

Special Section:

The COVID-19 pandemic: linking health, society and environment

Key Points:

- The seasonality of COVID-19 appears to follow seasonality of some environmental variables
- Seasonality of air drying capacity and ultraviolet radiation consistently matches the seasonality of COVID-19 across climatic zones
- Seasonality of air humidity and temperature matches the seasonality of COVID-19 in temperate climates but not in tropical monsoon climates

Supporting Information:

Supporting Information may be found in the online version of this article.

Correspondence to:

Y.-W. Choi,
choiyw@mit.edu

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Author Contributions:

Conceptualization: Elfatih A. B. Eltahir

Data curation: Yeon-Woo Choi

Formal analysis: Yeon-Woo Choi, Alexandre Tuel

Funding acquisition: Elfatih A. B. Eltahir

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On the Environmental Determinants of COVID-19 Seasonality

Yeon-Woo Choi¹ , Alexandre Tuel^{1,2} , and Elfatih A. B. Eltahir¹ 

¹Ralph M. Parsons Laboratory, Massachusetts Institute of Technology, Cambridge, MA, USA, ²Now at Oeschger Center for Climate Change Research, Institute of Geography, University of Bern, Bern, Switzerland

Abstract Viral respiratory diseases (VRDs), such as influenza and COVID-19, are thought to spread faster during winter than during summer. It has been previously argued that cold and dry conditions are more conducive to the transmission of VRDs than warm and humid climates, although this relationship appears restricted to temperate regions and the causal relationship is not well understood. The severe acute respiratory syndrome coronavirus 2 causing COVID-19 has emerged as a serious global public health problem after the first COVID-19 reports in Wuhan, China, in late 2019. It is still unclear whether this novel respiratory disease will ultimately prove to be a seasonal endemic disease. Here, we suggest that air drying capacity (ADC; an atmospheric state variable that controls the fate/evolution of the virus-laden droplets) and ultraviolet radiation (UV) are probable environmental determinants in shaping the transmission of COVID-19 at the seasonal time scale. These variables, unlike temperature and humidity, provide a physically based framework consistent with the apparent seasonal variability in COVID-19 and prevalent across a broad range of climates (e.g., Germany and India). Since this disease is known to be influenced by the compounding effect of social, biological, and environmental determinants, this study does not claim that these environmental determinants exclusively shape the seasonality of COVID-19. However, we argue that ADC and UV play a significant role in COVID-19 dynamics at the seasonal scale. These findings could help guide the development of a sound adaptation strategy against the pandemic over the coming seasons.

Plain Language Summary There is growing scientific interest in the potential seasonality of COVID-19 and its links to climate variables. This study aims to determine whether four environmental variables, namely, temperature, humidity, air drying capacity (ADC), and ultraviolet radiation (UV), are probable environmental determinants for the observed seasonal dynamics of COVID-19 prevalence, based on extensive country-level data spanning the first year of the pandemic. Although the influence of socio-economic factors may be dominant, we here suggest that ADC and UV are key environmental determinants of COVID-19 and can potentially affect the transmission and seasonality of the disease across a wide range of climates.

1. Introduction

Since the 2019 novel coronavirus responsible for COVID-19 was initially reported in December 2019 in Wuhan, the epicenter of the current pandemic (Li et al., 2020; Zhou et al., 2020), there has been growing scientific interest in the seasonality of this novel disease and the potential influence of climate variables. However, the analysis on this issue has been complicated by limited data. Nonetheless, based on epidemiological studies involving other viral respiratory diseases (VRDs; e.g., influenza), which, like COVID-19, are mainly transmitted by contact, droplets, and fomites (Dhand and Li, 2020; Stilianakis and Drossinos, 2010), it may be possible to provisionally infer not only the seasonal nature of COVID-19 but also the role of environmental factors in shaping this seasonality.

A well-known and well-studied VRD is influenza, which tends to peak during winter in temperate regions (e.g., Ballester et al., 2016; Choi et al., 2020; Shaman and Khon, 2009; Tamerius et al., 2011, 2013). Previous studies have attempted to understand its seasonality by considering the effects of environmental/weather conditions on virus survival and transmissibility. Based on experiments with inoculated guinea pigs, Lowen et al. (2007) reported that the transmission of the influenza virus was significantly suppressed under high absolute humidity and warm temperature conditions. Subsequent research based on similar laboratory

Investigation: Yeon-Woo Choi, Alexandre Tuel, Elfatih A. B. Eltahir
Methodology: Yeon-Woo Choi, Alexandre Tuel, Elfatih A. B. Eltahir
Project Administration: Elfatih A. B. Eltahir
Software: Yeon-Woo Choi
Supervision: Elfatih A. B. Eltahir
Validation: Yeon-Woo Choi, Alexandre Tuel, Elfatih A. B. Eltahir
Visualization: Yeon-Woo Choi
Writing – original draft: Yeon-Woo Choi, Alexandre Tuel, Elfatih A. B. Eltahir
Writing – review & editing: Yeon-Woo Choi, Alexandre Tuel, Elfatih A. B. Eltahir

experiments emphasized the role of absolute humidity over relative humidity as a key environmental factor for influenza transmission (Shaman and Kohn, 2009). The analysis of data from temperate regions further supported the hypothesis that low specific humidity conditions favored the survival and transmission of the influenza virus at the scale of the population, and it could be the main cause of winter epidemics (Shaman et al., 2010, 2011).

