



The COVID-19 Restrictions and Biological Invasion: A Global Terrestrial Ecosystem Perspective on Propagule Pressure and Invasion Trajectory

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Abstract: Biological invasions driven by climate change, transportation, and intercontinental trade, as well as land-use change and tourism, pose severe threats to biodiversity and ecosystem services worldwide. However, the COVID-19-induced shutdowns and cross-border restrictions could have significantly impacted some of these drivers. Thus, COVID-19-induced restrictions may potentially alter the invasion trajectories and propagule pressure of invasive alien species, yet very few studies have examined this possibility. Here, we provide a unique conceptual framework to examine how COVID-19-induced restrictions may influence the rate, magnitude, and trajectories of biological invasions. We also discuss the similarities between the high-hit regions of COVID-19 and the global hotspot of biological invasions. Additionally, we assessed whether previous predictions of biological invasions still hold despite the strong impact of COVID-19 on the drivers of invasive species, nature reserves, and national parks. The present study is a significant addition to the current understanding of the interplay between pandemic outbreaks and biological invasions in the context of both direct and indirect effects of global ecosystem change.

Keywords: intercontinental trade; pandemic lockdowns; invasion pathway; invasive alien species

1. Introduction

The severe acute respiratory syndrome, coronavirus or SARS-CoV2, commonly known as COVID-19, has quickly spread to most countries worldwide [1]. The World Health Organization (WHO) declared the virus infection a global pandemic on March 11 2020 [2,3]. The emergence of COVID-19 potentially led most countries into a severe economic downturn [4] as governments struggled to contain the ravaging virus. One such containment policy introduced was the lockdown policy [5], which prohibited mass social gatherings and restricted public movement via all significant transportation channels: land, sea, and air. The COVID-19-induced restrictions have had varying effects on the ecosystem via reduced human disturbances, decreased conservation measures, and disrupted long-term field experiments on invasive species [5,6]. However, recent studies indicated that restrictions on human mobility and anthropogenic activities have led to drastic reductions in greenhouse gases (GHGs) and atmospheric warming with a cascading improvement in the global climate [7,8]. Evidence is emerging on the direct and indirect effects of COVID-19 on social life [9], economic activities [10], biodiversity [11–14], and the environment [15,16]. However, very few studies have examined the linkage between the restrictions derived from coronavirus pandemic and biological invasions.

The COVID-19 and lockdown policies have tremendously influenced production activities, social lifestyles, and the economic growths of the nations of the world. For example, in a recent study, Shan et al. [4] reported a sharp drop of 34.3% and 12.1% gross domestic product (GDP) for the USA and the European Union, respectively, three months



Citation: Adomako, M.O.; Roiloa, S.; Yu, F.-H. The COVID-19 Restrictions and Biological Invasion: A Global Terrestrial Ecosystem Perspective on Propagule Pressure and Invasion Trajectory. *Sustainability* **2022**, *14*, 14783. https://doi.org/10.3390/ su142214783

Academic Editor: Giovanni Amori

Received: 20 September 2022 Accepted: 6 November 2022 Published: 9 November 2022

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Copyright: © 2022 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). after the virus was declared a pandemic in the year 2020, while China suffered a GDP drop of 6.8% in the first quarter. Despite these unexpected global economic downturns in productivity and livelihood, recent studies have also reported some unprecedented positive direct and indirect effects of the lockdown policies on major drivers of global climate change, particularly GHGs and atmospheric temperature [15]. It is projected that the global emission of CO₂ will experience a decline of 8%, which equalized the level of total CO₂ emission in the last decade [4]. Therefore, highlighting the impact (direct and indirect) of the COVID-19 pandemic restrictions on biological invasions from the global ecosystem perspective is critical, as it will assist in reviewing previous predictions on invasion pathways.

