation, expanding urbanization and industrialization, and so on. Often such human activities are changing the world's ecosystems and landscapes in drastic ways, and intensive research has revealed that the pressure of land use throughout the globe has influenced the environment, ranging from modification in the composition of the atmospheric gases to the extensive modification of the Earth's ecosystems [22]. The Millennium Ecosystem Assessment revealed that 60% of ecosystem services have been put under risk because natural resources have been affected by exploitation and unsustainable use [23].

The environmental processes and functions take place in various ecosystems regardless of the level of the naturalness of that particular ecosystem, including in urban and post-industrial ecosystems, and that in these less natural ecosystems, the type and strength of inter-relations, synergies, and processes that exist may vary widely [12]. As a result, there is an increasing awareness that is leading to the development of more effective management strategies, which consider the challenge of reducing the negative environmental impacts of increased land use and growing demand as well as maintaining the economic and social needs and benefits [24], especially in urban-industrial areas.

The issue of ecosystem services in urban-industrial areas has to be of particular consideration for several reasons:

- **i.** the majority of the world's population lives in urban-industrial areas, and two-thirds of the world's population is expected to be living in urban areas by 2050 [25];
- **ii.** urban-industrial areas comprise a small part of the Earth's terrestrial habitats, but they are responsible for a significant role in global carbon emissions, energy, and resource consumption [26];
- **iii.** the densely populated areas greatly contribute to environmental transformations, causing biodiversity loss, ecosystem degradation, and climatic change on an almost global scale [23, 27, 28].

The application of the concept of ecosystem services to urban and industrial environments has generated an increasing amount of research during the last decade [29–31]. Review papers on ecosystem services in urban and post-industrial environments have considered some specific issues such as water quality and resources [32]. Other studies on "the ecology of cities" [33–35] have considered the environmental balance between natural capital and ecosystem services in urban-industrial areas. Such studies have tended to focus on sustainable development in cities or the links between the urban areas and the rural landscape, with the suggestion that the links between the urban areas and the surrounding rural areas influence each other [35]. Often urban ecosystems include both the "gray" built-up infrastructure and the "green-blue" ecological infrastructure (parks, urban forests and woodlands, cemeteries, gardens, urban allotments, green roofs, wetlands, streams, rivers, lakes, and ponds) [36]. However, it is still a matter of discussion as to what extent peer-reviewed literature is able to currently provide the comprehensive and integrated research, which is capable of covering the diversity and interdisciplinarity of research approaches needed for a fuller understanding of urban-industrial ecosystem services [37].

It can be argued that in the urban-industrial environments, habitats and ecosystems have developed, which would not normally develop outside the urban-industrial areas or would become extinct elsewhere, including ecosystems developing initially on nutrient and mineral poor habitats. It is important to realize that apart from ecosystem services providing direct impact on human health and security, such as urban cooling, noise reduction, air purification, and runoff mitigation, there are also some services that are more difficult to assess. Nevertheless, these are important urban-industrial ecosystems at the initial stage of succession, with their unique microorganism-vascular plant relationships, and provide an important contribution into the overall ecological diversity.

According to the Millennium Ecosystem Assessment (MEA) [23], "Ecosystem services are indispensable to the well-being of all people in all places." Ecosystem services can only be provided by ecosystems, which are functioning effectively. However, there is a good evidence base that outlines the importance of biodiversity to ecosystem functioning, but less research is focused on the direct relationship between biodiversity and ecosystem services. Binner et al. [7] suggest, with reference to urban areas, that there is an evidence gap in the understanding of biodiversity in urban woodlands and the benefits that are accrued. Many of the world ecosystems have been damaged or disturbed by human activity, and those changed ecosystems need to be restored and/or managed accordingly [38, 39]. Knowledge regarding those ecosystems modified, transformed, or created by human influence is very limited. It is important that these changed ecosystems are restored and/or managed, but because of the lack of knowledge about the details of their functioning (**Figure 1**), the restoration practice is very complex and often unsuccessful [40, 41].

Even though there has been a sustained period of study, many of the mechanisms governing ecosystem functioning are still not fully understood. The general rule is that the relationships between the ecosystem elements are complex, and therefore, models have to be simplified, transformed, and translated into more accessible and informative formats for stakeholders and decision makers to incorporate the ecosystem principles into management practice. Improving management practice may facilitate the enhancement of ecosystem services for human well-being in urban-industrial sites. Urban and Industrial Habitats: How Important They Are for Ecosystem Services 173 http://dx.doi.org/10.5772/intechopen.75723



Figure 1. The basic inter-connected relationship between biodiversity and ecosystem functions, including the diversity (species richness, relative abundances of species, genetic diversity, and diversity of functional trait variability of vegetation types), impact, and interaction (species ecological role, species impact on ecosystem function, species impact on ecosystem services, variability of ecosystems, variation at landscape scales, abiotic or non-living diversity, and topography).

One of the relatively well-understood ecosystem principles, which has been substantiated in many studies, is that biodiversity, and in particular functional diversity, strengthens ecosystem stability, ecosystem services, and productivity [42, 43]. In this respect, the worldwide decline in biodiversity, caused mostly by human influence and anthropogenic factors, has to be of global concern [44, 45]. Decline in biodiversity is a global issue that has to be managed by local practice and within the local context [46, 47].

It has also been reported that the mechanisms that regulate biodiversity are complex and incorporate many potential interactions and feedback loops, which may even accelerate the loss of biodiversity, and should not be disregarded. One example of an important unsolved feedback relationship concerns whether producer diversity is related to the presence of consumers (top-down regulation) or related to the availability of resources (bottom-up regulation). The latest study suggests that the two relationships interact with each other [48–50] and seem to be habitat type dependent. However, whether and how biodiversity is related to ecosystem functional processes at higher trophic levels in different human transformed ecosystem types is arguable. It has been suggested [51, 52] that it is necessary to test if, in the complex communities with multiple trophic levels, diversity effects are governed by trophic interactions, including trophic processes, in order to gain a better understanding of functional diversity.

Politicians, business managers, and decision makers are increasingly aware of the need for the sustainable management of natural capital. However, they do not have the tools to evaluate the influence of different decisions [53], and there is a lack of knowledge and understanding of how abiotic and biotic elements of natural capital interrelate in ecosystems to provide different services. In addition, there is a growing concern that human needs are becoming detrimental to biodiversity conservation priorities [54] and that utilizing natural capital resources, required for necessary ecosystem services, are decreasing due to species loss and habitat fragmentation [23]. Therefore, the contemporary task for scientists is to provide the managers and stakeholders, if possible, with manageable protocols to help them understand the very complex links, synergies, and generally nonlinear relationships in ecosystem function. To date, research has shown that one management strategy will not work across all spatial, temporal, or cultural situations.