However, this perspective failed to account for influenza dynamics in tropical countries, where the disease typically peaks during the wet season (Tamerius et al., 2011). Further research argued that seasonality in tropical regions could be explained by a modulation of the effect of absolute humidity on temperature, with “cold-dry” and “warm-wet” conditions favoring influenza transmission (Deyle et al., 2016; Tamerius et al., 2013). Yet, it is still unclear why influenza would respond differently to absolute humidity at different temperatures, and why different statistical relationships would be needed for countries of different climates and latitudes. In addition, the exact mechanisms by which absolute humidity may affect the survival and transmission of the influenza virus remain unknown. Much of the attention has also focused on whether the environment affected virus survival and host contagiousness. Yet, since influenza and VRDs in general are transmitted in large part through respiratory droplets, environmental conditions may also affect VRD prevalence through their effect on the fate of these droplets. In an earlier study, we proposed by contrast that the prevalence of influenza, and VRDs in general, was likely to be shaped instead by the air drying capacity (ADC; see section 2.2), a state variable involving both temperature and humidity, which controls the evolution of respiratory droplets and is based on Maxwell’s theory of droplet evolution via coupled heat and mass transfer (Choi et al., 2020; Maxwell, 2003).

Regarding COVID-19, most of the virus prevalence during the initial stage of the pandemic was found in areas with specific climate conditions: Average temperatures of 5–11°C, combined with low specific humidity of 3–6 g/kg (Sajadi et al., 2020); temperature range of 3–17°C, with humidity between 4 and 9 g/m³ (Bukhari and Jameel, 2020); and temperature of 0–10°C, with relative humidity ranges within 70%–95% (Nath et al., 2021). Further studies also argued that low temperature and low humidity were major drivers behind the explosive increase in confirmed COVID-19 cases because they weakened the host’s immune system and increased virus stability and transmission (e.g., Araújo and Naimi, 2020; Chin et al., 2020; Moriyama et al., 2020; J. Wang et al., 2020; Wu et al., 2020). On the other hands, several studies have emphasized the effect of atmospheric humidity on the prevalence of this disease, consistent with influenza dynamics (Baker et al., 2020; Ma et al., 2020; Ward et al., 2020). By contrast, the spread of COVID-19 was found to be more correlated with temperature than with humidity in certain areas (Bherwani et al., 2020; Kaplin et al., 2020; Tosepu et al., 2020; Xie and Zhu, 2020). In addition, attention has also paid to ultraviolet (UV) radiation as a potential environmental factor impacting VRD transmission (Carleton et al., 2021). Laboratory and epidemiological studies have shown that strong UV radiation appeared to have a profound effect on the survival of severe acute respiratory syndrome coronavirus 2 (SARS-Cov-2) and other coronaviruses (Darnell et al., 2004; Duan et al., 2003; Ratnesar-Shumate et al., 2020; Seyer and Sanlidag, 2020; Schuit et al., 2020).

These studies provide some evidence that environmental variables play some role on COVID-19 transmission, even though it is generally agreed that many determinants, including social, biological, and environmental factors, shape the transmission of VRDs. In particular, the massive measures taken by governments in response to the COVID-19 pandemic have strongly impacted its dynamics (Bherwani et al., 2020; J. Wang et al., 2020). Additionally, most studies have focused on the initial months of the pandemic when the data were too limited to detect strong seasonal signals (Sajadi et al., 2020; Bukhari and Jameel, 2020; J. Wang et al., 2020). Therefore, at this stage, it remains unclear to what extent COVID-19 prevalence exhibits seasonality, whether this seasonality is shaped by environmental factors, and if so, which among them are the most important. Here, we focus on these questions by examining the relationships between COVID-19 prevalence and environmental variables across a wide range of climates based on available data covering the first year of the pandemic.

Table 1
List of Countries Used in This Study

	List of countries
Five representative countries of different climates and latitudes	Canada, Germany, India, Ethiopia, Chile
56 temperate countries in the Northern Hemisphere	Albania, Andorra, Armenia, Austria, Bahrain, Belarus, Belgium, Bhutan, Bosnia and Herzegovina, Bulgaria, Croatia, Cyprus, Denmark, Estonia, Finland, Germany, Greece, Hungary, Iceland, Iran, Iraq, Ireland, Israel, Italy, Japan, Jordan, Kazakhstan, South Korea, Latvia, Lithuania, Luxembourg, Mongolia, Morocco, Nepal, Netherlands, North Macedonia, Norway, Pakistan, Poland, Portugal, Qatar, Romania, Russia, Serbia, Slovakia, Slovenia, Spain, Switzerland, Tunisia, Turkey, Ukraine, United Arab Emirates, United Kingdom, Canada, China, US
6 tropical monsoon countries	Bangladesh, Ethiopia, Thailand, Ghana, India, Cote d'Ivoire

2. Data and Method

2.1. Data Sets

Six hourly temperature, dew point temperature and surface pressure data, and hourly UV fields are taken from the ERA5 reanalysis (Hersbach et al., 2018) at $0.25^\circ \times 0.25^\circ$ horizontal resolution for the period ranging from March 1st, 2020 to March 13th, 2021. With these data, we calculate daily mean temperature, specific humidity, and ADC (see section 2.2). Since population is not uniformly distributed within each country, we avoid simple country-averaged climate variables which do not correctly reflect the climate conditions to which the population is exposed. Instead, we calculate population-weighted average temperature, specific humidity, ADC, and UV across all grid cells contained in a given country, based on weights obtained from a gridded distribution of population density following Carleton et al. (2021). Population density data are taken from the gridded population of the world (GPW) v4 data set (CIESIN, 2018).

