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Review

A narrative review on the role of temperature and humidity in COVID-19: Transmission, persistence, and epidemiological evidence



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ABSTRACT

Since December 2019, the 2019 coronavirus disease (COVID-19) outbreak has become a global pandemic. Understanding the role of environmental conditions is important in impeding the spread of COVID-19. Given that airborne spread and contact transmission are considered the main pathways for the spread of COVID-19, this narrative review first summarized the role of temperature and humidity in the airborne trajectory of severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2). Meanwhile, we reviewed the persistence of the virus in aerosols and on inert surfaces and summarized how the persistence of SARS-CoV-2 is affected by temperature and humidity. We also examined the existing epidemiological evidence and addressed the limitations of these epidemiological studies. Although uncertainty remains, more evidence may support the idea that high temperature is slightly and negatively associated with COVID-19 growth, while the conclusion for humidity is still conflicting. Nonetheless, the spread of COVID-19 appears to have been controlled primarily by government interventions rather than environmental factors.

1. Introduction

Since December 2019, the 2019 coronavirus disease (COVID-19) outbreak caused by severe acute respiratory syndrome coronavirus-2 (SARS-CoV-2) has become an unfolding global pandemic [1]. At the time of writing, many governments are urging a reopening of society to rescue the economy. To achieve this goal, it is essential to understand the key drivers of COVID-19 spread [2,3]. Vaccination and pharmacological intervention have been deemed the most important means to reduce/eliminate the spread of COVID-19. However, although the vaccination rate in the population is increasing, some governments are vacillating between the policies of ‘living with COVID-19’ and ‘COVID-zero’. Apart from the vaccination, existing studies have demonstrated that the spread of COVID-19 could be significantly shaped by a mixture of other factors, including social distancing, travel restrictions, environmental conditions, variants, and others [4–6]. Hence, to aid the fight against COVID-19, the

relationship between the environmental conditions and COVID-19 spread has attracted mounting research attention.

Despite numerous studies, the evidence concerning the effect of weather on COVID-19 spread is still conflicting, probably because of considerable heterogeneities among data sources, methodology selection, study period, socio-economic status, and others. Although there have been several reviews and research studies on the associations between environmental factors and COVID-19 spread [7–12], most only covered parts of the research area and failed to offer a comprehensive and full picture of how temperature/humidity drives the spread of COVID-19. For example, the World Meteorological Organization (WMO) released the first report on meteorological and air quality factors affecting the COVID-19 pandemic. However, this report mainly focused on epidemiological evidence [13]. In addition, environmental factors may influence the stability of the virus, the transmission pathway, and the reactions of the body’s receptors. To elucidate the research status of

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the critical role of temperature and humidity, the most important factors among weather conditions, in the spread of COVID-19, this narrative review has merged evidence from model simulation and experimental and epidemiological studies. In particular, we first summarized the role of temperature and humidity in the aerosol and contact transmission of SARS-CoV-2, which have been considered the major pathways of COVID-19 spread. Meanwhile, we discussed the effects of temperature and humidity on human antiviral defense, and the associated findings from epidemiological studies. This review promises to assist policy-making in the global battle against COVID-19.

2. The role of temperature and humidity in aerosol transmission

The stability of SARS-CoV-2 in aerosols: One precondition to support the airborne transmission of SARS-CoV-2 is that the virus can remain infectious in droplets generally longer than the time it takes for the droplets to travel from person to person [14]: the infectious titer of SARS-CoV-2 was demonstrated to decrease exponentially from $10^{3.5}$ to $10^{2.7}$ TCID₅₀ (50% tissue-culture infectious dose) per liter of air after 3 h (21–23 °C and 65% relative humidity), with an estimated half-life of 1.1 h (95% confidence interval (CI): 0.64–2.64 h) [15] (Table 1). Furthermore, another study pointed out that SARS-CoV-2 could remain viable in respirable-sized aerosols for more than 16 h [16]. The SARS-CoV-2 variant in England was found to remain infectious for at least 1.5 h in experimental aerosols from artificial saliva and tissue culture mediums [17]. This study further illustrated that the SARS-CoV-2 was more susceptible at a higher relative humidity in tissue culture mediums, with the decay rate increasing from 0.91% per min (medium relative humidity: 40%–60%) to 2.27% per min (high relative humidity: 68%–88%) [17]. However, such findings were not observed for aerosolized SARS-CoV-2 from artificial saliva, where the decay rate was 75% lower at high relative humidity (1.59% per min at medium relative humidity and 0.40% per min at high relative humidity) [17].

Compared with humidity, fewer studies have reported the relationship between temperature and SARS-CoV-2 stability in aerosols. However, existing evidence has demonstrated that MERS-CoV in aerosols was far less active in a hot and dry environment [18]. Similarly, HCV/229E coronavirus appears to survive for shorter periods in aerosols when temperature increases [19]. In particular, when the temperature increased from 6 to 20 °C, the half-life of HCV/229E declined from 34.5 h to 26.8 h at a relative humidity of 30%, from 102.5 h to 67.3 h at a relative humidity of 50%, and from 86.0 h to 3.3 h at a relative humidity of 80% [19], respectively. Although similar studies regarding SARS-CoV-2 Delta and Omicron variants have not yet been published at the time of writing, existing evidence may suggest that a high temperature in the aerosol leads to a decline in SARS-CoV-2 infectivity and further impedes the spread.

The stability of the virus in experimental aerosols has also been confirmed by field studies, as viable viruses in the air were detected in

samples collected from hospitals worldwide [20–22]. A recent study collected air samples from eight groups of public and transportation locations: positive samples were detected in almost all regions, such as shopping malls (100%), subway trains (100%), airports (80%), buses (50%), and banks (30%). However, it failed to highlight that temperature was a determinant (the odds ratio was estimated to be 0.93, with a 95% CI of 0.72–1.17) for the presence of SARS-CoV-2 in the air [23]. A nationwide study in Turkey found that amounts of the virus in ambient particulate matter and humidity were both higher in Istanbul, Zonguldak, and Tekirdağ; however, the data were insufficient to address the association between humidity and virus exposure level in the air [24]. To date, field studies regarding how environmental conditions impact virus-laden aerosol concentrations remain scarce.