2. Urban-industrial environments uniqueness and ecosystem potential

Both urban and industrial areas represent complex land-cover mosaics, which are "novel ecosystems" in terms of their ecological component composition [55]. The community composition in urban-industrial areas, i.e., the below and above surface organism relationships developing on soil/soil substratum, is different to non-urban and non-industrial counterparts. In such new environmental situations, such as in habitats under constant human pressure in urban areas or created by human activities in industrial or post-industrial areas, the understanding of which features of particular organisms, communities, vegetation type, or habitat characteristics are most important (the service provider concept) is limited [56]. The most important point for understanding the urban-industrial areas' ecosystem function (ecosystem service providing mechanisms) is the biodiversity-ecosystem function-ecosystem service relationship. In the environment of urban-industrial areas, which are frequently modified, it might be expected that various aspects of the urban biodiversity-ecosystem service relationship are unique. There are many sites in urban-industrial areas that are poor in nutrients (oligotrophic) and are at the initial developmental stage, and these sites are valuable in terms of their potential for biodiversity enhancement (Figure 1). This uniqueness implies the urgent need for the study on the biodiversity-ecosystem function-ecosystem service relationship on one hand, and the need for the decision makers and stakeholders to take this uniqueness into account in policy and management recommendations on the other hand. This uniqueness also implies that there is a high potential for the enhancement of those habitats. However, ecosystem dynamics in urban and industrial landscapes are poorly understood [20, 57], especially when it comes to designing, creating, and restoring ecological processes, functions, and services in those areas [57, 58].

2.1. Urban areas – ecosystem service potential

Urban areas are more often related to high population density and high consumption, and these areas are more likely to be connected with a reduction in resource demand rather than the production of ecosystem services. However, the results in the recent studies indicate that cities, in general, can be important ecosystem service providers [59, 60]. The research of [61] presented unexpected results that indicate that cities are able to store a comparable amount of carbon per unit area as that found to be stored in tropical forests. The high biodiversity stored in the ruderal vegetation of urban sites (**Figure 2**) has been represented by Kompała-Bąba 2013 (modified [62]).

Research has enabled the recognition, quantification, and performance of ecosystem service assessments in urban areas [60, 63–65]. The ecology of urban areas that support ecosystem services is unclear [37], and the biodiversity-ecosystem service relationship should be clarified as to what extent, and how, biodiversity influences ecosystem service provision. The



Figure 2. The floristic diversity of vegetation of ruderal habitats expressed through the use of functional traits of species. Five functional groups of species in urban ruderal habitats are distinguished in relation to fertility and disturbance gradients: (A) comprised monocarpic and biennials that had a high seed weight and terminal velocity and that differed in relation to seed bank type and lateral spread; (B) and (C) groups comprised polycarpic species, which had many traits that are connected with competitive ability (high leaf area, canopy height, high seed number, and long-term seed bank), mainly nitrophilous ruderal and meadow species, which differ in relation to lateral spread, seed weight, and terminal velocity; (D) and (E) groups were mainly made up of species that possessed traits that enabled them to adapt to disturbances or other forms of stress that differ in relation to life span (modified [62]).

lack of a precise definition of biodiversity in its biological and ecological sense on one hand and a precise definition of biodiversity as understood by economists and sociologists on the other hand is a real challenge. A commonly used definition [66] (Convention on Biological Diversity) states that "Biological diversity means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are a part; this includes diversity within species, between species and of ecosystems," and it is sometimes understood that biodiversity can be given a numeric value. In particular, biodiversity in an industrial urban situation suggests that the principle that "more is better" is not working. Biodiversity should be understood as a complex mosaic of different habitats in which the species composition is appropriate for the abiotic site conditions. Such understanding of biodiversity may help to limit or avoid the spread of alien, invasive species, and the spread of expansive, ruderal organisms occurring in large numbers in different habitats. Research has shown that the spread of alien and invasive plant species causes a decrease in the species composition of native habitats [67, 68].

Apart from the serious contemporary constraints in understanding the biodiversity-ecosystem service relationship, there are reports concerning successful Blue-Green City projects. A Blue-Green City is a concept relating to the support or enhancement of natural potential, mostly by plants, and using them, for example, to reduce flood risk or to help improve air, soil, and water quality. When nature (plants or water) is used by people to help manage and enhance urban environments, e.g., in managing storm water, it is often referred to as blue-green infrastructure (**Figure 3**). Green infrastructure as a whole is a larger concept associated with the service provision of an ecological framework for the social, economic, and environmental health of the surrounding environment.

The aim of the Blue-Green City approach is to recreate a water cycle based on natural processes by joining water management with the green infrastructure in urban areas, for example, to manage flood risk by combining the hydrological and ecological potential of the urban landscape. The interaction between blue and green can enrich the urban environment as illustrated in the Blue-Green City project in Newcastle, UK [69]. In terms of ecology and hydrology, the aims of the Newcastle project are:

- **i.** the creation of an urban flood model to simulate the movement of water and sediment through blue-green features;
- **ii.** the improvement of water quality, habitat, and biodiversity by using a system of bluegreen features (http://www.bluegreencities.ac.uk). The Newcastle project takes into account both the ecological and hydrological elements, which are both equally important for the urban ecosystem.

The successful blue-green management projects undertaken on a larger scale (landscape scale) in cities are very important as scientific background is still unclear, and greater evidence and evaluation are required. Only 25% of papers deal with the biodiversity-ecosystem service relationship aspect of aquatic habitats in urban areas [37], in part, because it is difficult to set the boundaries of a water flow inside an urban area. A common operational definition of the term "urban area" and its boundary would be beneficial for further studies. At present, an "urban area" is defined either by taking into account the population size of the urban area (population density—population size to area size) or by the administrative boundary.

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Figure 3. The complexity of the Blue-Green City concept in relation to the special mosaic of urban-industrial sites, land management, land requirements, and demand.