Biological invasions could be described as the process whereby a species grows successfully, establishing, developing, and maintaining a certain level of population beyond its geographical borders of origin [17]. It is among the critical ecological disturbances threatening the global ecosystem's functioning and services [18–20]. Climate change, land-use changes (especially in agriculture), accelerated human mobility (e.g., transcontinental transportation), and cross-border trade have been linked with the thriving range expansion of invasive alien species into novel environments [21,22]. Invasive species have considerable adverse effects on the ecosystem worldwide by reducing native species' performances and productivities and altering community structures and compositions [23–25]. The main traits that cause invasive alien species to be successful in an introduced region are the high reproductive capacity, high nutrient use efficiency, and the capacity to induce priority effects on native soil communities [26,27]; such traits modify their competitive interaction with native communities [28]. Moreover, invasive alien species impose potential economic (i.e., the elevated cost of agriculture production) and health challenges in the invaded region [29,30]. Nevertheless, suppose the pandemic restriction policies have had critical impacts on these key drivers of biological invasions (i.e., climate change, transcontinental transportation, agricultural activities, and tourism) [31,32], then the COVID-19 pandemic may likely have indirect effects on biological invasions too. However, to date, very few studies have related the impact of the COVID-19 pandemic to biological invasions from the global ecosystem perspective. A clear insight into these unintended pandemic policies on the spread of invasive species could be harnessed to facilitate the management of invasive species, nature reserves, and national parks.

Both the COVID-19 pandemic and biological invasions share common characteristics in their mode of introduction and spread and thus call for a collective global effort for their eradication [33]. For instance, human mobility (local, regional, and transcontinental transportation and trade) is found to increase the infection rate of COVID-19 [34] and the spread of invasive alien species [21]. Additionally, climate change (e.g., extreme cold conditions) increases the susceptibility to COVID-19 infection [35,36] and, likewise, global warming underpins species invasions [37,38]. Again, the COVID-19 pandemic and biological invasions induce economic hardships and ecological and health impacts on the invaded regions [4,39,40]. Moreover, COVID-19 and biological invasions share typical hotspots in terms of occurrences (geographical area), infection rate (leading continents), and the magnitude of impacts (health, ecological, and economic). For example, one year after the virus was declared a pandemic, the European community had the most significant global confirmed infection cases, followed by the Americas ([41], https://COVID19.who.int/; last visited 9 March 2022). Likewise, North America is known to harbor the highest number of naturalized plants, followed by Europe (see Figure 3 of van Kleunen et al. [25]). In a recent study, van Kleunen et al. [25] reported that Europe has donated 288% of species from its native flora, while Butchart et al. [42] also reported an increase of about 76% of invasive species in Europe. Moreover, it is predicted that most emerging economies, such as those in China and India, will experience a surge in biological invasions owing to the increase in bilateral trade [22,43], with more invasive alien species expanding beyond their native range in the coming decades [43]. As the invasion hotspot countries tighten their entry regulations, especially

on intercontinental trade and tourism, one could expect a more remarkable shift in the invasion trajectory and propagule pressure.

In this paper, we first provide a unique conceptual framework to examine how the COVID-19 restrictions may influence the rate and trajectories of biological invasions (Figure 1). We also discuss the relatedness of the global hotspot of COVID-19 and biological invasions. Moreover, we assess whether past predictions of biological invasions still hold, despite the strong interactions of COVID-19 with the major invasion drivers, i.e., climate change, agriculture or land-use change, intercontinental or bilateral trade, tourism, and transportation. Finally, we highlight the possibility of harnessing such restrictive measures to manage invasive species, nature reserves, and national parks.