Temperature and humidity influence the SARS-CoV-2 trajectory in aerosols: Extensive evidence has suggested that one of the main pathways for COVID-19 spread appears to be airborne spread, including droplets (>5 μm) and droplet nuclei (≤5 μm) [25,26]. Hence, the trajectory of droplets and aerosols is crucial when addressing the transmission of SARS-CoV-2. The diameter is known to be an important parameter in the airflow patterns and trajectory of the virus from an infected source. In general, the larger droplets follow a ballistic trajectory regardless of flow in the gas phase, compared with the aerosols that are buoyant to a diverse degree within a turbulent gas cloud [7,27]. Apart from that, respiratory droplets are generated by various physical events, including talking, coughing, breathing, and sneezing [28,29], with initial speeds spanning from resulting in different distances at which droplets fall to the floor (Table 2). For example, sneezing was simulated to carry droplets larger than 100 μm and spread more than 2 m horizontally from infected persons, while droplets with a velocity of 1 m/s resulting from exhalation were found to fall to the floor within 1 m from the source [7].

Model simulations have well demonstrated that the evaporation mechanism, particle size distribution, and exhaled profile characteristics are the key drivers of airborne transmission [30]. By altering the size distribution and evaporation process, the temperature and humidity can alter the shape and magnitude of the airborne trajectory [31–34] (Table 2). Zhao et al. [31] suggested that droplets travel less than 1.8 m in a hot and dry environment. By contrast, in a low-temperature and high-humidity environment, the maximum distance of spread can be up to 3.6 m, and the number of aerosol particles also increases [31]. In a cold and damp environment, droplet sizes decrease due to the Kelvin effect, and finer droplets are capable of traveling further [35]. Notably, the reduction in the size of droplets may trigger a higher likelihood of deposition in human airways [36,37], which enhances infection risk. On the other hand, large droplets in conditions of low temperature and high humidity can be converted to numerous small droplets carrying fewer viruses, which are inclined to die out fast [38]. In addition, expelled droplets quickly lose water through evaporation. When humidity increases, the evaporation process becomes much slower because the higher relative humidity in the air has less potential to absorb water

Table 1
The stability of SARS-CoV and MERS-CoV in aerosols.

Virus strain	Temperature (°C)	Relative humidity	Inoculum	Stability (h)	T _{1/2} (h)	References
SARS-CoV-2	21–23	65%	10 ^{3.5} TCID ₅₀ /L air	15.8% survival at the end 3 h	1.1	[15]
SARS-CoV-1			10 ^{4.3} TCID ₅₀ /L air		1.2	
SARS-CoV-2	23	53%	NR	16	NR	[16]
SARS-CoV-2	19–22	40%–60%	(1.11–1.63) × 10 ⁶ TCID ₅₀ /mL aerosol of tissue culture mediums	1.5	1.25	[17]
England-2 variant	19–22	68%–88%			0.5	
	19–22	40%–60%	(0.77–2.28) × 10 ⁶ TCID ₅₀ /mL aerosol of artificial saliva		0.7	
	19–22	68%–88%			2.95	
MERS-CoV	25	79%	10 ^{5.5} TCID ₅₀ /mL eluate	63% at the end 1 h	NR	[10,18]
	38	24%		4.7% at the end 1 h		
MERS-CoV	20	40%	10 ⁶ TCID ₅₀ /mL suspension	93% viability at the end 10 min	NR	[58]
	20	70%		11% at the end 10 min		

NR, not reported; TCID₅₀, 50% tissue-culture infectious dose.

Table 2

The simulated spreading distance under various environmental conditions from a SARS-CoV-2 spreader in typical scenarios.

Events	Size diameter (μm)	Velocity (m/s)	Temperature (°C)	Humidity	Horizontal distance (m)	Remark	References
Sneezing	60–100	50	20	50%	about 5	Using Wells evaporation-falling curve	[33]
Coughing	45–80	10	20	50%	about 1.5–2		
	30	10	20	30%	1.25–1.5		
	30	10	20	70%	about 2.25		
Speaking	20	5	20	50%	about 1		
Breathing	20	1	20	50%	<0.5		
Model assumptions	Size Distribution [109]	4.1	30	20%	<1.8	Under most regions proposed by the authors, the spreading distance may exceed 1.8 m	[31]
			30	60%	1.8–2.4		
			30	90%	>3.6		
			20	20%	<1.8		
			20	20%	about 1.8		
			20	60%	>2.4		
Coughing	60	10	25	35%	>2		[110]
Coughing	100 (droplet size)	10	30	84%	6.6	Outdoor, wind speed of 2 m/s	[111]
					0.8	Outdoor, wind speed of 0 m/s	
Coughing	1000 (droplet size)				1.3	Outdoor, wind speed of 2 m/s	
Coughing	About 80–100	10 m/s at 0.1 s and	25	60%	Probably <1 m	Considering evaporation	[30]
	About 2–80	decays to zero at 0.5 s	25	60%	Probably >1 m		

vapor [39]. In particular, droplets of about 60 μm appear more sensitive to relative humidity than those of other sizes [34]. However, when the air is dry, droplet nuclei may also be generated that are sufficiently fine to remain suspended in the air for a long time [40]. Regarding the temperature, low temperature in the environment provides less heat source for evaporation.

Moreover, Pal et al. [32] pointed out that most existing research has considered the droplet a pure water droplet, neglecting the formation and trajectories of aerosols. Given that the formation of crystals further delays the evaporation of droplets, hot and dry conditions appear to be more dangerous situations than previously speculated, and cold and humid circumstances may allow the droplets to travel up to 2–3 fold farther than previous estimations [32].

Generally, in flowing fluids in the respiratory tract, high viral loads reduce the minimum size of virus-laden respiratory secretions, indicating that more virus-laden aerosols are anticipated under conditions of high viral load [41]. Given that a relatively high viral load was found for Delta and Omicron [42], these variants of concerns (VOCs) are prone to cause quick and massive spread in enclosed spaces [43]. Furthermore, if these novel VOCs satisfy the four fundamental principles (asymptomatic host, high viral load, stability of viruses in the air, and binding affinity of viruses to human cells), associated rapid outbreaks of COVID-19 should be considered [41].

3. Contact transmission: SARS-CoV-2 on inert surfaces is affected by temperature and humidity

Besides airborne transmission, SARS-CoV-2 spread may occur indirectly via touching surfaces in the environment. High contact surfaces, including the touchscreens on electronic equipment, elevator push buttons, and handles of public utilities, potentially carry the virus from infected persons. An early experiment demonstrated that the transmission efficiency from the fingertip to the mouth was greater than 30% for bacteria and phages on fomites [44], suggesting that fomite transmission appears to be a highly efficient pathway [45].