The different definitions are used depending on specificity of a particular county or research purpose [70, 71]. For more comprehensive results, particularly when the hydrological aspect of the natural capital is taken into account, a broader definition for an urban ecosystem service study should be used [6, 72–74]. The most important reason is that administrative boundaries rarely coincide with ecological function "boundaries" [20, 75]. The broader understanding of the target area that is indicated as urban, sub-urban, or peri-urban is required [76].

2.2. Industrial and post-industrial areas - ecosystem service potential

Restoration and regeneration of areas transformed, changed, and/or degraded by industry can be a long and complicated process. Post-industrial sites generally represent heavily affected ecosystems, which have lost their biodiversity and most of their ecosystem functions and services [77].

The wide range of aspects of biodiversity restoration and ecosystem services in post-industrial (particularly post-mining) sites has received wide attention among restoration scientists [78–81]. Although the scientific attention to ecosystem services has been growing, there has been a strong tendency to conduct short-term experimental studies in which biodiversity was experimentally manipulated (in the laboratory or in the field) [28]. However, some studies on vegetation development and spontaneous succession on urban and post coal-mine waste sites were conducted over 10 years providing interesting results about the mechanisms of concerning spontaneous ecosystem development and biodiversity enrichment in a broad spatiotemporal context [62, 82].

Increasing the biodiversity and ecosystem services, which are dependent on ecosystem functions, is the main aim of ecological restoration [83, 84]. In post-mining and post-industrial sites, the biodiversity and ecosystem function restoration and/or enhancement are related to the wider landscape (**Figure 4**), and various local micro-habitats in a broad spatiotemporal context.

The important prerequisites of soil/soil substratum physical features included:

- erosion control;
- water infiltration;
- recognition, assessment, and, when necessary, the improvement of the biotic spoil (spoil substratum) parameters including bacteria, arbuscular mycorrhiza fungi (AMF) diversity, and abundance;
- micro- and meso-climate, etc.

All of which are the prerequisites for the establishment of permanent vegetation [67, 85–88]. The restoration and/or enhancement will be the basis for the re-establishment of primary productivity of post-industrial sites, carbon sequestration, and the increase of the esthetic value of the site and the landscape. Ecologists [78, 89] prefer to emphasize the re-establishment or the increase of biodiversity as a goal of restoration.



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Figure 4. The main landscape factors affecting vegetation diversity during spontaneous ecosystem development on coalmine heaps in a broad spatiotemporal context (modified [82]). Biodiversity is often considered to be closely linked with the increase in ecosystem functions or ecosystem services [90]. Biodiversity is also commonly used as a main driver or as a surrogate of ecosystem functioning and informs the understanding of ecosystem health (understood as overall description of the condition of an ecosystem) [91, 92]. However, society finds difficult to evaluate biodiversity because it is unquantifiable in monetary terms.

Among different definitions of the term biodiversity, including diversity of species, food webs, or genetic structure of populations, particularly meaningful is the definition on the diversity of functional groups [93]. Functional diversity reflects the importance of an ecosystem's diversity as it may occur that many species can fulfill the same role within the ecosystem (**Figure 5**), and so regardless of the number of species, a system may not necessarily function properly. However, species diversity is a useful and often adopted measurement in restoration projects, but unfortunately, it can be insufficiently informative and even misleading, particularly in highly transformed and modified urban and industrial ecosystems.

An understanding of biodiversity measurements of these ecosystems is needed because of the high number of species (species diversity), which may include both species appropriately adjusted to the particular habitat conditions (e.g., grassland species on grassland habitat, wetland species on wetland habitat, i.e., the target species), regardless of whether the sites are of natural or anthropogenic origin [67] and are dominated by competitive generalists, ruderals, and sometimes alien species. Alien, invasive, and expansive species may indicate an unwanted developmental and/or restoration pathway [94]. Selecting biodiversity indicators in restoration projects requires detailed study and understanding of the mechanisms governing spontaneous processes existing on post-industrial sites (**Figures 5** and **6**) [95–97]. The management proposed has implications for choices made based on certain values and focusing on some specific aspects, e.g., restoration or spontaneous succession [82, 98].

Post-industrial sites need to be managed, and the consideration of which restoration method is the most effective in terms of environmental/ecosystem recovery is necessary and site specific. The restoration/reclamation approach presents a type of gradient, or a continuum, of ecological restoration. There are intervention levels that range from technical reclamation (which involves heavy interventions, such as the restructuring of landforms, importing soil, and planting or sowing of plants) on one hand, and on the other hand, the spontaneous succession of the ecosystem that might be expected to recover principally through natural processes [79, 82, 99].

It can be expected that for post-industrial ecosystem development and functioning and the ecosystem services that may be accrued, the primary succession through natural processes is the most appropriate for several reasons:

- the site conditions of post-industrial sites are so different from the natural ones that it is inappropriate to use the experience from natural habitats for reclamation practice;
- the high microsite heterogeneity on post-industrial sites would require low-scale action that is not economically beneficial;
- recognition and increasing understanding of spontaneous succession enable the facilitation of natural processes by assisted restoration, in order to speed up the natural regeneration and the recovery of the ecosystem under adverse environmental conditions [86];

- it should be accepted that the target ecosystem may not always be a replacement of the original ecosystem that was lost by mining or industrial activities, but a system of living organisms that is best adjusted to the new post-industrial conditions;
- factors influencing spontaneous succession of post-industrial sites have to be assessed, through the studies of various measures and approaches, and this should be the basis for the planning of effective ecological restoration [100–103];
- at the beginning of spontaneous succession, the early successional stages create a mosaic of species group composition that is of high-conservation value [47, 96, 104];
- the maintenance of early successional stages should be a goal of restoration projects;
- technical reclamation, when compared with spontaneous succession, can negatively influence the local biodiversity since it decreases the amount of habitats that affect the specialized threatened species [101, 104] or even enhance and maintain the pool of seeded alien species that may spread to the surrounding environment [105];
- spontaneous natural succession on post-industrial and urban areas often leads to the establishment of a self-sustained, well-functioning ecosystem. However, they may be different ecosystems from those that occur in natural and semi-natural habitats;
- the differences caused by the adverse environmental conditions, such as contamination of the surroundings, are also a reason why technical reclamation fails;
- in some post-industrial sites, the conditions are so extreme endemism, and microevolution could be expected—still an issue to be studied;



Figure 5. Aspects of functional diversity of vegetation development on post coal-mining heaps (modified [82]).