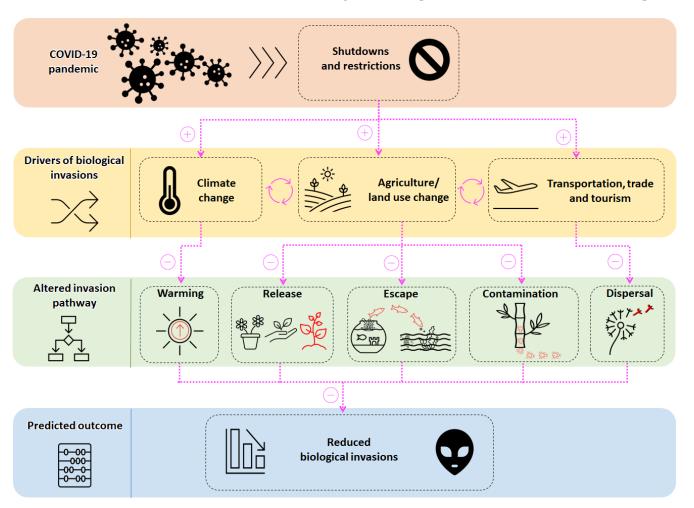


Figure 1. The conceptual framework of how the impact of COVID-19 may influence the propagule pressure and invasion trajectories of invasive alien species. Recent studies have indicated some positive effects (denoted positive signs) on climate change, agriculture or land use change, transportation, trade, and tourism, which are critical drivers of biological invasion. Notably, each invasion driver can promote the other (denoted ring arrows). These invasion drivers can facilitate biological invasions (denoted negative signs) via warming, release, escape, contamination, and dispersal. However, COVID-19 restrictions-derived effects on these invasion drivers can alter the invasion pathway, thereby reducing biological invasions.

2. Conceptual Framework: Interplay between COVID-19 and Drivers of Biological Invasions

2.1. COVID-19 Restrictions and Global Climate Change

Notably, in the 21st century, anthropogenically induced disturbances and environmental change have resulted in the explosion of many organisms moving beyond their native range [44,45]. Climate change will undoubtedly be one of the main factors influencing the occurrence and impacts of biological invasions in the future [31].

For example, atmospheric warming, melting of glaciers, and altered rainfall patterns have caused a considerable shift in propagule pressure, as many invasive alien species are moving beyond their native boundaries, particularly towards higher altitudes [46–48]. The elevated global warming in recent decades presents huge climatic suitability for establishing current and future invasive alien species in an environment previously deemed unsuitable for their survival and establishment [47,48]. Both global climate change and biological invasions pose an emerging threat to human livelihood, economic growth, biodiversity, and ecosystem services [49]. However, the pandemic-induced reductions in the impact of climate change will likely alter the trajectories of range-expanding species.

Currently, the COVID-19 pandemic is considered among the most devastating events (e.g., the world wars and the flu pandemic of 1918–1919) because of its destructive nature and global spread in the history of our world. Despite the extent to which the COVID-19 pandemic and its interventions have disrupted and altered the social lifestyle and economies of nations, there have been unprecedented reports of both direct and indirect interactions between COVID-19 and global climate change. The majority of this literature focused on the reduction of global emissions of greenhouse gases [15], atmospheric warming [50-52], and the restructuring of the ozone layer [7,53]. For example, about a 11-58% reduction in particulate matter across major cities of the world has been recently reported and attributed to the COVID-19 pandemic [54,55]. While 77.3% and 54.3% reductions in NO and NO_2 , respectively, have been recorded in Sao Paulo, Brazil [55], ~50% and 20.5% increases in ozone have been observed in Italy [53] and China [56], respectively. Large quantities of elemental particles and compounds such as SO₂, NOx, and CO, which constitute the primary driving force behind climate deterioration, have considerably declined [52]. These findings suggest that the COVID-19-mediated atmospheric emissions, coupled with the substantial improvement of the ozone system, could potentially have positive cascading effects by decreasing the range expansion, establishment rate, and invasion trajectory of alien species. However, we recognize that these documented positive effects on air quality could easily be reversed as most countries ease their entry restriction. Consequently, the potential impact of biological invasions that we suggest here could also dissipate.

