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Unraveling Plant Invasion: Insights into Major Pathways and Mechanisms of Invasive Species Spread

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Abstract

Invasive non-native species, commonly referred to as invasive alien species (IAS), pose a significant threat to ecosystems, economies, and human well-being due to their ability to outcompete native species, disrupt ecological balance, and incur substantial economic and social costs. In particular, invasive alien plant species (IAPS) have a pronounced detrimental impact on biodiversity, highlighting the urgent need for ongoing research efforts to comprehend their ecological interactions, devise effective management strategies, and safeguard the integrity of natural ecosystems. In this frame, this review aims to evaluate the current state of knowledge on IAPS ecology, with a specific focus on the pathways and mechanisms by which they propagate and establish themselves in new environments. Additionally, recognizing the existing gaps in understanding IAPS dynamics, we propose future directions and priorities for research within the current epoch of the Anthropocene and climate change. This comprehensive synthesis of the latest research findings and insights into IAPS provides an up-to-date understanding of the field, offering valuable insights for researchers, policymakers, and conservationists engaged in this scientific field.

Keywords: biodiversity, biological invasion, competition, dynamics, plant species, threats.

1. Introduction

IAS encompass animals, plants, or other organisms introduced by human activity, either intentionally or unintentionally, into environments beyond their native range. Their presence often results in adverse effects on native biodiversity, ecosystem services, and the well-being of human societies and economies [19]. These species often outcompete native flora and fauna for resources, resulting in declines in native populations and the modification of natural habitats [19,43]. Consequently, over 44.000 species are currently threatened with extinction, constituting 28% of all assessed species [20]. The International Union for Conservation of Nature (IUCN) Red List, recognized by the IUCN as a crucial indicator of global biodiversity health [21], now encompasses more than 157.100 species, with over 66.500 being plant species, representing approximately 16% of the world's known plants [21]. Just in the year 2023, the IUCN Red List published assessments for approximately 4.000 new tree species, bringing the total number of tree species assessed on the Red List to over 40.000 [22]. According to the IUCN Red List of Threatened Species (2022), one in ten species listed on the IUCN Red List faces threats from IAS. In response to this concern, the IUCN developed The Global Invasive Species Database (GISD) between 1998 and 2000. The GISD functions as a freely accessible online repository of information on alien and invasive species that adversely affect biodiversity. Its primary objectives include enhancing public awareness of IAS and facilitating effective prevention and management efforts by disseminating specialized knowledge and experience to a global audience. The database focuses on IAS that pose threats to native biodiversity and natural habitats, covering all taxonomic groups from microorganisms to animals and plants. Among its features, the database highlights the "100 of the World's Worst Invasive Alien Species," providing a comprehensive compilation that sheds light on the most detrimental non-native species and supports global endeavors to control their spread and conserve biodiversity [15].

The introduction of IAS can disrupt intricate ecological relationships, resulting in cascading effects throughout entire ecosystems [32,10]. Moreover, IAS can directly prey upon native species, introduce diseases, and alter habitat structure, further exacerbating their detrimental effects [10,39,41,4]. Such disturbances can lead to reduced species richness and genetic diversity, compromising the resilience of ecosystems to environmental changes.

The economic toll of biological invasions is staggering, as underscored by figures published by Diagne et al. [8]. Between 1970 and 2017, the minimum economic cost of biological invasions amounted to a staggering USD 1.288 trillion. These costs encompass a wide array of factors, including but not limited to direct expenses incurred in controlling invasive species, losses in agricultural productivity, impacts on human health, and damage to infrastructure and ecosystems. The financial burden imposed by invasive species extends across various sectors and industries, affecting both developed and developing economies worldwide [4,33]. Moreover, these figures only represent the minimum estimate of the economic impact, suggesting that the actual costs may be even higher.

Biological invasions are widely expected to become a greater problem in the future [35,26,42]. Consequently, it is evident that the world is now entering what can be termed as the 'Era of Globalization,' representing the third phase of biological invasions, succeeding the earlier phases associated with the Middle Ages and the Industrial Revolution [18,12]. Although it is acknowledged that IAS rank as the second most prevalent threat linked to species that have gone extinct entirely since the year 1500 after habitat destruction [2], prospects for the near future remain concerning. According to a 2020 study, the number of established IAS is projected to increase by 36% between 2005 and 2050 [20].