- not all parameters are the only the negative products of human disturbances. Some of the post-industrial sites may provide refuges for specialized wildlife [101, 104, 106–111];
- It is possible to use high-resolution remote sensing data and LIDAR scanning; together with
 the wide range of ecological data (microorganisms including bacteria, arbuscular mycorrhiza
 fungi, mezofauna, vascular plant species, plant chlorophyll content, photosynthesis potential,
 vegetation species composition, and biomass production), in order to build a biodiversity
 model of urban industrial sites, with coal-mine heaps as an example (InfoRevita project) [112].

The above list suggests the need for a detailed study and the analysis of spontaneous development of ecosystems on post-industrial waste sites. Such research could provide scientific information on environmental and plant characteristics that may influence the regeneration and succession for restoration (**Figure 7**) and reclamation practice. These data can be used in developing effective ecological restoration under adverse site conditions resulting from postindustrial sites [100, 103, 107, 113, 114].

Post-industrial subsidence (**Photo 1**) and wetlands (**Photo 2**) have particular environmental, ecosystem function, and ecosystem service potential. These aquatic and wetland habitats of anthropogenic origin can provide opportunities for using ecosystem services to improve



Figure 6. The example of predicted changes in vegetation development on coal-mine heaps depending on the TWINSPAN analysis of 2567 vegetation records performed on unclaimed post coal-mine heaps [82].



Figure 7. Divergence or convergence of biodiversity/ecosystem function recovery on post-industrial sites. The probable development pathway.

the quality of human life and minimize climatic change in urban-industrial areas. The study [115–117] conducted on the coal-mine subsidence included:

- identification of the ecological status of waters with the use of selected parameters, including biodiversity;
- identification of the potential of photosynthesis of aquatic plants;
- modeling of the functionality of biodiversity;
- identification of habitat conditions including the humidity of the ground and areas of water accumulation, based on high-resolution remote sensing data and LIDAR scanning;
- the role of vegetation diversity in modifying humidity conditions (including the water balance of the area), taking into account the results of modeling the species niche and the digital vegetation model;
- conditions of soil moisture in regeneration and creation of habitats in the revitalization of urban-industrial areas;

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Photo 1. Post coal-mine subsidence. The visual impression is misleading and does not refer to the real biodiversity potential of these anthropogenic habitats (photo: Edyta Sierka).



Photo 2. The peatbog vegetation with many rare and protected plant species developing spontaneously on wetland habitats of anthropogenic origin (photo: A. Błońska).

- the variety of vegetation in terms of functional features of species and their importance in water retention [67];
- diversification of habitat conditions and aquatic properties of anthropogenic peatlands [67];
- creating wetlands habitats and their role in local water retention.

Flooded mine subsidence is one of the effects of underground 'deep' coal mining. The subsidence results from the gradual sinking of the ground over the mine workings and takes the form of shallow (3–4 m deep) basins with gently sloping sides. Subsidence can occur in woodland, farmland, or industrial areas. However, the few studies conducted so far suggest that subsidence basins are unique enclaves, which facilitate the development of new ecological systems, thereby contributing to the biodiversity of such areas [77, 115, 116].

The study conducted on flooded mine subsidence showed that despite similar origins, subsidence pools differ substantially when it comes to the level of plant diversity. In contrast, there is no difference in terms of the average share of various functional groups (FGs). Plant diversity was substantially affected by the size and depth of the subsidence pools and habitat humidity, C/N ratio, concentration of P total in the soil, water, and water clarity. Subsidence pools differ significantly in terms of the number of dominant species. The importance and value of ecosystem services provided by 10 subsidence pools on the post-industrial area in Poland and Czech Republic, and their vicinity was estimated on an average of \in 521,000 [\notin × ha × year⁻¹]. The most important ecosystem service that the pools fulfill is the water supply and habitat creation (**Figure 8**) [75].



Figure 8. The example of predicted changes in species composition of vegetation developing on coal-mine flooded mine subsidence [75].

It has been shown that the development of reservoirs in the subsidence troughs within postmining areas, contributes to the enrichment of environmental potential of these areas, provides new possibilities for their use by living organisms, and improves the quality of human life.

3. Conclusions and perspectives

In ecological restoration, the biggest challenge is to find a general consensus of suitable biodiversity indicators and economically viable measures, which will produce multiple socially and ecologically guided environmental benefits. There is difficulty in reaching such consensus because of the complexity of the biodiversity concept. In an effort to restore sites disturbed by industrial (mining) activities, restoration projects should involve ecologically based methods and approaches, which would be able to fulfill many stakeholders' expectations for sustainable development and human well-being.

In this respect, it would be useful to employ integrated natural and human models to understand the dynamics of ecosystems including most of biodiversity and trophic levels (including such trophic levels like the mid-trophic consumer) in order to simulate management scenarios in relation to biodiversity and ecosystem services. Another crucial point will be the increasing understanding of the role of biodiversity and ecosystem service identification as important factors influencing the relationships between them. Both the models and the knowledge could be used to develop predictive scenarios of system-level impacts under a range of possible management policy scenarios in order to assess and to explore which management policy provides the greatest impact on sustainable ecological, social, and economic aspects.

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Integrating Ecosystem Services in Historically Polluted Areas: Bioremediation Techniques for Soils Contaminated by Heavy Metals

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Abstract

Bioremediation of soils contaminated by heavy metals is based on the use of specially selected plants able to reduce the hazards of toxic metals. Depending on the mode of action on the heavy metals existing in the soil and the place where the action takes place, the following mechanisms for soil phytoremediation are distinguished: phytostabilization, phytoextraction, phytoimobilization, rhizofiltration, or evapotranspiration. These mechanisms are complex and include the plant ability to reduce the mobility and bioavailability of heavy metals and other pollutants, to extract large amounts of heavy metals from the soil or to evaporate water together with various pollutants already reached in the rhizosphere. Decontamination of polluted soils by using bioaccumulative plants is proposed as an environmental-friendly alternative to the traditional physicochemical methods, being a sustainable method with a great potential in the terms of environmental protection and cost management.

Keywords: contaminated sites, hyperaccumulators, phytoextraction, phytoremediation, phytomining, soil contamination

1. Introduction

Pollution has become a worldwide concern because its effects can lead to ecological imbalances, affecting flora, fauna, and the health of people living in the vicinity of the contaminated sites. Soil pollution with heavy metals is as old as human ability to melt and process ores. Each

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stage of cultural development of humanity left behind its pollution with metals, mainly stored in soil, sediments, and ice [1].