Mounting studies have reported positive results for SARS-CoV-2 in environmental samples, including tables, handles, chairs, glasses, personal protective equipment [46], cell phones [20], room window ledges [20], light switches [47], and the food supply chain [48]. A recent review pointed out that hospitals and healthcare facilities with COVID-19 patients have the highest detection rates, yielding about 17.3% positive samples (n = 533) for SARS-CoV-2 RNA detected in 3077 surface samples [9]. Contrastingly, the rate of positive samples (n = 174) was 10.1% among samples collected in non-hospital settings (n = 1724) [9].

However, viable viruses have not been commonly confirmed in these environmental samples because viral infectivity assays were not always performed: they require propagation of SARS-CoV-2 in cell culture, which is only allowed in biosafety level 3 facilities [9].

The existence of SARS-CoV-2 in the environment has also been supported by its stability on a large array of inert surfaces, including metal, plastic, wood, paper, masks, and various other materials (Table 3). As summarized, the stability of SARS-CoV-2 ranges from <1 h to a couple of weeks. For example, on metal surfaces, the duration of SARS-CoV-2 stability was determined to be 4 h for copper and 72 h for stainless steel [15]. The low stability of SARS-CoV-2 on the copper surface may be due to the copper ions being able to aggregate virus particles [49]. Meanwhile, free copper ions may generate reactive oxygen species [50]. Active oxygen can attack the spike and envelope proteins and lipids of SARS-CoV-2, destroy the integrity of the virus, and inhibit its infection. A fall in temperature and humidity appears to strengthen the stability of the virus on stainless steel [51,52] (Table 3). Concerning plastic surfaces, an early study reported that infectivity lasted up to 3 days but had decayed at the end of the 4th day, under 40% relative humidity [15]. Later research reported that when the relative humidity increased to 65%, the duration of stability of SARS-CoV-2 increased to 4 days [51]. Notably, as displayed in Table 3, the stability of SARS-CoV-2 on non-porous surfaces appears to be similar to that of SARS-CoV-1.

Scientists have also investigated the stability of SARS-CoV-2 on porous surfaces. On facemasks, two studies reported that the SARS-CoV-2 could survive for 96–504 h, indicating that the infectious virus can possibly be recovered even after 21 days (Table 3). Publications have revealed relatively short durations of stability of SARS-CoV-2 on paper, banknotes, cards, woods, cloths, and cotton (Table 3). Although SARS-CoV-2 survived for less than 1 h on paper, the SARS-CoV-1 could remain viable on newspaper and filter paper for more than 96 h [50,53], illustrating some disparities between the two viruses.

It is well known that the protein coat of the virus may be impaired at high temperatures, and the virus, therefore, may lose its infectivity, which further validates the survivability of SARS-CoV-2 in response to temperature [10]. Shane et al. [45] found that the virus remained viable for up to four weeks on a paper note at 20 °C, while the virus survived for less than 48 h at 40 °C. This study also found a low half-life at higher temperatures on stainless steel and glass [45]. Using a simulated clinically relevant matrix with SARS-CoV-2 dried on nonporous surfaces at a room temperature of 24 °C, Jennifer et al. [54] noted that the virus half-life was 6.3–18.6 h, depending on the relative humidity. In contrast, the half-life reduced to 1.0–8.9 h when the temperature increased to 35 °C [54]. At room temperature (20–25 °C), Chan et al. [55] suggested

Table 3
The stability of SARS-CoV on different surfaces.

Type of surface	Strain	T (°C)	Humidity	T _{1/2} (h)	S (h)	Time of 100% decay (h)	References
Plastic	SARS-CoV-2	21–23	40%	6.8	72	96	[15]
		22	65%	11.4	96	168	[51]
	SARS-CoV-1	21–23	40%	7.6	72	96	[15]
		21–25	NR	NR	96	120	[50, 53]
		21–25	NR	NR	144	216	[112]
		22–25	40%–50%	NR	28 days	NR	[10, 57]
		33	>95%	NR	24	NR	[10, 57]
		33	80%–89%	NR	24	NR	[10, 57]
		38	>95%	NR	24	NR	[10, 57]
		38	80%–89%	NR	24	NR	[10, 57]
Stainless Steel	SARS-CoV-2	21–23	40%	5.6	72	96	[15]
		22	65%	14.7	72	96	[51]
		20	35%–40%	NR	336	504	[52]
Copper	SARS-CoV-1	21–23	40%	4.2	48	72	[15]
	SARS-CoV-2	21–23	40%	0.8	4	8	[15]
Glass	SARS-CoV-1	21–23	40%	1.5	8	24	[15]
	SARS-CoV-2	22	65%	4.8	48	96	[51]
Cardboard	SARS-CoV-1	21–25	NR	NR	96	120	[50, 53]
	SARS-CoV-2	21–23	40%	3.5	24	48	[15]
Metal	SARS-CoV-1	21–23	40%	0.6	8	24	[15]
	SARS-CoV-1	21–25	NR	NR	120	NR	[10, 53]
Mosaic		21–25	NR	NR	72	96	[10, 53]
Paper	SARS-CoV-2	22	65%	NR	0.5	3	[51]
Paper (H) *	SARS-CoV-1	20	NR	NR	NR	24	[113]
Paper (M) *		20	NR	NR	NR	3	[113]
Paper (L) *		20	NR	NR	NR	<5 min	[113]
Tissue paper	SARS-CoV-2	22	65%	NR	0.5	3	[51]
Press paper	SARS-CoV-1	21–25	NR	NR	96	120	[50, 53]
Filter paper		21–25	NR	NR	120	NR	[50, 53]
Wood	SARS-CoV-2	22	65%	NR	6–24	24–48	[51]
Wood boards	SARS-CoV-1	21–25	NR	NR	96	120	[50, 53]
Cloth	SARS-CoV-2	22	65%	NR	6–24	24–48	[51]
Cloth	SARS-CoV-1	21–25	NR	NR	120	NR	[50, 53]
Banknote	SARS-CoV-2	22	65%	7.9	48	96	[51]
Mask, inner layer		22	65%	9.9	96	168	[51]
Mask, outer layer		22	65%	23.9	168	NR	[51]
Plastic face shield		20	35%–40%	NR	504	NR	[52]
N95 mask				NR	504	NR	[52]
N100 mask				NR	504	NR	[52]
Nitrile gloves				NR	168	336	[52]
Chemical gloves				NR	96	168	[52]
Disposable gown (H) *	SARS-CoV-1	20	NR	NR	NR	48	[113]
Disposable gown (M) *		20	NR	NR	NR	24	[113]
Disposable gown (L) *		20	NR	NR	NR	1	[113]
Cotton	SARS-CoV-2	20	35%–40%	NR	4	24	[52]
Cotton gown (H) *	SARS-CoV-1	20	NR	NR	NR	24	[113]
Cotton gown (M) *		20	NR	NR	NR	1	[113]
Cotton gown (L) *		20	NR	NR	NR	5 min	[113]
Tyvek	SARS-CoV-2	20	35%–40%	NR	336	504	[52]