Daily data on confirmed COVID-19 cases, number of tests, stringency index (i.e., a composite index of political measures; Hale et al., 2021), and the population for each country are from the “Our World in Data” database (available at <https://ourworldindata.org/>). Subnational-level COVID-19 epidemiological data for Australia, China, and Canada are available at the Johns Hopkins University Center for Systems Science and Engineering (JHU CCSE; <https://data.humdata.org/>). Daily COVID-19 data at the scale of different states within the United States are provided by the COVID Tracking Project (available at <https://covidtracking.com/>). A threshold of at least 10,000 cumulative COVID-19 tests per 1 million people was retained to discard countries with unrepresentative data. This criterion can somewhat ensure the reliability of the data, although it still has severe limitations (see discussion). This approach yields 56 countries in the temperate Northern Hemisphere, and six tropical countries (Table 1), which are predominantly influenced by tropical monsoon systems with hot-humid summers. To isolate the role of environmental factors in modulating the spread and potential seasonality of COVID-19, five representative countries are carefully selected, which have different climate conditions and constant social controls (i.e., stringency index does not change significantly) over the analysis period (Figure S1). The list of analyzed countries is provided in Table 1. To consider the incubation period of COVID-19, which is generally regarded as 4–7 days, we mainly use weekly average or weekly cumulative values (Li et al., 2020).

2.2. Air Drying Capacity

The current mechanistic understanding of VRD transmission assumes that VRDs are mainly transmitted through virus-laden droplets between infectious and susceptible individuals (Bourouiba, 2020; Wells, 1934; Xie et al., 2007). Since droplets tend to evaporate more quickly under high temperature and low humidity conditions (B. Wang et al., 2020), these two variables could theoretically affect the spread of the VRD by controlling the fate of droplets in their surrounding environment (Choi et al., 2020; Maxwell, 2003). In our earlier study, we proposed a physically based atmospheric state-variable, ADC, as a relevant environmental determinant for the transmission of VRD (Choi et al., 2020). We define ADC, (in mm^2/hr) as the rate of decrease of the droplet surface area, under given temperature and humidity conditions. ADC is an integrated

Table 2
Relationship Between Weekly Environmental Variables Including Temperature (°C), Specific Humidity (g/kg), ADC (mm²/hr), and UV (W/m²) for the Period From March 1st, 2020 to March 13th, 2021 Across Countries in the Temperate Northern Hemisphere

	Temperature	Specific humidity	ADC	UV
Temperature	1 (1)	0.8 (0.7)	0.6 (0.0)	0.6 (0.0)
Specific humidity		1 (1)	0.2 (0.3)	0.3 (0.0)
ADC			1 (1)	0.6 (0.5)
UV				1 (1)

Note. The values in parentheses is same as those without parentheses, but for tropical monsoon countries.
Abbreviations: ADC, air drying capacity; UV, ultraviolet radiation.

measure of temperature and humidity and is nonlinearly proportional to temperature but inversely proportional to humidity (Table 2). ADC is defined as follows:

$$ADC(T_a, RH) \equiv -3.6 \times 8\pi \times 10^9 \times \frac{(RH - 1)}{\left(\frac{L_v}{R_v T_a} - 1\right) \frac{L_v \rho}{K T_a} + \frac{\rho R_v T_a}{e_s (T_a) D}}$$

where T_a is the ambient temperature, RH the ambient relative humidity, L_v the latent heat of vaporization, R_v the specific gas constant for water vapor, ρ liquid water density, K the thermal conductivity of air, e_s the saturation vapor pressure at temperature, D is the diffusion coefficient of water vapor. More details can be found in the work of Choi et al. (2020).

3. Results

The prevalence of COVID-19 tends to exhibit a distinct seasonality in the five representative countries (see section 2.1 for a selection of countries), similar to that of influenza (Figures 1 and S2; Choi et al., 2020; Tamerius et al., 2011, 2013). For example, temperate countries in both hemispheres (i.e., Canada, Germany, and Chile) experienced peak COVID-19 incidence in their respective winter months. These regions in temperate climates exhibited, over the past year, opposite evolutions of COVID-19 and the four environmental variables we consider (temperature, specific humidity, ADC, and UV). That is, low values in temperature, humidity, ADC, and UV generally occurred in the months with the highest COVID-19 incidence.