2.2. COVID-19 Restrictions and Agriculture

The advent of the Green Revolution substantially reduced global food shortages, especially grain production [57], but is detrimental to global environmental integrity owing to the introduction of large quantities of agrochemicals into the soil [58]. Throughout history, agriculture has been considered one of the most common arenas by which humans have directly interacted with the ecosystem worldwide [58]. Besides its contribution to the deteriorating global climate [59], agriculture has enormously influenced the range expansion of many alien species via altered land use and habitat homogenization, as well as the release, escape, and contamination of novel habitats [60,61]. Moreover, soil tillage, seed propagation, and the application of agrochemicals have modified the natural environment, disrupted the soil ecosystem, created a conducive atmosphere for introduced alien plants to thrive, and caused varying degrees of economic damage and disruption to ecological virtues.

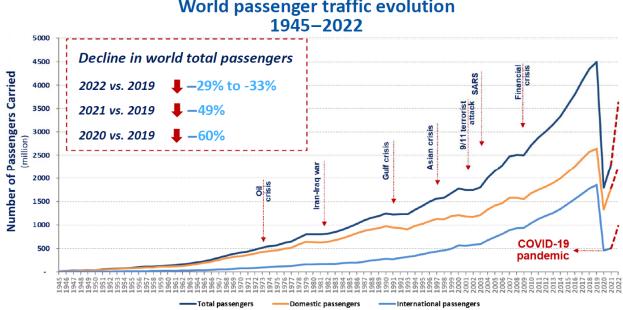
Nevertheless, agriculture represents a vital infrastructure in both developed and developing economies by ensuring food stability and security and providing employment opportunities to people. Agricultural activities were essential to ensure stable and sustainable food and nutrition security amidst the lockdowns and social distancing policies to tackle the coronavirus. More importantly, government subsidies on agrochemical inputs and animal feed and reduced taxes on product processing of industries, transportation, and toll levies were able to stabilize the food system without adding starvation to the woes of COVID-19. For example, in China, to ensure food security and strictly adhere to various interventions to contain the virus, the Chinese government ordered the agricultural industry to swing into action to produce enough to feed over 1.4 billion people [62].

Despite these countermeasures to boost food security, the restriction policy disrupted significant aspects of the agricultural industry, such as farm labor availability and the cancellation of many invasive species eradication projects (e.g., the Gough Island mouse eradication project) [5,63,64]. For example, approximately 95% of rice-growing sectors in India rely heavily on manual labor [65]. The COVID-19 restrictions saw about 1 million immigrant workers returning home with no prospects of coming back [2,65]. Globally, seasonal migrant labor shortages, especially in the United States, Europe, Australia, and India, are likely to impact the agricultural economy negatively [66]. Additionally, in Eastern Africa, the fight against locusts was compromised because of the high cost (i.e., more than tripled the usual price) of transporting pesticides to the affected farming communities [10]. Although such a coronavirus-induced reduction of human interaction and disturbances of farmlands have significant shortfalls in economic growth and livelihood, there could be positive effects on ecosystem health and biodiversity restoration [11,67].

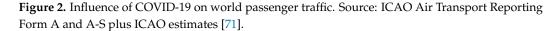
2.3. COVID-19 Restrictions and Transportation, Trade, and Tourism

Transportation, trade, and tourism are among the many factors that initiate the interaction of people across local, regional, and continental boundaries. These socio-economic factors have contributed hugely to the globalization of our world, where people from diverse backgrounds are operating on common grounds of development and cooperation. However, due to trade and tourism, large quantities of live plants, animals, and insects have been exported across the globe, thereby increasing the richness of alien species into novel ecosystems [68]. Trade and transport have been identified as the most relevant drivers of alien species impacts until 2050 for most biomes and taxonomic groups [31]. By 2050, global shipment due to trade will cause more negative effects compared to climate-driven environmental change on marine invasions [21,68]. Moreover, owing to the solid integral role of bilateral trade in socio-economic development, most developed countries will experience an increasing growth of invasion risk [21]. For example, Work et al. [69] reported a 50–98% arrival of alien insects into the USA, while Sardain et al. [27] predicted an 80% surge of invasions from Northeast Asia to Northern Europe by 2050. Therefore, an increase in the rate of international trade, tourism, and transportation, particularly air transport (as the fastest and most efficient way among others), will concomitantly increase the rate of biological invasions and their environmental and social cost [70].