Heavy metal pollution is a major public health concern, and although efforts have been made to limit the population exposure, the problem persists due to the accumulation of these substances in the environment [2]. Especially long-term industrial and mining activities are the preponderent sources for heavy metal environmental contamination worldwide. Unlike other pollutants (organic compounds and radionuclides), heavy metals are considered to be the most persistent contaminants in soil because these elements tend to accumulate in the soil and then, through the plant and animal food chain, the population is exposed to their toxic effects [3, 4].

Heavy metals are defined as elements with metallic properties (conductivity, ductility, cation stability), atomic number greater than 20, and density greater than 5 kg/dm³ [5, 6]. Recently, the term "heavy metal" is used as a general term for those metals and semi-metals with toxic potential on the human body or the environment [7]. The most common elements in heavy metal contamination of environment are Cd, Cr, Cu, Hg, Pb, and Zn. They occur naturally in the soil in relatively small concentrations but can occur in much higher quantities as a result of human activities.

Some heavy metals, in small amounts, have a physiologically beneficial role for plants or in the human body (e.g., Zn, Mn, and Se), and others are potentially toxic to organisms and humans regardless the concentration [8].

Expansion of areas affected by mining and industrial activities contaminating the environment with heavy metals makes the application of traditional technologies inappropriate due to the high costs associated with soil remediation. The majority of conventional methods such as incineration, vitrification, or land replacement are extremely expensive. Also, the potential impact on the environment must be considered, in particular the change of agricultural soil properties and damage to the landscape [9]. In historically polluted areas, the challenge is to decontaminate soils in order to resume agricultural practices and protect the population health. Thus, in addition to soil remediation, it is necessary to remedy the water or wastewater used for crop irrigation [10].

The importance of biodiversity, both below and above ground, is currently increasing for the cleaning of metal-contaminated ecosystems [11]. The concept of ecosystem services may be integrated in this field, having implications for the practice of soil remediation [12, 13]. There is a close connection between soil, plants, and other ecosystem components. In fact, ecosystem services include the services provided by air, water, soil, and biota. Of these, the soil functions are important for the ecosystem good functioning and refer to some valuable properties: the capacity of storing, filtering, or transforming nutrients, substances, and water; biomass production (crops and forestry); host of biodiversity (habitats, species, etc.); source of raw materials; physical and cultural environment for humans; and human activities [14]. Ecological consequences of soil pollution apply not only to soil functions, such as its biological activity, but have also negative effects on soil-crop-animal-human system [5]. On the other hand, plants and microorganisms play a crucial role in restoring the specific soil functions and also other ecosystem components, being considered as ecological or ecosystem engineers [15].

A wide range of biodegradation processes of soil contaminants are currently available, an advantage of these biological treatments being their potential to be cost-effective [16–18]. Initially, research is focused on bacteria, taking into account catabolic reactions mediated by bacterial enzymes. The first investigations into phytoremediation have been confronted with some opinions that if a contaminant cannot be degraded by bacteria that have a wide range of catabolic enzymes, it can certainly not be by plants [19]. Plant remediation features include three common strategies for "treating" heavy metal-contaminated soils: immobilization, removal, and destruction [20].

Phytoremediation, also known as green remediation or agro-remediation, uses vegetation to remove pollutant substances such as heavy metals, organic compounds, and radioactive compounds from the soil, sediments, or water [21]. Phytoextraction, one of the most important phytoremediation techniques, is defined as the extraction of contaminants from soils by plants and is known as a mild, ecological remediation method. It uses the plants to take pollutants from the soil through the roots, with their subsequent accumulation on the upper part of plant, generally followed by the harvesting and elimination of plant biomass [22].

The applicability of phytoremediation depends on the possibility of identifying plants that have the ability to tolerate high concentrations of heavy metals, to extract and accumulate important quantities of heavy metals from the soil, or to immobilize contaminants at the soilroot interface, thus reducing the possibility of groundwater contamination.

2. Soil pollution in industrial and mining areas

Soil is the most important compartment for all terrestrial ecosystems, providing essential nutrients for plant growth, plant degradation, and transport of biomass. A significant role of the soil is also as natural buffer within the transport of chemical elements and substances in the atmosphere, hydrosphere, and biota [3].

The persistence of contaminants in soil is much higher than in other compartments of the biosphere, and soil pollution by heavy metals appears to be permanent in soils [23]. Heavy metals are native components of the earth crust, existing in different concentrations in all ecosystems [24].

The period of existence of metals in soil in temperate climatic conditions can be estimated for the metal elements, as follows: Cd between 75 and 380 years, Hg between 500 and 1000 years, and between 1000 and 3000 years for Ag, Cu, Ni, Pb, Se, and Zn [3, 25].

The sources of heavy metals in the environment are very diverse and can be of both natural and anthropogenic origins. The main natural sources are rocks and soils [26], and the anthropogenic sources are represented by socioeconomic activities; some of these are illustrated in **Table 1**. The problem of this type of pollution derives in particular from the exploitation of minerals and the use of metals by the human population.

Historically contaminated areas by heavy metals are found all over the world, especially caused by mining and ore processing activities. Consequently, the metal pollution is not

Source	As	Cd	Cr	Cu	Pb	Hg	Ni	Zn
Mining and processing of ores	\checkmark			\checkmark	\checkmark	\checkmark		\checkmark
Metallurgy	\checkmark							
Chemical industry	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark		\checkmark
Alloy industry					\checkmark			
Paint industry		\checkmark	\checkmark		\checkmark			\checkmark
Glass industry	\checkmark				\checkmark	\checkmark		
Paper industry			\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	
Textile industry	\checkmark		\checkmark			\checkmark		\checkmark
Chemical fertilizer industry	\checkmark	\checkmark		\checkmark	\checkmark	\checkmark	\checkmark	\checkmark
Petroleum industry	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark		\checkmark
Burning of coals	\checkmark							

Table 1. Industrial sources of the most important heavy metals in the soil [27].

attributable exclusively to mining activities, although these are preponderent in many regions [28–30]. Most of these activities are currently closed, remaining behind enormous quantities of heavy metals that have been deposited in the soil. The volume of tailing dumps discharged has exceeded 10 billion tonnes per year [31]. Usually, these mine tailings are not covered by vegetation caused by a poorly structured soil, being potential sources of heavy metal spreading through water infiltration or wind [32].