NR, not reported; * H, high inoculation, 10^6 TCID₅₀/mL; M, medium inoculation, 10^5 TCID₅₀/mL; L, low inoculation, 10^4 TCID₅₀/mL; T, temperature; S, stability.

that dried SARS-CoV-2 retained viability for a couple of days, with a prolonged survival duration of more than two weeks at 4 °C. By contrast, the virus lost its infectivity within 24 h when the temperature was set at 37 °C [55]. Another study verified the inverse association between SARS-CoV-2 stability and temperature by incubating fomites with SARS-CoV-2 at different temperatures. The long stability of the virus at low temperatures illustrates that more caution is required for low-temperature environments, for example, the food cold chain [56]. On the other hand, despite fewer studies being available on modification of the infectivity of SARS-CoV-2 by humidity, evidence from SARS-CoV-1 [57] and MERS [58] may indicate that viability would be impaired at extremely high relative humidity.

4. The effects of temperature and humidity on human antiviral defense

On infection, SARS-CoV-2 binds to the angiotensin-converting enzyme 2 (ACE2) receptor of respiratory epithelial cells through the S

protein, replicates in large quantities, and migrates to the lower respiratory tract to enter alveolar cells [59]. The rapid and sustained replication of SARS-CoV-2 resulting in alveolar cell death can elicit an intense immune response [60]. When type II alveolar cells die, they release specific inflammatory mediators and stimulate immune cell activation which secretes a large amount of interleukin 1 (IL-1), interleukin 6 (IL-6), tumor necrosis factor (TNF- α), and other pro-inflammatory factors, threatening to trigger a cytokine storm or cytokine release syndrome [61].

Human antiviral defenses may also be sensitive to temperature and humidity. Previous studies have pointed out that dry and cold conditions impair nasal and bronchial mucociliary clearance and further hinder the ability of the body to defend against inhaled virus-containing particles [13,62]. In general, the temperature of the air we breathe is below body temperature, causing heat loss in the nasal passages. It is well known that mucociliary clearance is the first line of defense against respiratory infection [63]. A reduction in temperature may slow metabolic activity, thus reducing both ciliary beat frequency and the rate of secretion of

mucus, which further alters the rate of mucociliary clearance [63]. One report has demonstrated that the inhalation of dry air impairs innate antiviral defense and tissue repair [64].

The response of the immune system may also be associated with temperature. The expression of interferon-stimulated genes is vital to triggering an antiviral state [65], and findings from single-cell RNA sequencing have indicated that induction of type I interferon (IFN)—stimulated genes in response to viral infection was decreased in various cell types in the lungs of mice housed in low-humidity conditions [64]. Upon exposure to an environmental temperature of 36 °C, the mice reduced their food intake and showed a reduced adaptive immune response to influenza virus infection [66]. This may be because increased temperature inhibits virus-specific CD8⁺ T cell responses and antibody production after influenza infection [13,66]. In addition, airway cells with genetic deficiencies in RIG-I-like receptor or IFN receptor signaling support much higher levels of viral replication at 37 °C [67]. Another study demonstrated that, in the absence of IFNs, temperature-based rhinovirus amplification largely resulted from host cell antiviral restriction mechanisms operating more effectively at 37 °C than at lower temperatures [68].

5. Modifying effects of temperature and humidity on COVID-19 spread: Evidence from epidemiological studies

As summarized above, while the effect of humidity on COVID-19 spread remains controversial, hot temperatures may reduce COVID-19 spread by reducing the dispersal distance and impairing virus infectivity. Compared with summer, the spread of COVID-19 is anticipated to be higher in winter, and a recurrent outbreak of COVID-19, therefore, is highly probable.

Therefore, direct epidemiological research on the alteration of COVID-19 spread by temperature and humidity has become a research focus, with a rapid increase in the number of associated publications. Fig. 1 illustrates the general research framework used to unveil the associations between COVID-19 spread and the two environmental conditions. Besides some descriptive studies, most studies can be divided into two types: 1) cross-sectional studies, in which the association was determined for the COVID-19 pandemic over a certain period in many areas, with statistics on the temperature, humidity, and other confounding variables; and 2) longitudinal studies, in which the associations of COVID-19 incidence or mortality were studied versus a daily measure of temperature and humidity. Furthermore, the longitudinal studies can be classified as: 1) purely temporal associations, either because the study was in a single region or a study performed in a single region was

analyzed at the first stage, and a pooled analysis was implemented at the second stage; and 2) spatio-temporal associations, which simultaneously combined the temporal variables regarding temperature/weather and other spatial variables as a random term. Thus, the choice of model parameters is related to the study design. For instance, some confounding variables, including demographic and population factors that differ over regions but not at temporal scales, are capable of modifying the associations, as exemplified by how the age structures of European and North American population increased their COVID-related death rates [69]. An earlier study also pointed out that the study design does not significantly bias the findings estimated by previous studies [70].

Given that the number of relevant publications is increasing sharply, this section mainly focuses on the findings of studies conducted at a global or national scale. Meanwhile, as the novel VOCs have spread rapidly worldwide, the findings from associated epidemiological studies are discussed in this section.

Associations between COVID-19 cases and temperature/humidity: Using the keywords of ‘COVID-19 or SARS-COV-2’ AND ‘temperature or humidity’ AND ‘Global or nationwide or national or worldwide’ on 19 March 2022, 29 remaining studies were tabulated in Table 4 after the examination of the titles, abstracts, full text and the removal of low-quality articles (Fig. 2).

Based on global COVID-19 cases prior to 6 May 2020, an early descriptive study [71] noted that 60% of the confirmed cases were concentrated in regions where air temperature ranged from 5 to 15 °C, with a peak at 11.5 °C. Furthermore, approximately 74% of the cases occurred in places with absolute humidity in the range of 3–10 g/m³. The authors speculated that COVID-19 might spread cyclically, and outbreaks might recur in large cities in the mid-latitudes in autumn 2020 [71], as confirmed by later observations. When using various statistical approaches and data sources, conclusions on the correlations between daily confirmed COVID-19 cases and meteorological factors varied. For example, Pan et al. [72] employed wavelet coherency analysis for eight countries with 202 locations, finding no significant association between basic reproductive number and weather conditions. In contrast, by analyzing data between 25 March and 18 April 2020, a cross-sectional study [73] reported strong inverse correlations between monthly average environmental temperature and multiple COVID-19 indexes, such as total nationwide cases, active cases, and cases per million.