Given the multitude of concerns surrounding the significant threats linked with the invasion of plant species, it becomes imperative to prevent the introduction of IAPS and effectively manage their impacts to mitigate biodiversity loss. This matter is not only pivotal for safeguarding biodiversity but also crucial for human health, food security, livelihoods, and economies. To effectively tackle the ecological risks posed by IAPS, it is paramount to gain a comprehensive understanding of their traits and characteristics. Following these concerns, this review aims to synthesize the latest research findings and insights into IAPS, specifically focusing on the pathways and mechanisms through which they spread and establish themselves in new environments. Additionally, acknowledging the current gaps in understanding IAPS dynamics, we suggest future research directions and priorities, particularly within the current epoch of the Anthropocene and climate change.

2. Methodology

The methodology employed in this review involved a rigorous approach comprising comprehensive literature search and critical analysis focused on IAPS. A systematic search was conducted across major international databases, including Web of Science Core Collection, Scopus, ScienceDirect, and Google Scholar. The search strategy involved utilizing a combination of relevant keywords such as "invasive alien species", "invasive plant species", "mechanisms for plant species invasion" and "major pathways for plant species introduction."

Initially, a broad pool of scientific papers was identified based on the predefined keywords. Following this, a thorough screening process was implemented to ensure the inclusion of studies directly pertinent to the scope of the review. Inclusion criteria encompassed relevance to the mechanisms and pathways associated with the invasion of plant species, publication in peer-reviewed journals, availability of full-text articles in English, and.

Ultimately, a total of 156 scientific papers were selected for detailed examination and critical analysis. Additionally, to ensure the robustness and comprehensiveness of the review, supplementary searches were conducted through reference mining and consultation of relevant review articles and book chapters. This multifaceted approach aimed to capture a broad spectrum of research findings and perspectives, thereby facilitating a comprehensive synthesis of the existing literature on the topic.

3. Advancements in Understanding Invasive Plant Species Dynamics

3.1. Pathways for IAPS introduction. IAPS finds entry into new ecosystems through both intentional and accidental means facilitated by human activities. The intentional introduction by humans, whether for ornamental, agricultural, or pest control purposes, stands as a significant cause of species invasions across various ecosystems [6]. Additionally, IAPS can inadvertently infiltrate ecosystems as by-product of the import through accidental transport via international trade, shipping, road transport, and outdoor recreation [31,27]. These are the so-called 'hitchhiker' species [31]. Amongst these IAPS introduction sources, several studies pointed out the important contribution shipping trade to biological invasion, especially through the ballast water. Ruiz et al. [37] underscored the critical role of incidental transport in the dissemination of marine invasive species within the San Francisco Bay. Their study emphasized the adverse effects of non-native organisms introduced through the ballast water of commercial vessels, significantly impacting marine biodiversity and ecological equilibrium.

Small insular states are widely recognized as being particularly vulnerable to biological invasions, owing to their unique ecological characteristics and limited resources for invasive species management. Islands typically harbor simplified ecosystems with fewer native species, rendering them more susceptible to the introduction and establishment of invasive species. Moreover, insular states often lack natural barriers to prevent the arrival of invasive species and may experience high levels of human activity, including tourism and trade, which elevate the risk of unintentional introductions. Additionally, the limited land area and biodiversity of islands magnify the impacts of invasive species on native ecosystems and species. Consequently, insular states frequently encounter significant challenges in controlling and mitigating the consequences of biological invasions [31].

Upon introduction into new habitats, some IAPS facilitate the ingress of other invasive species through interactions and associations. A seminal study by Wang et al. [45] delved into the interaction dynamics between two invasive plant species, *Erigeron annuus* L. pers. and *Solidago canadensis* L., shedding light on their influence on native vegetation in China. The research demonstrated that the invasive species' rapid growth and prolific reproductive capabilities fostered dense populations, swiftly colonizing the studied ecosystems. Furthermore, the study identified key factors defining the resistance of native plant communities to invasion, including the relative abundance, growth performance, and diversity of native species.

Additionally, climate change, a pressing global challenge, profoundly influences the spread and establishment of IAPS [28]. The changing climate presents unprecedented challenges, as rising temperatures, altered precipitation patterns, and extreme weather events creating sometimes favorable conditions for the expansion and proliferation of IAPS into new habitats by altering environmental conditions in ways that favor their establishment and spread. Recent studies, such as that by Lenzner et al. [25], have elucidated how these extreme weather events create favorable conditions for the adaptation and proliferation of IAPS in novel geographic regions. More recently, Essl et al. [11] employed a comprehensive approach to assess potential shifts in the geographic distribution of IAPS amidst changing climatic conditions, indicating a trend of expansion towards colder regions or higher altitudes. Conversely, IAPS may face challenges in maintaining their presence in regions undergoing warming or drying trends. Furthermore, the emergence of Arctic shipping routes resulting from melting ice caps is projected to significantly decrease the duration of ship voyages from Asia to Europe, increasing the risk of IAPS surviving the journey [22].