On the other hand, in tropical regions (i.e., India, and Ethiopia), COVID-19 appears to have peaked during summer in the Northern Hemisphere, specifically at the time of the monsoons when the specific humidity

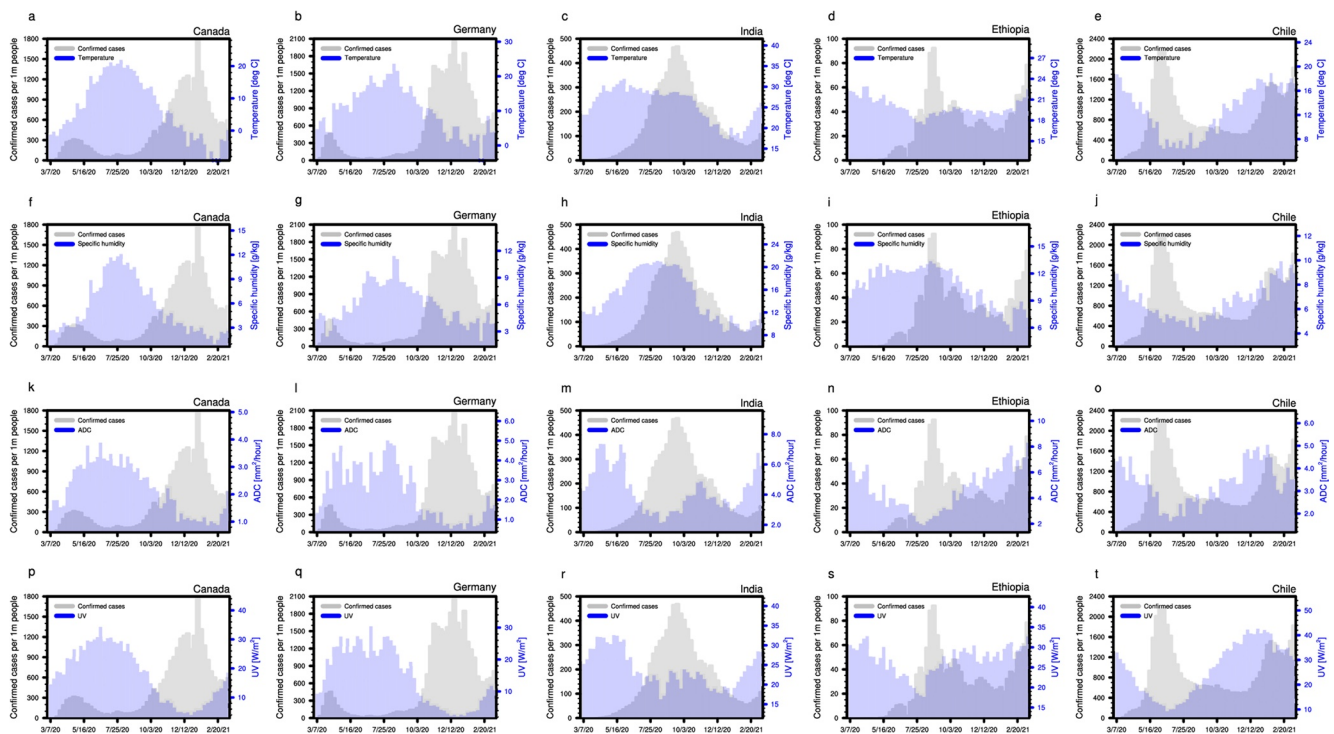


Figure 1. Seasonal variation of COVID-19 prevalence and environmental variables. Seasonal variation of weekly COVID-19 prevalence alongside weekly (a–e) temperature, (f–j) specific humidity, (k–o) air drying capacity, and (p–t) ultraviolet radiation across COVID-19 hotspots, such as (a, f, k, and p) Canada in North America, (b, g, l, and q) Germany in Europe, (c, h, m, and r) India in Asia, (d, i, n, and s) Ethiopia in Africa, and (e, j, o, and t) Chile in South America.