3. Phytoremediation: a green technology to remove heavy metals from the soil

Many remediation techniques have been used to respond to the growing number of soils contaminated with heavy metals [33–35].

Decontamination methods currently applied in the majority of sites are mainly characterized by the manipulation of enormous quantities of soil or heavy metal extraction by using chemical reagents. These practices are very expensive and also lead to the loss of soil fertility by changing its physicochemical properties (structure, cationic exchange capacity, etc.), destroying at the same time the microorganisms from the soil and, ultimately, the humus layer [36]. In this situation, other less brutal methods for heavy metal extraction were searched and developed. Bioremediation and phytoremediation in particular are such "mild" remediation methods that maintain or even restore the natural soil fertility [21].

Thus, methods by which plants, natural or genetically modified, alone or in the presence of auxiliary substances cause polluted soils to become less dangerous for humans have been developed [37, 38].

Phytoremediation is defined as a phenomenon of polluting substances extraction by using plants. With all these, there are many types of phytoremediation, so we can state that phytoremediation represents a much broader defined term [39, 40]. Phytoremediation of soils, waters, and sediments is not a new concept; for decades it has been found that some plants can degrade or extract heavy metals and other pollutants from these environmental compartments. Plants have been used for the decontamination of wastewater about 300 years ago. *Thlaspi caerulescens* and *Viola calaminaria* were the first species of plants used in the nineteenth century and found to accumulate large concentrations of metals [4].

A strong motivation to apply phytoremediation in historically contaminated sites, in addition to other advantages, is the particularly low cost of this method compared to conventional ones. **Table 2** highlights the costs of different soil remediation techniques. Nevertheless, the most frequently applied remediation techniques for contaminated soil in Europe include land excavation or disposal [41].

3.1. Phytoremediation process and techniques

The metal extraction or accumulation by plants involves a variety of biological mechanisms and requires direct knowledge of plant physiology and soil science.

Through the rhizosphere (the interface between plant roots and soil), the water is absorbed by the roots to replace the evaporated water from the leaves. The metals in the soil solution (free ions or organometallic complexes) can move together with water (by convection or mass transfer) as the plant absorbs the water needed for vital processes. Absorption of water from the rhizosphere creates a hydraulic gradient directly from the ground to the surface of the roots. This concentration gradient or hydraulic control ensures the diffusion of ions from the soil particles to the deficient layer surrounding the roots [45, 46].

The elimination by plants of exudates and metabolites play an important role in the phytoremediation process. Thus, enzymes such as dehydrogenase, hydrolase, peroxidase, and phosphatase are released at the plant-soil interface and contribute to the degradation of

Remediation method	Remediation costs (in US dollars/m ³ soil)
Excavation and disposal	140–720
Vitrification	360–1.370
Soil washing, ex situ	80–860
Soil washing, in situ	20–270
Solidification and stabilization	40–200
Electrokinetic methods	30–290
Bioremediation	10–310
Phytoremediation	1–150

Table 2. Costs of different soil remediation methods [42-44].

some soil compounds [47]. Plant enzymes named metallothioneins and phytochelatins bind the heavy metals increasing the extraction of these elements [48, 49].

In fact, phytoremediation is based on the extension of already existing processes in different ecosystems, with other processes that occur under different conditions, different degrees of contamination, different pollutants, and plant species.

Depending on the mode of action on the pollutants and the place where the action takes place, the following phytoremediation mechanisms and biological processes are distinguished: phytoextraction, phytostabilization, phytoimobilization, evapotranspiration, rhizodegradation, rhizofiltration, phytodegradation, and phytovolatilization [35, 50, 51].

Heavy metals in the soil are only suitable for phytoextraction, evapotranspiration, phytostabilization, and phytoimobilization [35, 52]. Phytoextraction is by far the most studied and applied method. Phytodegradation and rhizodegradation processes, as well as phytovolatilization, are specific to organic pollutants; the major difference between these and other processes applicable to metals is the complete mineralization of the pollutant after degradation.

From the point of view of the place where the remediation takes place, this procedure is exclusively in situ, without excavation of contaminated site, in all types of phytoremediation [52, 53]. Also, from the point of view of the processes that occur, they can be either in plant, by the absorption of the metals in the plant (phytoextraction, rhizofiltration, phytovolatilization), or ex plant due to the action of the excreted enzymes by the plants or the microorganisms associated with the plants (phytoimobilization), either combined (in the case of phytostabilization).

Phytoextraction is based on the cultivation of large biomass plants and the ability to extract large amounts of heavy metals from the soil, accumulating them in the plant tissues. These plants are harvested using conventional farming methods and then dried and incinerated, the resulting ash being stored [54].

Starting from the necessity of finding solutions for the decontamination of areas polluted with heavy metals of anthropogenic origin, the concept of "heavy metal phytoextraction" was introduced for the first time by Baker and Brooks in 1983 [55].

Phytostabilization refers to plant ability to stabilize pollutants, thereby reducing their mobility and bioavailability. In the case of nonagricultural land, especially those with a high degree of pollution, a method of mitigating the risk of pollution can be the reduction of the possibility of moving heavy metals into the soil [56].

From the point of view of the area where the pollutant fixation takes place, phytostabilization can take place in the rhizosphere, on the root membranes, or in the root cells. This method applies especially to tailings dumps, but the main disadvantage of this technique is that the metals remain in the soil.

Phytostabilization research is still in the laboratory phase, with very few applications in the field. These include the use of plants as *Brassica juncea* for the stabilization of lead and cadmium from both mine and tailing dumps; *Rubus ulmifolius* to stabilize arsenic, lead, and nickel; or lemon grass to stabilize copper in mine tailings [49, 57, 58].

Phytoimobilization represents a combination of phytoextraction (heavy metals are extracted from the soil by perennial plants, but they are not harvested) and phytostabilization (fallen leaves are collected, the soil being treated to immobilize heavy metals). This technique uses tolerant species to the target pollutant which will form a "vegetal carpet" in areas where natural vegetation is absent due to the high concentration of pollutants. The method is already successfully used in the case of tailing dumps from the mining industry [59].

Evapotranspiration – plants also have the ability to influence local hydrogeological conditions. Thus, plants are capable of intercepting a significant amount of rain on the surface of their leaves. This intercepted water is evaporated directly into the atmosphere, not reaching the ground. Simultaneously, infiltrations are reduced, so the method can also be used to limit the accumulation of water in the ground.