Extreme weather events, such as droughts, floods, and storms, associated with climate change can disrupt ecosystems and facilitate the dispersal of IAPS [29,9]. For example, flooding events can transport seeds and plant fragments over long distances, aiding the rapid expansion of IAPS along waterways and floodplains. To date, Bellard et al. [3] investigated the influence of increasing temperatures and fluctuations in water levels on the distribution and invasion success of aquatic species. Their findings underscored the advantage held by IAPS possessing greater ecological plasticity and adaptability to changing environmental conditions, enabling them to proliferate and colonize new habitats more effectively.

3.2. Mechanisms of alien plant species invasion: competitive relationships between invasive and native species. Competitive interactions between invasive and native species are paramount in ecosystem ecology and conservation. IAPS exerts significant pressure on native counterparts by competing for vital resources, such as water, food, space, and light [30,43,24]. These competitive dynamics profoundly impact biodiversity and ecosystem functioning, influencing the growth, survival, and reproductive success of native species. As such, understanding these competitive interactions between invasive and native species is crucial for elucidating the dynamics of biological invasions and informing effective management and conservation strategies.

There are specific concerns regarding the competitive advantage of IAPS over native species. Still, the mechanisms underlying the competitive advantage of IAPS are diverse and contingent upon species-specific traits and environmental conditions [36]. IAPS often possess physiological and morphological adaptations that confer a competitive edge in resource utilization. For instance, they may exhibit accelerated growth rates, early maturity, enhanced fecundity, efficient seed dispersal mechanisms, deeper root systems for optimal nutrient absorption, and leaves optimized for sunlight capture. Additionally, some IAPS demonstrate faster growth rates and heightened aggressiveness in resource exploitation compared to native counterparts [38,44], facilitating their rapid colonization of new habitats and restricting native species' access to essential resources. Furthermore, IAPS may display greater resilience to environmental stresses, including drought, nutrient deficiencies, and temperature fluctuations, thereby enhancing their ability to persist and thrive in conditions where native species struggle to maintain competitiveness.

The phenomenon of rising temperatures specific to climate change exacerbates the growth potential of IAPS, amplifying their competitive advantage over native counterparts in the quest for essential resources such as water and nutrients. As temperatures increase, IAPS often exhibit enhanced physiological activity and metabolic rates, leading to accelerated growth rates and heightened resource acquisition capabilities. This accelerated growth enables IAPS to rapidly outcompete native vegetation for limited resources, thereby exerting greater pressure on native ecosystems. While underrepresented in the scientific literature, it has been demonstrated that climate warming can exacerbate the impact of species invasions on plant pollination. To date, Giejsztowt et al. [14] demonstrated in their study that warming trends have the potential to intensify competition for pollination between invasive and native plant species. Their findings suggest that increasing phenological overlap, especially in areas with high floral density, may exacerbate the invasive species' impact on native plants. This highlights the importance of considering not only the direct effects of climate change but also its indirect effects on ecological interactions, such as competition for pollination resources. Moreover, the heightened competitive intensity resulting from rising temperatures can exacerbate ecological imbalances, further compromising the resilience of native plant communities to invasive encroachment.

Recent studies have shed light on the intricate mechanisms of competition, the ensuing impacts on biodiversity, and the complex interactions that shape ecosystem dynamics. IAPS can significantly alter resource availability for native counterparts through their efficient utilization of water and nutrients, rapid spread, and adaptation to local conditions [46,40,16]. Consequently, native species may experience diminished growth and survival rates as a result of intensified competition.

The impact of competition between invasive and native species extends beyond individual survival to encompass broader implications for biodiversity, ecosystem structure, and functioning. Studies have revealed that species diversity in invaded plots versus uninvaded areas is largely influenced by the invading species' identity. Furthermore, declines in Shannon diversity and evenness are primarily attributed to factors such as the cover and height of IAPS, as well as disparities in height and cover between invasive and dominant native species, irrespective of species identity [16].

Furthermore, it is widely acknowledged that IAPS typically exhibit greater ecological plasticity compared to native species, enabling them to adapt more effectively to changing environmental conditions and resource availability, thus conferring a competitive advantage [5]. The detrimental impact of IAPS on native counterparts, including reductions in growth and survival rates, has been well-documented. However, it's important to recognize that morphological characteristics and superior physiological traits are not the sole contributors to the competitive advantage of IAPS. The dynamic response of these species' traits plays a significant role as well [13]. Invasiveness often correlates with the greater plasticity of plant traits in response to environmental changes [48]. Phenotypic plasticity, defined as the ability of organisms to modify their morphology and/or physiology in response to environmental variations, significantly influences the success of IAPS. Daehler [7] demonstrated that increased phenotypic plasticity can expand the ecological niches of invasive species, further enhancing their invasive potential.