However, such predicted increases in the spread of alien species mediated by transportation, trade, and tourism are likely to shift owing to regional and international crossborder closure and restrictions, which are deemed the surest way of curtailing the crossborder importation and exportation of COVID-19. Despite the effectiveness of these countermeasures in limiting the spread of the pandemic, travel restrictions have tremendously influenced most aviation-tourism-dependent economies by affecting employment, lifestyle, and state revenues (Figure 2).



World passenger traffic evolution



For example, the SARS epidemic in 2003 reduced tourism revenue in China by USD 16.9 billion and significantly declined aviation passenger traffic by nearly 50% [72]. Accordingly, the European airports suffered a significant sum of USD 40.8 billion loss of revenue, while Asian/Pacific airports suffered a deficit of USD 29.6 billion in gross income for 2020 [66]. Therefore, such a massive margin of reduction in air transportation and tourism may likely exert a proportionate decreasing effect on the propagule pressure of potential range-expanding species. This decreasing effect on range-expanding species suggests that the impact of COVID-19 and its associated containment measures on drivers of biological invasions may equally impose a cascading impact on propagule pressure.

3. Relationship of High-Hit Regions of COVID-19 with Hotspots of Plant Invasions

COVID-19 has wreaked significant havoc on the USA and European community regarding the number of infections and deaths than in any other region. The virus, which was first detected in Snohomish County, Washington, USA, on 21 January 2020 [73] and in nine European countries with 47 cases on 27 February 2020 [74], has since killed hundreds of thousands of people in these regions. Two years after the first cases were reported in these regions, subsequent variants of the virus (e.g., Delta and Omicron) are still threatening both social life and the economy of the United States and the European community. Coincidentally, these regions (America and Europe) represent the hotspot of invasive alien plants (see Figure 3 of van Kleunen et al. [25]). For example, North America is recently found to harbor the highest number of naturalized plant species (i.e., alien species reproducing naturally in the recipient ecosystems) [25].

Although the cross-border movement is partially easy in these countries, many people, out of fear of contracting the virus, prefer to remain in their respective regions to cross to the other site. Therefore, we argue that, as countries ensure strict entry regulations in these hotspots of COVID-19, the rate at which invasive species leak out of these invasion hotspots will equally be reduced. Despite the lack of annual data on the number of invasive species that spread out of the European community and the Americas, restricting human movement for more than two years will strongly impact the propagule pressure, which can alter the trajectories of biological invasions.

4. Past Predictions of Biological Invasions in the Face of COVID-19

Predicting biological invasions has equally been challenging with the eradication of the species after its establishment; however, understanding the magnitude and direction of the range-expanding species is critical to managing these invasive species. Ecological predictions to fathom the movement of alien species invasions have become necessary due to the fast-changing global climate, increasing land-use changes, and upsurging intercontinental trade, maritime transportation, and tourism [75]. For example, in a recent study, Sardain et al. [21] predicted a 3- to 20-fold increase in the global invasion risk by 2050 owing to the emerging global shipping network. Sardain et al. [21] indicated that Northeastern Asia would account for approximately ~80% of invasive species in Northern Europe by 2050. About the socio-economic activities 20 years ago, Seebens et al. [76] projected a surge of naturalized species for the emerging economies owing to trade in the next 20 years, with an increase in the spread of invasive species in the northern temperate due to global climate change. Moreover, nonindigenous establishment has also been predicted to increase by 16–24% in the United States from 2000–2020 due to international trade [77]. Last but not least, the global environmental change-induced impacts of biological invasions in the United Kingdom are expected to increase by 2050 [61]. Such projections were produced based on the current trend and magnitude of the factors that drive the invasions of alien species.