The presence of vegetation above a groundwater body has the effect of a "pump," on the one hand reducing the amount of water in the area of the rhizosphere; on the other hand, extracting the heavy metals the groundwater may have lower heavy metal concentrations [60]. The presence of plants at the surface of the soil also prevents its erosion.

Rhizodegradation, also called photosynthesis or plant-assisted degradation, represents the transformation of existing organic contaminants into the soil due to the bioactivity in the rhizosphere. Plants metabolize organic pollutants (including with the help of associated microorganisms) at the level of the roots, turning them into less or no toxic compounds. A symbiotic relationship is established between plants and microorganisms in the soil. Plants increase the pH of the soil and provide the nutrients needed for the microorganisms. These contribute to soil clean-up, thus providing the rhizosphere more conducive to the development of the roots [61]. Many pollutants can be degraded into harmless products or can be transformed into energy and feed sources for plants or soil organisms. But then, natural substances removed from plant roots (e.g., sugars, alcohols, phenols, carbohydrates, and acids) contain organic carbon that feeds soil microorganisms, stimulating their biological activities.

Rhizofiltration is based on the property of plant roots that grow in well-aerated water to precipitate and concentrate toxic metals from the pollutant effluents.

Phytodegradation, also known as phytotransformation, refers to the absorption of organic pollutants from soil, sediments, and water and their subsequent transformation by plants. Depending on the concentration and composition, as well as the plant species and local conditions, an organic pollutant may be able to pass through the protective barrier of the rhizosphere. In this case, it may suffer a transformation process inside the plant. The transforming mechanisms are very diverse, the resulting products being stored in vacuoles or embedded in plant tissues [50].

In order to be absorbed by the plant through the roots, an organic pollutant must be soluble in the soil solution. Once the pollutant has reached the plant, it can be stored and/or biotransformed in the plant biomass through lignification (binding the pollutant or its byproducts within the plant lignin) or can be further metabolized to carbon dioxide and water (mineralization) [35]. Plants capable of causing pollutant degradation are the phreatophytes (species of *Populus, Salix*) or grains (rye, *Sorghum*) [62, 63].

Phytovolatilization is applied exclusively for the treatment of soils contaminated with As, Hg, or Se, metals that may exist in the gaseous phase. This method uses plants capable of extracting these metals from the soil and volatilizing them in the atmosphere [64]. Plants extract volatile compounds from soil, including metals, and evaporate them through the leaves. Due to the particular toxicity of these metals, which once released can no longer be controlled, the method is still subject of controversy.

3.2. Metal accumulative plant species

The ability of plants to accumulate extraordinarily high levels of some metals and other pollutants has reached an increase interest over the past few years.

In general, heavy metals are phytotoxic to plants, but there are plants capable of absorbing and storing metals in their various tissues (roots, leaves), used successfully in soils rich in heavy metals and known as hyperaccumulative plants. Brooks and his colleagues used this term for the first time in 1977 to describe plants that are able to accumulate more than 0.1% Ni (>1000 μ g/g) in their leaves. Hyperaccumulative plants (hyperaccumulators or metallophytes) are those plants capable of accumulating 100 times larger quantities of metal than common plants considered non-accumulating [65, 66].

Hyperaccumulative plants are spread all over the world, although they are very rare plants and are found only in certain areas. The approximately known number for these plants is about 500 species belonging to a number of plant families. The majority are "obligate metallophytes," species that occur only on metalliferous soils; a smaller, but increasing number of plant species are "facultative hyperaccumulators" that hyperaccumulate heavy metals when occurring on metalliferous soils, although they commonly grow on normal, non-metalliferous soils [67].

To be considered a hyperaccumulator, the concentration of heavy metal should be 2–3 times greater than in leaves of most species growing on normal soils and at least one order higher than the usual range found in plants from metalliferous soils. The proposed threshold criteria (in g metal per g of dry leaf tissue) are 100 for Cd, Se, and Tl; 300 for Co, Cr, and Cu; 1000 for As, Ni, and Pb; 3000 for Zn; and 10,000 for Mn [68].

The growth of certain plants on soils contaminated by heavy metals leads to their adaptation to the pollution conditions and the assimilation of toxic elements into the vegetal organism. Of course, not all plants are resistant to the action of pollutants, as not all are able to accumulate significant amounts of toxic elements. The vast majority of plants are able to overaccumulate only one heavy metal from the soil, even if the soil is polluted with several such elements. Special abilities for the simultaneous bioaccumulation of several heavy metals have been proven by *Thlaspi caerulescens* for zinc, cadmium, and copper and *Brassica juncea* (Indian mustard) for lead and cadmium [49, 66]. Other hyperaccumulative plant species are shown in **Table 3**.

Thlaspi caerulescens has been extensively studied and is used in most studies as a model plant for assessment the mechanisms of metal translocation, accumulation, and tolerance and for investigating the physiological and biochemical mechanisms of metal accumulation in plants [72].

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Hyporacoumulators	Heavy motal	Patarancas
	Heavy metal	Kelelences
Thlaspi caerulescens	Zn, Cd, Cu	[66, 69]
Brassica juncea	Pb, Cd, Ni	[49, 70]
Arabidopsis halleri	Cd, Zn	[71, 72]
Phytolacca acinosa	Mn	[73]
Alyssum bracteatum	Ni	[55, 74]
Brassica napus	Zn	[75]
Sedum alfredii	Zn	[76]

Table 3. Examples of hyperaccumulative plants and the targeted heavy metal/heavy metals.

3.3. Factors that are influencing the phytoremediation process

The success of extensive application of phytoextraction depends on several key factors: the soil physicochemical properties, the degree of soil contamination, the possibility that the metal is absorbed in the roots, and the ability of plants to accumulate metals and then translocate them into the air [77, 78]. The soil properties affecting the bioavailability of heavy metals to plants include soil pH, redox potential, organic matter, clay content, and cation exchange capacity [79].

The low bioavailability of metals in the soil represents a major factor that is limiting the potential for the use of phytoextraction in the case of many heavy metals [77, 80, 81]. A major objective of the phytoremediation studies in historical areas contaminated by heavy metals is to increase the availability of metals to be absorbed from the soil by plants. On the other hand, in the case of phytostabilization, it is preferable to reduce the heavy metal availability in soils.