However, the two studies did not control the effects of confounding variables. Given that COVID-19 spread is strongly shaped by policy intervention, physical distancing, use of face masks, and some other factors, concerns were raised about the robustness of the results. After controlling influences from wind speed, nationwide population structure,

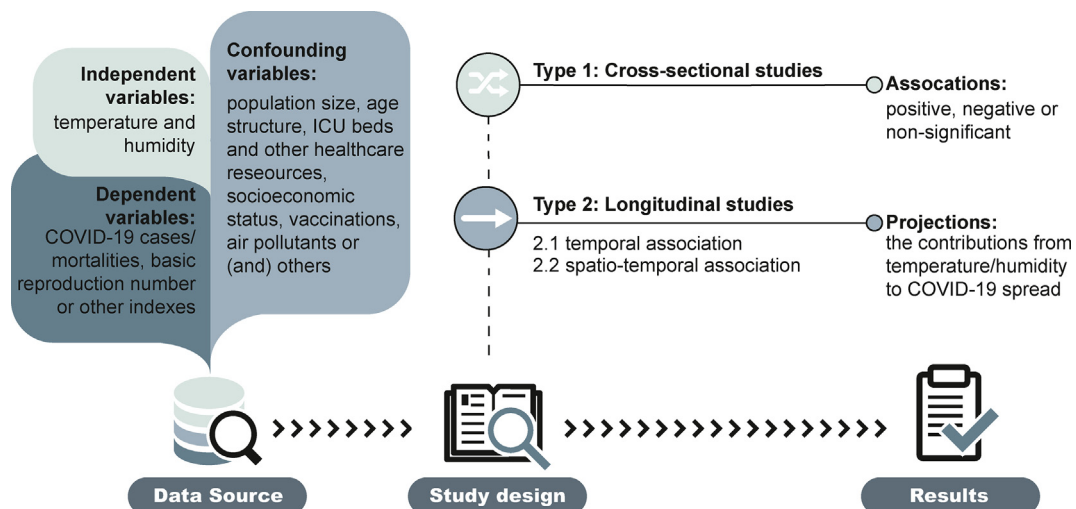


Fig. 1. The general study framework used to determine the associations between COVID-19 spread and temperature/humidity.

Table 4
Selected literature on global epidemiological analyses regarding COVID-19 spread and temperature/humidity.

Region	Timespan	Meteorological variables	Outcome variable	Confounding variables	Study Type*	Inferences	References
3739 global locations	December 12, 2019 to April 22, 2020	Temperature, humidity, precipitation, snowfall, moon illumination, sunlight hours, ultraviolet index, cloud cover, wind speed and direction, pressure data	Effective reproduction number	Air pollutants, population density, and using models to control for estimating effective reproduction number	b	A moderate negative (coefficient: 0.037% with 95% CI of 0.019–0.054) relationship between the estimated reproduction number and temperatures above 25 °C was obtained	[3]
277 global regions	December 1, 2019 to April 14, 2020	Humidity, temperature, wind speed, and visibility data	Defined growth rate	Location, population, people aged over 65, area, life expectation, the number of hospital beds, GDP, and governmental policy	a	Temperature sensitivity of COVID-19 spread was only –2.7% (–5.2%–0%), indicating warm summer is unlikely to eliminate COVID-19 transmission naturally	[2]
1236 regions	By the end of May 2020	Daily mean temperature and humidity	New daily case and basic reproductive number	Gross regional product, population, government response, elevation and suspected population, working population, and school-age group	b	Temperature and relative humidity were negatively associated with the COVID-19 spread	[114]
409 cities across 26 countries	January 1, 2020 to May 31, 2020	Temperature, dewpoint temperature, surface solar radiation, downwards, precipitation, and wind	Effective reproduction number	Government response index, total population, population density, the elderly population (>65 years), and GDP and PM _{2.5}	a	Meteorological conditions influenced little COVID-19 spread. Population behavior and government interventions were more important drivers of transmission.	[78]
202 locations in 8 countries	As of the early stage of the global pandemic	Daily temperature, humidity, and UV radiation	Basic reproductive number	–	b	Meteorological conditions did not statistically alter the COVID-19 spread	[72]
Global, first-level administrative division	As of March 17, 2020	Daily temperature and humidity	Confirmed cases	Exposure day; the median age of the national population, population density, the capacity of the country to detect an emerging infectious disease	b	A negative association with COVID-19 incidence for temperatures of –15 °C and above was found	[76]
Global	Data on April 2, 2020	Temperature	Proportion of cases	GDP, latitude, and longitude	a	The temperature may be negatively associated with both the proportions of COVID-19 cases/mortalities in the population	[75]
50 cities	From at least 10 reported deaths in a country to March 10, 2020	Mean temperature and humidity	Total number of cases	–	a	The distribution of substantial community outbreaks along restricted latitude, temperature, and humidity measurements was consistent with the behavior of a seasonal respiratory virus.	[115]
144 geopolitical areas worldwide, excluding China, South Korea, Iran, and Italy	From at least 10 COVID-19 cases to March 20, 2020	Temperature and humidity	Epidemic growth rate	Elevation, GDP, health expenditure as a percent of GDP, life expectancy, rate of people aged over 65 years or older, the infectious disease vulnerability index, urban population density, number of flight passengers per capita, and closest distance to a country with an already established epidemic	a	COVID-19 spread was not associated with temperature but maybe weakly and negatively associated with humidity.	[77]
249 countries	December 1, 2019, to March 30, 2020	Daily data of precipitation, average temperature, maximum temperature, and minimum temperature	COVID-19 transmission and deaths	Exposure time, population density, and dummy month	b	The average temperature per country was negatively associated with the number of cases of SARS-CoV-2 infections	[116]