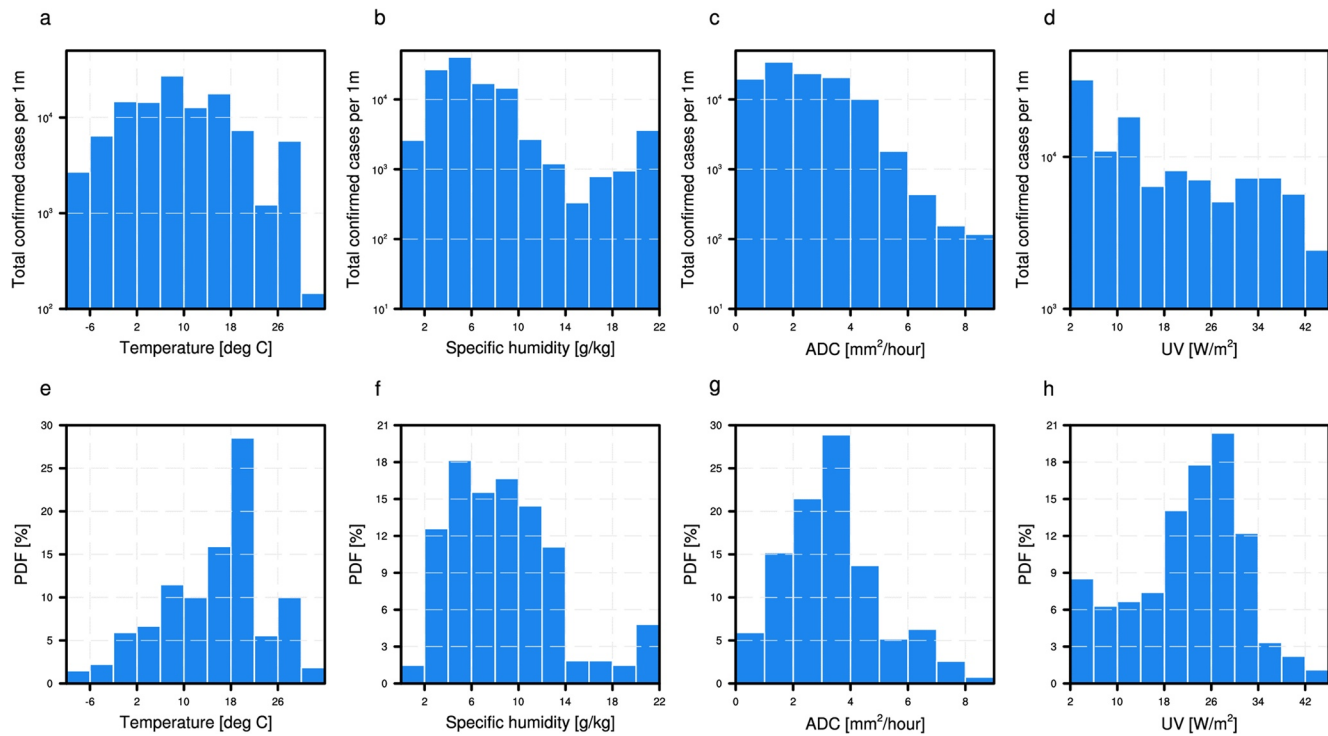


Figure 2. Environmental variables and COVID-19 prevalence. Sum of weekly new confirmed COVID-19 cases per 1 million people (i.e., total confirmed cases per 1 m) across the five representative countries (i.e., Canada, Germany, India, Ethiopia, and Chile) for the period from March 1st, 2020 to March 13th, 2021 as a function of weekly mean (a) temperature, (b) specific humidity, (c) air drying capacity (ADC), and (d) ultraviolet radiation (UV). Probability density function of weekly mean (e) temperature, (f) specific humidity, (g) ADC, and (h) UV over the region for the same period.

was at its highest. There, the seasonality of COVID-19 and that of temperature and specific humidity, thus, turn out to be inconsistent with what is observed in temperate regions, as is the case for influenza (Tamerius et al., 2011). The seasonal evolution of ADC and UV, by contrast, is consistent with COVID-19 prevalence in all countries (Figure 1k–1t). High UV and high ADC are linked to lower prevalence and vice-versa, although this relationship is weak over a certain period in winter over Ethiopia. The associated inconsistency in Ethiopia appears to be due to less strict policy measures during this period (Figure S1). This result is in line with the expected effect of these two variables on the survival and transmissibility of SARS-CoV-2 (e.g., Choi et al., 2020; Ratnesar-Shumate et al., 2020; Schuit et al., 2020; Seyer and Sanlidag, 2020). The case of India in particular is quite striking, especially since the country attracted much attention due to the explosiveness of its COVID-19 outbreak and its different timing of peak incidence (e.g., Bherwani et al., 2020) compared to those in temperate regions.

Pooling the data for the five representative countries together and conditioning weekly new COVID-19 cases on the various environmental variables yield further insights consistent with the previous analysis (Figure 2). While COVID-19 spread appears lowest at high temperatures, the peak in COVID-19 spread occurs at somewhat average temperatures and the relationship is altogether inconsistent. Similarly, new cases are at their highest at low specific humidity values but almost as high when specific humidity is large as well. By contrast, the conditioning on ADC and UV stands out as much more consistent: (a) COVID-19 prevalence nonlinearly increases as ADC approaches zero, in keeping with its effect on virus-laden droplets exhaled by infected patients (Choi et al., 2020); (b) similarly, low UV values appear to provide favorable conditions for the spread of the disease, consistent with the impact of UV light on the survival of SARS-CoV-2 (Carleton et al., 2021; Schuit et al., 2020; Seyer and Sanlidag, 2020) and (c) the lowest ADC (0–2 mm²/hr) and UV (2–14 W/m²) values with a probability less than 15% are systematically linked to the largest numbers of COVID-19 infections (Figures S2, 2c, 2d, 2g, and 2h). Given the relatively similarity and constant level of social control in the five analyzed countries, these findings suggest that ADC and UV, unlike temperature and humidity, are likely environmental determinants of COVID-19 spread and its seasonality.