A more recent study by Ren et al. [34], analyzed the phenotypic plasticity and vigor of *Solidago canadensis* (garden sedge) in the context of different nitrogen supply and temperature variations. The results of the study showed that *Solidago canadensis* exhibits significant phenotypic plasticity in response to variations in N and temperature. The plant has demonstrated the ability to adapt to environmental changes by adjusting its morphological, physiological and reproductive characteristics. This research are of outstanding importance, demonstrating that global warming and N fertilization could make the invaded habitat more suitable for this species to grow and even increase the invasion risk of *Solidago canadensis* through enhanced phenotypic plasticity, which is a crucial factor in helping the species to cope the changing environment.

A significant contribution to the understanding of the importance of phenotypic plasticity to the success of the invasion of IAPS was made by Zheng et al. [49]. The authors investigated how *Mikania micrantha* (vine/climbing hemp) plant respond to defoliation, aiming to identify the role of phenotypic plasticity in the adaptation and invasiveness of this species. The study is of particular importance because it highlights that some IAPS have the ability to adapt the photosynthesis process at the stem level in stress conditions, allowing the plant to continue the photosynthesis process and survive in unfavorable conditions.

Furthermore, the study by Hiatt and Flory [17] highlights the importance of understanding the differences in phenotypic plasticity between IAPS and native species for ecosystem management and conservation. The research aimed to study the differences that exist in the manifestation of phenotypic plasticity between 12 populations of the IAPS *Imperata cylindrica* and 6 native species that coexist in the same habitat. The research authors concluded that the IAPS exhibited greater plasticity in response to environmental variables, which gave it an adaptive advantage in colonizing and spreading across a wider range of habitats. On the other hand, native species exhibited lower levels of phenotypic plasticity, suggesting a more specific adaptation to local environmental conditions.

4. Challenges and Future Directions

As previously detailed, significant progress has been achieved in the realm of research concerning IAPS, indicative of a burgeoning knowledge base spanning various disciplines. These advancements have shed light on the intricate ecological dynamics governing plant invasions, elucidating the mechanisms through which IAPS establishes and proliferate in new environments. However, there remains a notable gap in our understanding of the introduction pathways for many IAPS [23]. As previously discussed, preventing the introduction of IAPS is paramount, prompting the implementation of effective measures for eradication and control. Future directions in research regarding IAPS introduction pathways should prioritize comprehensive investigations into human-mediated vectors such as trade routes, transportation networks, and horticultural practices, particularly in regions susceptible to invasion. Understanding these pathways is crucial for devising effective prevention and management strategies.

Additionally, research should delve deeper into the mechanisms underlying the competitive relationships between invasive and native species. Understanding the interactions between IAPS and native species and other invasive species, as well as their responses to ongoing environmental changes like climate change and land use modification, is crucial. Addressing these research gaps is pivotal for formulating comprehensive and effective strategies to combat the spread of IAPS and mitigate their ecological and socio-economic impacts. The economic costs associated with biological invasions (detailed in the first section of the article) underscores the need for concerted efforts in prevention, early detection, and effective management strategies to mitigate financial burdens and safeguard ecosystems and livelihoods from further harm. Moreover, recognizing the intricate interplay between climate change and IAPS introduction and spread emphasizes the necessity for integrating IAPS into climate change policies. This entails implementing biosecurity measures to prevent the introduction of IAPS to new regions due to climate change and implementing rapid response measures to monitor and eradicate alien species that may become invasive due to climate change.

5. Conclusions

The threat of IAPS looms large, contributing significantly to biodiversity loss, species extinctions, and global food security concerns. Extensive research has delved into the ecological ramifications of IAPS, highlighting their detrimental effects on native biodiversity, ecosystem functioning, and ecosystem services. Moreover, studies have elucidated the genetic, physiological, and behavioral attributes that confer invasiveness, informing the development of innovative management strategies aimed at curbing their adverse impacts.

As pointed out by numerous studies, climate change exacerbates the spread and invasiveness of many IAPS, creating new challenges for management. In light of these complexities, there is an urgent need for comprehensive management strategies to mitigate the ecological impacts of IAPS proliferation in a warming world. By understanding the mechanisms of adaptation and response to the environment, effective strategies for the management and control of IAPS can be developed, especially in the context of global climate change and biodiversity loss.

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