More than 200 countries	Counts on specific days	Monthly average temperature	COVID-19 cases	–	a	The temperature may be negatively associated with COVID-19 transmission	[73]
166 countries, excluding China	As of March 27, 2020	Temperature, humidity, wind speed	Daily new cases and deaths	The median age of the national population, population density, global health security, human development index, and exposure day	b	The temperature may be negatively related to COVID-19 transmission	[74]
Global, top 20 countries	January 22 to April 27, 2020	Daily Temperature, dew/frost point, wind speed, precipitation, relative humidity, surface pressure	COVID-19 outcomes	–	b	High temperature and high relative humidity reduced the viability, stability, survival, and transmission of COVID-19, whereas low temperature prolonged the activation and infectivity of the virus	[117]
Global	The number of reported cases and deaths in April 2020	Temperature and humidity	Reported positive cases and deaths	Human development index	a	Surface air temperature and Specific humidity do not have any statistically significant association with COVID-19 transmission, though there is a weak relationship between temperature and the pandemic's mortality	[118]
Global	January to April, 2020	Temperature, humidity, and UV	Growth rate	Population data	a	Without intervention, COVID-19 will decrease temporarily during summer, rebound by autumn, and peak next winter	[119]
Global, 209 countries	In the first 16 weeks of the infection	Climatic zone, temperature, solar irradiation, relative humidity, wind speed, surface pressure, precipitation	COVID-19 Incidence or prevalence	population size, land area	a	Climatic factors significantly influence the spread of SARS-CoV-2	[120]
Global, 52 countries	December 31, 2019, to April 13, 2020	Temperature, relative humidity, and solar radiation	Basic reproduction number	Global Health security index	a	A negative association is found between the incidence of COVID-19 and temperature.	[121]
Global, 206 regions/countries	January 8, 2020 to April 20, 2020.	Temperature, relative humidity, UV index, wind speed, cloud cover, precipitation, sea-level air pressure, and daytime length	newly reported COVID-19	GDP per capita, and the Global Health Security Index	b	The positive association between COVID-19 and 14-day lagged temperature and a consistently higher rate of COVID-19 cases in absolute humidity of 5–10 g/m ³	[122]
35 OECD countries and all US states	–	Ambient temperature, relative humidity, cumulative precipitation, and air pollution	COVID-19 mortality	Population size, population density, days of social distancing prior to first reported COVID-19 death, the Gini index as a measure of socioeconomic inequality, ICU beds, the prevalence of obesity, smoking prevalence, and proportion of the population older than 75 years.	a	A 1 °C increase in ambient temperature was associated with 6% lower COVID-19 mortality at 30 days following the first reported death	[96]
Global, 159 countries	January 22 to June 15, 2020	Air temperature, specific humidity	Growth rate	Population density, size, and structure, per capita government health expenditure, and global airport connection	a	The role of environmental conditions on COVID-19 transmission is controversial.	[123]
Global, 188 countries	As of 31 December 2020	Mean temperature, maximum temperature, minimum temperature, dew point temperature, precipitation, and wind speed	The number of daily new cases	Population density, government response stringency index, human development index, categorical variable for the country, and date	b	The mean temperature, wind speed, and relative humidity were negatively correlated with daily new cases of COVID-19,	[124]

(continued on next page)

Table 4 (continued)

Region	Timespan	Meteorological variables	Outcome variable	Confounding variables	Study Type*	Inferences	References
Global	–	UV radiation, temperature, specific humidity, and precipitation	The daily growth rate of confirmed COVID-19 cases	Social and economic characteristics	a	Temperature and specific humidity cumulative effects are not statistically significant	[125]
144 countries	At least 21 days of death until April 27, 2020.	Maximum temperature, relative humidity, and UV Index	COVID-19 mortality rates	Population structure, the number of hospital beds, governmental immigration restrictions, and GDP	a	The temperature has a negative association with the COVID-19 mortality rate.	[126]
47 countries	February 22 to June 22, 2020	Temperature, air pressure, and wind speed	Effective reproductive number	Human mobility, country, and date	b	A negative relationship between temperature and COVID-19 transmission rate	[127]
615 cities	January to June 2020	Temperature, pressure, humidity, dew, wind gust	Total number of COVID-19 confirmed cases	–	b	High ambient temperature and relative humidity have a mitigation effect on COVID-19.	[128]
153 countries	January to May 2020	Temperature, humidity, air pressure, wind speed, precipitation	Daily COVID-19 cases, basic reproductive number	Day, policy	b	The temperature was positively related to daily new cases at low temperature but negatively related to daily new cases at high temperature	[129]
191 countries	Until January 22, 2021	Temperature	Mortality rate	Daily test, political regime, urban population, GDP, air pollutant, and DALYs	a	Mean annual temperature showed a significant inverse association with the COVID-19 mortality rate	[130]
150 countries	A minimum of 90 days since the first confirmed case	Temperature	Mortality rate	The probability of mortality due to respiratory disease, the stringency of government measures, countries' hemisphere, DALYs, human development index, population density, and the proportion of people aged 65 and older	b	The increase in ambient temperature decreases the incidence of COVID-19 deaths	[131]
58 countries, at least 30 daily cases as of July 29, 2020	–	Temperature, precipitation	Basic reproduction number	Demographics, disease, economics, air pollution, habitat, health, and social factors	a	Temperature and humidity did not have strong relationships with R_0 but were positive.	[132]

* a, cross-sectional study; b, longitudinal study.

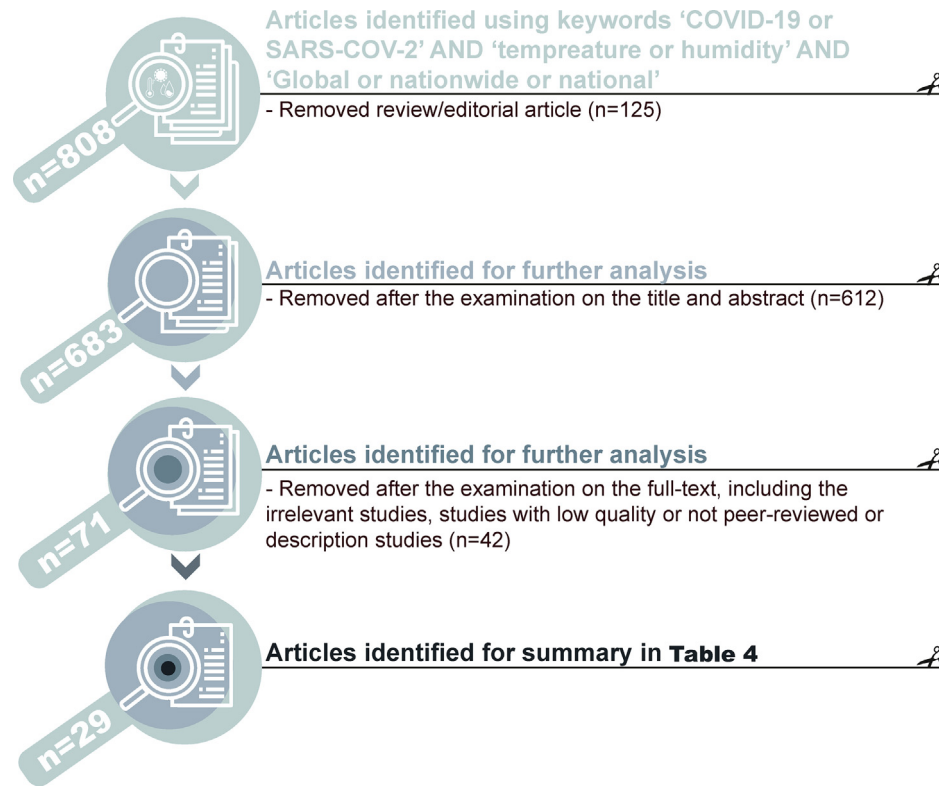


Fig. 2. The framework to identify global analyses on the association between temperature/humidity and COVID-19 transmission in this study. n, sample size.