However, the COVID-19-induced shutdowns and restrictions have significantly altered the potency of most of these invasion drivers. Once COVID-19 lingers with the intermittent outbreak of new variants, these restrictions and cross-border shutdowns will persist or be re-activated. Therefore, past predictions that depended on invasion drivers, such as intercontinental trade via shipping, air cargo, tourism, and climate change may require further validation in the face of COVID-19 (see Table 1). The entire world has come to accept "the new norm" created by the pandemic owing to the disruption of lifestyle and socio-economic activities that could potentially exacerbate the rate of biological invasions. New predictions and further assessment of the past predictions on the introduction, establishment, and spread of invasive species will be highly acceptable. Although some of the impacts may be temporal, the combined positive influence on the global ecosystem and biodiversity may extend beyond decades. We recommend that such restrictive strategies are adopted to manage our nature reserves, parks, and conservation forests.

Predicted Factor	% Increase or Decrease	Time-Lapse	Reference
Shipping traffic	A 240–1209% increase in the global invasion risk	By 2050	[21]
Bilateral trade	A 36% surge in plant naturalization in emerging economies	Between 2005–2050	[76]
Climate change and global trade	Strong increase in naturalized plants	Next 20 years (2015–2035)	[22]
Warmer temperature	European catfish becoming widespread invasive species	By 2050	[78]
Climate change	Ambrosia artemisiifolia to increase across lowland Britain	By 2080	[79]
Horticultural trade	Massive export of new invasive species to the USA	Variable	[80]
Land-use change	The emergence of new invasive species into novel habitats	By 2050 and 2100	[29]
Climate change	More range-expanded species (Chilean needle grass) into Britain due to favorable climate	By 2080	[81]
Agriculture	A 70–100% increase in demand for agricultural goods	By 2050	[82]

Table 1. Recent predictions of biological invasions that COVID-19-derived restrictions are likely to change.

While we know that the level of restrictions will not be permanent over time on a global scale, our work can explore how the local implementation of these rules can mitigate severe and costly environmental problems, such as biological invasions. Thus, actions

that include the rigorous control of mobility and trade and appropriate land use, could be beneficial to avoid new processes of biological invasions in local areas of particular conservation interest, such as protected areas.

Globalization has grown unstoppably over recent decades, increasing economic activity and productivity generally, with consequent benefits for part of human societies. However, in parallel with this enormous economic activity, globalization has also undoubtedly negatively impacted the environment and, consequently, the ecosystem services nature provides. The processes of biological invasions and the spread of emerging diseases are closely linked. On the one hand, invasive species can act as vectors of these diseases, as could be the case of American mink in Europe infected by COVID-19 [83,84], where escaped infected animals from fur farms could spread COVID-19 in the wild. On the other hand, there is precise parallelism between the phases associated with the process biological invasions and the occurrence and expansion of emerging infectious diseases, such as COVID-19, from introduction to impact [33]. Here, and following this similarity, we propose that management actions to contain the spread of COVID-19 could also contain the spread of biological invasions.

The economic costs due to COVID-19 restrictions have been enormous. However, it is also necessary to consider the potential collateral benefits arising from this situation. In this sense, the economic costs of biological invasions are also massive, even when these costs remain strongly underestimated [85]. Therefore, if restrictions can somehow reduce new biological invasion events, these benefits should also be considered in the cost/benefit balance. So far, COVID-19 restrictions have proven that previous pandemics and natural and human-caused events had the potential to alter the invasion pathways of invasive species. Nevertheless, such pandemic-mediated impacts on the trajectories of biological invasions may depend on the time scale, as the effects observed within short-terms are likely to resurface.

Author Contributions: Conceptualization, M.O.A. and F.-H.Y.; methodology, M.O.A.; software, M.O.A. and S.R.; validation, M.O.A., S.R. and F.-H.Y.; formal analysis, M.O.A.; investigation, M.O.A.; resources, F.-H.Y.; writing—original draft preparation, M.O.A.; writing—review and editing, M.O.A., S.R. and F.-H.Y.; visualization, M.O.A. and S.R. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Acknowledgments: We thank three anonymous reviewers for their comments.

Conflicts of Interest: The authors declare no competing interest.

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