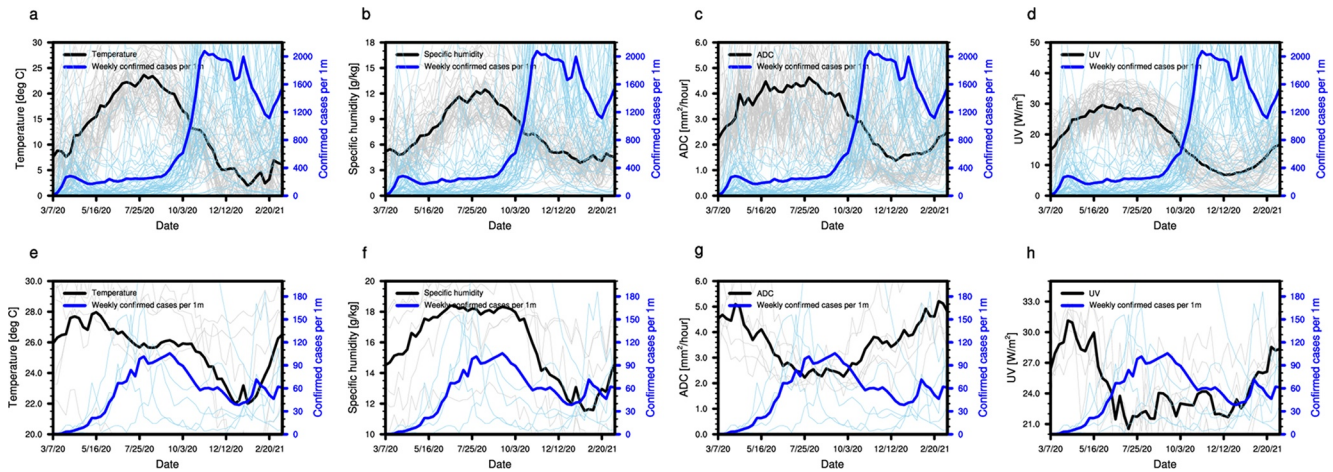


Figure 3. Seasonal variation of COVID-19 prevalence and environmental variables. Seasonal variation of weekly COVID-19 prevalence alongside weekly (a and e) temperature, (b and f) specific humidity, (c and g) air drying capacity, and (d and h) ultraviolet radiation across (a–d) 56 temperate countries in the Northern Hemisphere (Table 1) and (e–h) six tropical monsoon countries (Table 1).

To further advance our understanding of the possible link between COVID-19 seasonality and the four environmental variables, we now analyze data from all available countries with sufficient number of tests, divided into temperate countries in the Northern Hemisphere, and tropical, monsoon-dominated countries (see section 2.1; Table 1). We find supportive evidence for strong negative relationships between all four environmental variables and COVID-19 spread in the temperate group (Figures 3a–3d and 4a–4d). Interestingly, in the early stages of the pandemic (i.e., first half of the year), ADC and UV exhibit more consistent variability with COVID-19 infections rather than temperature and humidity (i.e., COVID-19 prevalence, ADC, and UV does not change very much, while temperature and humidity increase sharply; Figures 3a–3d). The discrepancy

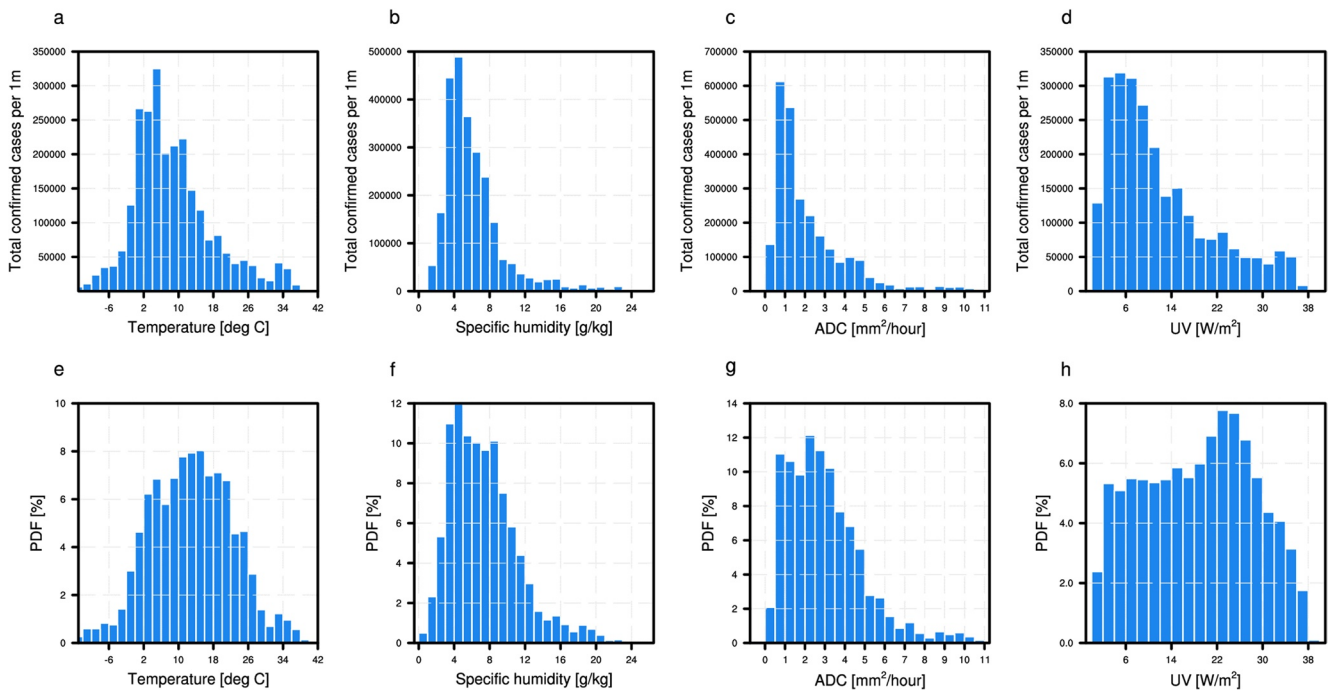


Figure 4. Environmental variables and COVID-19 prevalence. Sum of weekly new confirmed COVID-19 cases per 1 million people (i.e., total confirmed cases per 1 m) across the 56 temperate countries (Table 1) in the Northern Hemisphere for the period from March 1st, 2020 to March 13th, 2021 as a function of weekly mean (a) temperature, (b) specific humidity, (c) air drying capacity (ADC), and (d) ultraviolet radiation (UV). Probability density function of weekly mean (e) temperature, (f) specific humidity, (g) ADC, and (h) UV over the region for the same period.