Particularly, the mobility of metals in soil is directly influenced by their chemical species. The chemical characterization of metals determines their behavior and toxicity in the environment [82]. The metal species represent the specific forms of an element including isotopic composition, electron or oxidative state, and complex or molecular structure [3]. Several chemical forms of metals include free metal ions, metal complexes dissolved in solutions and adsorbed on solid surfaces, and metal species coprecipitating in their own solids or in other metals with much higher concentrations. The metal species modify both toxicity and certain processes such as volatilization, photolysis, adsorption, atmospheric deposition, acid-base balance, polymerization, electron transfer reactions, solubility and precipitation equilibrium, microorganism transformations, and diffusion [82, 83].

There are also plant-related factors contributing to the efficiency of phytoremediation: rapid growth and high biomass producers, the presence of an extensive root system capable of exploring large soil volumes, a good tolerance for high metal concentrations, a high transfer factor (TF > 1), and adaptability to polluted areas under different climatic conditions [82–87].

The availability or retention of a metal in soil and plants can be expressed by several indices [88, 89]:

• *The modified distribution coefficient (Kmd),* defined as the ratio between the metal concentration in the soil and its concentration in the soil solution.

- *The bioavailability factor (BF),* defined as the ratio between the metal content in mobile phase and the total metal concentration in the soil. This value indicates the fraction of the total metal concentration in the soil that is considered available for plants.
- *The retention factor (RF),* the ratio between the amount of metal in the residual fraction (after mineralization and then sequential extraction) and the total amount of metal in the soil. Its value reflects the amount of metal retained in the solid phase. Normally, the retention factor is lower in soils with low pH and low clay content.
- *The transfer factor (TF) or bioaccumulation factor,* the ratio between the metal content of certain plant tissues and the total amount of metal in soil. It expresses the degree to which a plant absorbs the metal in the roots and other tissues, usually having much higher values for roots than for stem or seeds. Currently, the accumulation factor in the edible parts of the plants is of maximum interest.

3.4. Other bioremediation techniques

Phytoremediation can be used in combination with other remediation techniques: chelateassisted remediation, microbial-assisted remediation, and the use of transgenic plants [90, 91].

The 1990 EPA Manual on In situ Treatment of Contaminated Soils mentions the remediation term or ecological restauration, limiting the definition to the physicochemical methods of immobilizing or extracting heavy metals from the soil [92].

The purpose of the biological remediation process is to degrade contaminants and transform them into harmless intermediates and byproducts. The last step is to complete the mineralization of contaminants to carbon dioxide, water, and simple, inorganic compounds. Microorganisms in the rhizosphere can symbiotically interact with roots to increase the absorption of metals from soil or to biodegrade or immobilize certain toxic compounds for plants [93, 94].

The low solubility of heavy metals in the soil solution is an important impediment to their extraction by plants. In order to make the phytoextraction process more efficient, it is necessary to find methods to solubilize the heavy metals, increasing their bioavailability and therefore the ability to be extracted from plants, preferably with accumulation in the aerial parts, easy to remove by harvesting. Until now, besides soil pH reduction, the only viable solution for increasing the mobility of heavy metals in soil is the addition of substances that form soluble compounds with heavy metals existing in the soil in different forms, thus increasing their bioavailability. The use of chelators for soil remediation has started from the finding that these heavy metal complexes are more soluble in aqueous solutions than other combinations. Applying some ligands to the soil, such as EDTA, citrate, or tartrate, results an increased heavy metal mobility, an immediate increase of the mobile fraction amount in the soil and then in the roots and aerial parts of the plants [95, 96].

The use of amendments and fertilizers is also useful to increase the phytoextraction capacity of plants. Adding organic amendments such as compost, green fertilizer, and biosolids is playing an important role in metal mobility and plant growth [97, 98].
4. Future developments

Phytoremediation requires a greater effort than simply plant cultivation with minimal maintenance, assuming that the concentration of heavy metals in the soil will decrease. In addition, phytoextraction also refers to phytomining. A limited definition of the term "phytomining" is the possibility to use the crop plants to achieve economical production of metals, both from contaminated soils and also from soils that naturally have a high concentration of metals [66]. This extraction for commercial purposes of heavy metals from crop plants is not widely used. Several plant species are used by geologists for mineral prospecting, as indicator plants for the presence of different metals in soils: *Equisetum arvense* (horsetail) for gold, *Alyssum bertolonii* and *Thlaspi* L. for nickel, *Viola calaminaria* for zinc, and *Pteridium aquilinum* for arsenic [99, 100].

Another method of improving the cost-benefit of phytoremediation is to extract active principles from plants and used before plant processing. Obviously, if any useful substances (metals or oils) are recovered from the plants or by using the harvested plants for biofuel production, this practice can reduce the related costs of phytoremediation [101, 102].

Recent research in the phytoremediation application includes the use of transgenic plants and removal of metallic nanoparticles from soils [37, 103]. The challenge is to identify genes coding the specific heavy metal hyperaccumulation in plants.

5. Conclusions

The goal of phytoremediation is to improve the functioning of ecosystems. Plants are considered veritable "ecosystem engineers," and bioremediation by using plants is appreciated as a special applied form of ecosystem services. Assessment of the bioremediation applicability and effectiveness may be required for specific ecosystems, at least until the technology becomes firmly demonstrated and established. Extensive studies of field conditions are required in order to implement this technique in historically heavy metal-contaminated areas.

Thus, further research is still needed before implementing this technique in a large scale. Before becoming a commercially widely applicable process, phytoremediation requires a commitment to resident population and to local authorities in polluted regions, as well as financial and time resources. At the same time, it has the potential to offer low costs for its application and is considered a green alternative to conventional technologies for soil remediation.

Decontamination of polluted soils by using bioaccumulative plants is proposed as an environmentalfriendly alternative to the traditional physicochemical methods, being a sustainable method with a great potential in the terms of environmental protection and cost management.

Conflict of interest

The authors declare no conflict of interest.

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The aim of *Ecosystem Services and Global Ecology* is to give an overview and report from the frontiers of research of this important and interesting multidisciplinary area.

Ecosystem services as a concept plays a key role in solving global environmental and human ecological crises and associated other problems, especially today when the sixth major extinction event of the history of the biosphere is in progress, and humanity can easily become a victim of it. Human activity is rapidly transforming the surface of the Earth, its biosphere, atmosphere, soil, and water resources. Ecological processes happen over a long time scale, thus damage caused by human activity will be perceptible after decades or even centuries.

We hope that our book will be interesting and useful for researchers, lecturers, students, and anyone interested in this field.

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