the security index and exposure period, a longitudinal analysis in 166 countries concluded that both the temperature and relative humidity were negatively related to daily new cases [74]. In detail, each unit increase in temperature would significantly trigger a 3.08% (95% CI: 1.53%, 4.63%) reduction in daily new cases, while an increase in relative humidity resulted in a 0.85% (95% CI: 0.51%, 1.19%) decrease in daily new cases [74]. In addition, model assumptions on the lag structures did not significantly alter the results, suggesting that elevated temperature and humidity may partially influence the COVID-19 pandemic [74]. Various other cross-sectional studies, relying on daily confirmed or accumulated cases as dependent variables [75,76], have yielded homogeneous results. On the other hand, Jüni et al. [77] performed a prospective cohort study including 144 geopolitical areas worldwide and indicated that there was no association between COVID-19 growth and temperature but a weak negative effect for relative or absolute humidity.

In addition, some studies did not directly use daily cases as dependent factors. Generally, the authors first estimated the local effective reproduction number (R_t) or transmission rate and then linked these indexes to spatial and temporal variables. One merit of such studies is that these estimated indexes can better describe the growth of the COVID-19 pandemic, which promises to narrow the uncertainties raised by test coverage or incubation period. A cross-sectional analysis first evaluated the R_t in 409 cities in 26 countries [78]. After controlling the impacts from selected confounding parameters including the government response index, total population, population density, elderly population (>65 years), GDP, and particulate matter, a slight decrease of 0.087 (95% CI: 0.025, 0.148) in R_t caused by mean temperature was observed, as well as less evidence for relative humidity [78]. The authors concluded that population behavior and government interventions rather than meteorological conditions were the key drivers for COVID-19 spread [78]. In line with this study, Su et al. [6] found that the estimated transmission rate of COVID-19 at an early stage was slightly associated with temperature rather than humidity. An ancillary finding is that the proportion of people over 65 was a crucial driver of COVID-19 spread and those elderly

people may face an approximately 2.5-fold higher infection risk than younger people [6]. By calculating the daily R_t at 3739 global locations, a recent global analysis considered the co-effects of air pollutants and weather conditions [3]. The authors stated that a moderate negative association between the estimated R_t and a temperature higher than 25 °C, whereas no obvious relationship was found for humidity, and weaker positive associations were found for sulfur dioxide and ozone [3]. Similarly, findings from Fontal et al. [79] supported the notion of a uniform summer recession of COVID-19 spread, indicating that COVID-19 may become a seasonal low-temperature infection. To date, it appears that the relationships between temperature and COVID-19 observed in most global analyses were negative, but associations for humidity remain unclear.

Besides global analysis, more studies have been carried out at national, provincial, or city scales, as summarized in a previous study [70]. Compared with global analysis, the spatial variations in studies with smaller scales may produce lower levels of bias when estimating the associations. In China, Fang et al. [80] found that the median value of R_t was 0.46 in the north, much higher than the 0.2 in southern cities. Meanwhile, the transmissibility of COVID-19 was negatively associated with temperature, and an increase in humidity from 40% to 75% would increase the spread of COVID-19 by 47% [80]. A modeling study also revealed that higher temperature was associated with decreased COVID-19 spread by a lag effect and concluded that a temperature increase in China made a key, but not determining, contribution to impeding the COVID-19 outbreak [81]. In 211 counties of 46 states in the USA, the mean R_t was estimated to be 5.7 in the first two weeks, and research showed that the R_t declined when the temperature was in the range of 0–11 °C and >20 °C, while the R_t was increased when the temperature was between 11 and 20 °C [82]. Similarly, another study revealed that cold and dry conditions might be moderately associated with increased SARS-CoV-2 transmissibility [83]. Research implemented in 15 countries in Europe estimated that a unitary increase in temperature can result in a 0.9% decline in COVID-19 transmission [84]. In

Table 5

Typical study weaknesses in research on the associations between COVID-19 spread and weather conditions.

Issues	Details
Independent variables	The treatments of temperature and humidity varied, including daily measurements and aggregated averages. In addition, some studies considered the lag effects, while some did not.
Dependent variables	a) Owing to the incubation period, diagnostic technique, and capability, the quality of the data on the number of positive cases and mortality rates is questionable, especially in the early stage of the pandemic. b) There is no uniform guideline for choosing the appropriate indexes (cases, mortality, cases per person, basic reproduction number, transmission rate, or others) to represent the COVID-19 spread.
Confounding variables	Most ecological studies did not control the important confounding factors related to the COVID-19 spread.
Methodologies	Although some statistical models were utilized, the comparisons between these methods/models remain unclear.
Result interpretation	Sensitivity and uncertainty analysis was required in most studies.
Exposure period	Generally, a short study period was preferred, which is not able to account for long-term trends.
Research areal unit	Results may be quite different when studies are performed at the city, provincial, national, or global scale.
Other issues	Geographical variation in viral strains; cluster infections; the role of transmission in indoor environments, etc.

England, Nottmeyer et al. [85] pointed out that dry and cold conditions may elevate the COVID-19 incidence. In Africa, relative humidity and temperature appeared to be inversely correlated with COVID-19 growth [86]. Similar results were observed in India [87], Bangladesh [88], Indonesia [89], Mexico [90], and Brazil [91]. To some extent, although the conclusions derived from local studies become increasingly heterogeneous, it appears that inverse associations between temperature and COVID-19 have been demonstrated by many studies, while relationships for humidity are controversial.

At the time of writing, only one publication has reported the association between temperature/humidity and the transmission of SARS-CoV-2 Delta or Omicron variants. In Sydney, Australia, an observational study suggested that humidity was negatively associated with SARS-CoV-2 Delta cases [92]. Furthermore, when the humidity was below 70%, a relationship between temperature and cases of the Delta variant was also apparent [92].