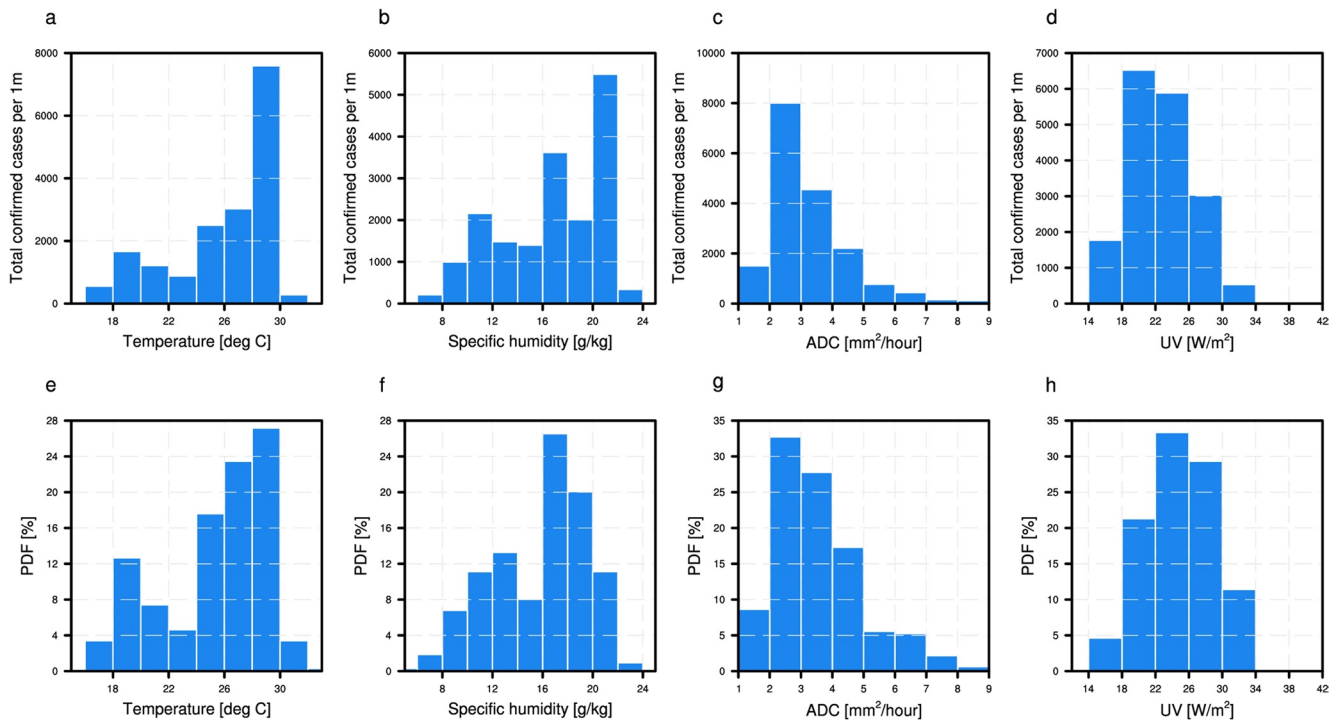


Figure 5. Environmental variables and COVID-19 prevalence. Sum of weekly new confirmed COVID-19 cases per 1 million people (i.e., total confirmed cases per 1 m) across the 6 tropical monsoon countries (Table 1) for the period from March 1st, 2020 to March 13th, 2021 as a function of weekly mean (a) temperature, (b) specific humidity, (c) air drying capacity (ADC), and (d) ultraviolet radiation (UV). Probability density function of weekly mean (e) temperature, (f) specific humidity, (g) ADC, and (h) UV over the region for the same period.

among them is more obvious in tropical monsoon regions, as expected from the results shown in Figures 1 and 2 and from previous influenza studies (e.g., Tamerius et al., 2011). Consistent with the previous 5-country analysis, the tropical group, with a sharp rise in new COVID-19 cases during the wet season, stands in contrast to the temperate group. Only ADC and UV, unlike temperature and humidity, show seasonal variations consistent with those of COVID-19 spread across the two groups of countries (Figures 3g–3h).

On conditioning COVID-19 cases once more on the values of the four environmental variables, different statistical relationships are found for the two selected climate zones. The temperate Northern Hemisphere is characterized by a nonlinear decrease of COVID-19 cases with all four variables (Figure 4), whereas in the tropical monsoon regions, COVID-19 cases increase with both temperature and humidity (Figure 5). By contrast, ADC and UV both show consistent negative relationships with COVID-19 regardless of the region (Figures 4 and 5). The spread of COVID-19 seems, in particular, to be very constrained at ADCs of 5 mm²/hr or larger. Its sensitivity is also obviously nonlinear, consistent with the observation by Choi et al. (2020). Additionally, low UV values (0–15 W/m²), though quite rare at the annual scale, systematically occur in conjunction with high numbers of new COVID-19 cases, especially in the temperate regions (Figure 3d).