Associations between COVID-19 mortality rates and temperature/humidity: Wu et al. [74] illustrated that a unit increase in temperature might lead to a 1.19% (95% CI: 0.44%–1.95%) decrease in daily new deaths. Similarly, a study conducted in Nigeria yielded a significantly weak negative correlation between temperature and cumulative mortality [93]. A recent global analysis covering 149 countries reported a negative association between temperature and COVID-19 mortality in high-income economies [94]. Contrastingly, the diurnal daily temperature was positively related to COVID-19 in low- and middle-income countries [94]. In China, a longitudinal analysis addressed the non-linear association between temperature and COVID-19 mortality rates, and a unitary increase in temperature may decrease daily cumulative relative death risk by 12.3% (95% CI: 3.4%–20.4%) [95]. Research conducted in multiple countries suggested that a unitary increase in temperature triggered a 6% lower COVID-19 mortality [96]. Such combined evidence indicates that temperature may be inversely associated with the COVID-19 mortality rate. In addition to the notion that a high temperature may potentially reduce COVID-19 cases, another reason may be that the immune system functions differently under various ambient temperatures.

Compared with temperature, the associations between humidity and COVID-19 mortality have been studied to a lesser extent. A study in Wuhan suggested that humidity was negatively associated with daily death counts [97]. A worldwide study indicated that a 1% increase in humidity resulted in a 0.51% (95% CI: 0.34%–0.67%) decrease in daily new cases [74]. In Pakistan, the humidity was found to be insignificantly associated with daily death rates [98]. Thus, with respect to the associations for humidity, results from existing studies appear to be conflicting.

Data-related, methodological and other obstacles: Table 5 lists some common study limitations, which have also been well-reviewed previously [70,99]. In general, the study weaknesses in existing publications can be divided into three types: data, methodology, and others. Commonly, most studies have struggling with inconsistent data on COVID-19 cases, mortality rates, and other health-related indicators [13]. For example, all data

used in models, including the independent, dependent, and confounding variables, should be treated with caution (Table 5). Using the daily confirmed cases as an example, insufficient test coverage at an early stage would reduce the number of positive samples. Hence, spatially varied test capability will bias the estimation in ecological studies. Similarly, the temporally varied test coverage has introduced uncertainties in time-series analysis. In addition, the incubation period of COVID-19 cases means that it is challenging but necessary to determine the lag effects of environmental factors. Another critical problem with the data is the quantification of confounding variables. Population behavior and government interventions have contributed significantly to impeding the COVID-19 outbreak, and these factors can therefore mask the effects of environmental conditions. Although effects for some confounding variables have already been evaluated [100–102], these results have not been well applied to the estimation of the associations between COVID-19 spread and environmental conditions.

With respect to the methodological obstacles, some studies did not follow standardized approaches for specific study designs. In existing publications, although correlation analysis, generalized additive models, Bayesian inference, meta-analysis, and some other statistical models were usually adopted, the preconditions for these approaches were seldom validated. In addition, most studies used empirical models rather than process-based models such as compartmental models that address interactions among susceptible, infectious, and recovered individuals within a population [13]. A weakness of an empirical model is that it only considers the fit to observed data without a priori hypotheses. Although it is difficult to quantify some parameters in a process-based model (for example, public health interventions), such an approach is useful for exploring transmission dynamics and epidemic trajectories.

To date, few studies have investigated transmission of SARS-CoV-2 in a cold chain-related environment, although several outbreaks in China were linked to food transported in the cold chain from abroad [103–105]. More than 10 provinces have detected SARS-CoV-2-positive samples collected from imported frozen food or its packaging [104]. As shown in Table 3, SARS-CoV-2 is relatively stable on plastic and stainless steel, where the virus has been reported to remain viable even after 72 h. Under a temperature of $-20\text{ }^{\circ}\text{C}$, the titer of the infectious virus did not decline significantly [103]. An earlier study concluded that the infectivity of viruses in food might remain for up to 2 years during frozen storage and transport at $-20\text{ }^{\circ}\text{C}$ [104]. Hence, public health officials should be alerted to the infection risk of SARS-CoV-2 in contaminated refrigerated or frozen food.

6. The way forward: Possible research directions

Although research on the role of environmental conditions in the spread of COVID-19 has yielded some results, several critical questions remain unanswered. In particular, some research directions require special attention:

- 1) The stability of SARS-CoV-2 variants and associated transmission, especially for VOCs or variants of interest. To date, a couple of variants have been identified whose properties, including spread, diagnostic tools, associated disease severity, therapeutics, and vaccine performance (<https://www.who.int/en/activities/tracking-SARS-CoV-2-variants/>), are raising concerns for public health. For example, the Delta (B.1.617.2) variant, which first emerged in India, is now spreading rapidly worldwide and has even resulted in resurgence in nations with highly vaccinated populations [106]. The basic reproductive number (R_0) of the Delta variant was estimated to reach 5.08, much higher than that of the ancestral SARS-CoV-2 [106]. Although there are available epidemiological studies on the spread of the VOCs, how environmental conditions influence the spread of these variants remains unclear. To date, there have been few studies on the stability of VOCs in aerosols or on inert surfaces.
- 2) The study design or guidelines used in epidemiological studies. Owing to existing study limitations [70] (Table 5), most epidemiological research has failed to provide a robust scientific basis for the role of environmental conditions in COVID-19 spread. For example, do the modifying effects of temperature/humidity on different scales vary? Is it possible to use temperature and humidity as risk indicators for COVID-19 spread? What are the true interactive effects between temperature/humidity and other environmental factors? Meanwhile, the merits, demerits, and suitability of statistical methods should be compared and elucidated, and methodological guideline is highly encouraged.
- 3) The role of environmental conditions in the spread of COVID-19 from the environment. High virus loads have been detected in wastewater, sediments, soils, and non-human animals [107,108]. These environmental mediums may become potential reservoirs for viruses. However, the possibility of the virus recycling from these pathways into the human population under suitable environmental conditions remains unclear.
- 4) Adaptive strategies for COVID-19 control. To reduce or eliminate the COVID-19 risk requires multifaceted effort. The spread of COVID-19 appears to have been controlled primarily by government interventions rather than environmental factors. At this stage, when the vaccination rate in many populations is high, it is possible to consider how to control the spread of COVID-19 to achieve low or zero frequency and to reduce the cost of epidemic prevention derived from dynamic strategies, taking into account the combined effects of environmental conditions, non-pharmaceutical interventions and population behavior.

Declaration of competing interests

The authors have declared no conflicts of interest.

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