4. Discussion and Conclusion

Through extensive country-level data spanning the 1-year pandemic period, this study evaluates and compares the role of four environmental variables (temperature, humidity, ADC, and UV) with the potential to influence the spread of COVID-19. Three important results that emerge from this study are that (a) the spread and prevalence of COVID-19 appears to display some seasonality consistent, to some extent, with the seasonality of the analyzed environmental variables and their known relationships to influenza seasonality; (b) two environmental variables in particular, ADC and UV, evolve consistently with COVID-19 spread across the selected countries in all climates and at both the weekly and the seasonal timescales, and their relationship to COVID-19 spread is consistent with their respective effects on the fate of the respiratory droplets (ADC, Choi et al., 2020) and on virus survival (UV, Schuit et al., 2020; Seyer and Sanlidag, 2020;

Ratnesar-Shumate et al., 2020). Therefore, ADC and UV may provide the basis for a physically based framework shaping seasonal variations in COVID-19 prevalence across the world; and (c) we also find that, as was the case for influenza, absolute humidity and temperature do not exhibit a consistent relationship with COVID-19 cases across all climate zones. Their statistical relationships change directions whether one considers temperate or tropical monsoon countries, which casts doubt as to their true relevance for COVID-19 spread at the country scale, all the more so as the physical mechanisms that could explain these relationships and why they differ depending on the background climate remain unknown. By contrast, the statistical relationship between COVID-19 prevalence and ADC or UV is both consistent across climate zones and is well-supported by the known physical effects of these two variables on disease transmission. The quantitative assessments of the relationships between environmental variables and COVID-19 seasonality across the selected countries of all climates are summarized in Table S1. This result additionally supports our main findings. Naturally, all four variables are, to some extent, correlated with each other (Table 2). Temperature and humidity tend to evolve in concert as warmer air generally holds more moisture. Similarly, for temperate countries, both ADC and UV tend to reach their minimum during winter when both temperature and specific humidity are also at their lowest. But such is not the case in tropical, monsoon-dominated countries.

Before concluding, it is important to mention that this study naturally presents several important caveats. First, as for any COVID-19-related study, the quality, extensiveness, and uniformity of the data are subject to caution. COVID-19 case data are strongly impacted by testing rates and policies, which differ in space (between different countries) but also in time since testing protocols have evolved over time. Although this study applied the threshold of at least 10,000 cumulative COVID-19 tests per 1 million people to discard countries with unrepresentative data, considering all the countries without quality control may provide other conclusions that are inherent with high uncertainty. Influenza data also suffer from the same biases, which are inevitable in any global study. Additionally, the spread of COVID-19 cannot be described by environmental factors alone, but instead, like that of many other diseases, it is known to be influenced by the compounding effects of social, biological, and environmental determinants. For instance, the spread of COVID-19 is largely shaped by several factors like population density, social distancing, international travel routes, school closures, event cancellations, mask mandates, and hygiene (Bherwani et al., 2020; Nath et al., 2021; Poirier et al., 2020). Recent studies have suggested that environmental conditions might be related to the spread of the pandemic at the initial phase of the outbreak (Nath et al., 2021; Sasikumar et al., 2020). In this study, in an attempt to isolate the effect of environmental factors from that of the other determinants of COVID-19, we considered five representative countries (i.e., Canada, Germany, India, Ethiopia, and Chile) which have relatively constant social controls over the analysis period (Figure S1). The result confirmed that the seasonality of COVID-19 appears to follow the seasonality of environmental variables, specially ADC and UV (Figure 1). Finally, we did not consider the effects of indoor environments (e.g., heating and air conditioning), which may also influence the seasonality of VRD (e.g., Shaman and Kohn, 2009; Xie et al., 2007). As always in such cases, one must be careful in concluding the role of environmental variables in shaping VRD dynamics (Carlson et al., 2020; Zaitchik et al., 2020). Even though vaccines have recently been developed and are currently being administered, and although it is hoped that SARS-Cov-2 will soon be controlled effectively, there is still a possibility that this virus will stay with us as a seasonal disease with milder effects, like influenza. Our findings could therefore help guide the development of a sound adaptation strategy against COVID-19 in the coming years.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

ERA5 reanalysis data were obtained from the European Center for Medium Range Weather Forecasts (EC-MWF) (<https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-single-levels?tab=overview>). Population density data were taken from the gridded population of the world (GPW) v4 data set (<https://sedac.ciesin.columbia.edu/data/collection/gpw-v4>). Daily data on confirmed COVID-19 cases, number of

tests, stringency index and population for each country were from the “Our World in Data” database (available at <https://ourworldindata.org/>). Subnational-level COVID-19 epidemiological data for the Australia, China, and Canada are available at the Johns Hopkins University Center for Systems Science and Engineering (JHU CCSE; <https://data.humdata.org/>). Daily COVID-19 data at the scale of different states within the United States were provided at the COVID Tracking Project (available at <https://covidtracking.com/>). Correspondence and requests for materials should be addressed to choiyw@mit.edu.

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