Introduction

Establishment rates of invasive alien species (number of new invasive alien species discovered or reported per annum for a recipient region [1]) have been increasing worldwide during the past century. These trends have been widely attributed to increased rates of international trade and associated species introductions, but rarely linked to environmental change. To better understand and manage the bioinvasion process, it is crucial to understand the relationship between global warming and establishment rate of invasive alien species, especially for poikilothermic invaders such as insects.

Methodology/Principal Findings: We present data that demonstrate a significant positive relationship between increases in average annual air temperature and the establishment rate of invasive alien insects in mainland China during 1900–2005. This relationship was modeled by regression analysis, and indicated that a 1 °C increase in average annual surface temperature in mainland China was associated with an increase in the establishment rate of invasive alien insects of about 0.5 species year⁻¹. The relationship between rising surface air temperature and increasing establishment rate remained significant even after accounting for increases in international trade during the period 1950–2005. Moreover, similar relationships were detected using additional data from the United Kingdom and the contiguous United States.

Conclusions/Significance: These findings suggest that the perceived increase in establishments of invasive alien insects can be explained only in part by an increase in introduction rate or propagule pressure. Besides increasing propagule pressure, global warming is another driver that could favor worldwide bioinvasions. Our study highlights the need to consider global warming when designing strategies and policies to deal with bioinvasions.
mic animals and thus should be sensitive to changes in ambient temperature.

**Materials and Methods**

**Data collection**

Establishment rate (unit: species year⁻¹) was calculated using the first-year an IAI was recorded or recorded within the recipient region during 1900–2005 (inclusive). To build this series for China, we compiled a list of IAI's and their first-recorded dates of occurrence in China from professional literature, particularly from checklists of invasive alien species and journal articles.

Additional data were obtained for the United Kingdom and the continental United States mostly from professional publications. Information described as “date of introduction”, “arrival date”, or “year of first record” was considered to represent the year of establishment [19–22]. However, we recognize that the year of establishment often occurs many years before the year of first record. When the time of first record was described as a decade then we entered the midpoint of the decade (e.g., 1930s was entered as 1935), and when the time was reported as prior to a specific year then we entered that year (e.g., prior to 1940 was entered as 1940) [20].

Overall, we collected data for 54 IAI's that are of economical and environmental importance in China (Table S1), for 296 invasive and non-invasive alien insects in the United Kingdom (Table S2), and for all 44 invasive and non-invasive alien bark and ambrosia beetles (Coleoptera: Scolytinae) recognized as established in the continental United States during 1900–2005 (Table S3). To minimize potential confounding effects from human activities, we excluded species introduced intentionally into the region (Table S4 provides summary data for the response and explanatory variables used in this study).

Our explanatory variable, annual change in average annual surface air temperature (unit: °C year⁻¹) in China, the United Kingdom, and the United States were calculated using data derived from references [23], [24] and [25], respectively. For the United Kingdom and United States, updated datasets are publicly available at http://www.metoffice.gov.uk and http://data.giss.nasa.gov, respectively. The years covered by these datasets are 1873–2005 for China, 1659–2011 for the United Kingdom, and 1880–2011 for the United States. We adjusted all raw data relative to 1961–1990 for each country, which is a widely-used reference period [26, 27]. Next, we took an 11-year moving average of temperature for each country during the period 1905–2000, and used the resulting series as a metric to explore for trends along with the 11-year moving average of IAI's over the same time period.

We also explored the relationships between changes in average annual surface air temperature and establishment rate of IAI's after accounting for changes in levels of international trade during the period 1950–2005. For trade data, we used the International Financial Statistics of imported merchandise (unit: million US$ year⁻¹) for the three study regions during the years 1950–2005. The years covered by these datasets are 1950–2010 for China, and 1948–2010 for the United Kingdom and United States. These data are publically available at http://www.imf.org/external/data.htm.

**Statistics**

Cross-correlation function (CCF) was used to identify potential associations between the establishment rate of IAI's and changes in temperature in each country. Linear least-square regression analysis was conducted to model the relationship for each country. We used the following equation that links establishment rate of IAI's (r) in year t to temperature change (h) in year t.

\[ r_t = a h_t + b \text{trend}_t + c + [\varepsilon_t] \]  

(1)

\[ r_t = a h_t + \text{byear}_t + c + [\varepsilon_t] \]  

(2)

where c represents fixed effects accounting for time-invariant characteristics that might explain differences in the baseline level of bioinvasion risk, \( btrend_t \) suggests a common time trend of bioinvasion risk associated with the growth of human activities, \( \text{byear}_t \) reflects a region-specific time trend used to control for variables that could evolve over time (e.g., international trade) and thereby alter the risk of bioinvasion, and \([\varepsilon_t]\) is the residual error term. We first ran model [1] using only \( btrend_t \) to determine the effect of global warming without the variable \( \text{byear}_t \), and then we ran model [2] including international trade without the variable \( btrend_t \).

**Results**

CCF analysis detected a significant positive relationship between the establishment rate of IAI's and annual mean temperature change in China during the study period 1905–2005 (Table 1). All CCF values were significant (P<0.05) when testing the model with time lags of 0 to 5 years. All analyses using

| Pair | Time lag (year) | CCF1 | CCF2 |
|------|----------------|------|------|
| f_{CN} ~ h_{CN} | 0 | 0.4317* | 0.7657* |
|       | 1 | 0.2590* | 0.6965* |
|       | 2 | 0.3170* | 0.6234* |
|       | 3 | 0.3071* | 0.5512* |
|       | 4 | 0.2673* | 0.4817* |
|       | 5 | 0.2435* | 0.4164* |
| f_{UK} ~ h_{UK} | 0 | 0.3745* | 0.7201* |
|       | 1 | 0.3973* | 0.6554* |
|       | 2 | 0.3464* | 0.5830* |
|       | 3 | 0.2303* | 0.5147* |
|       | 4 | 0.1732* | 0.4539* |
|       | 5 | 0.1759* | 0.4021* |
| f_{US} ~ h_{US} | 0 | 0.3261* | 0.6666* |
|       | 1 | 0.3180* | 0.6338* |
|       | 2 | 0.1717* | 0.5895* |
|       | 3 | 0.1999* | 0.5476* |
|       | 4 | 0.2815* | 0.5002* |
|       | 5 | 0.1812* | 0.4481* |

Establishment rate and temperature change (deviation from the 1961–1990 mean) were indicated by r and h, respectively. In CCF1, r and h are based on annual data during the period 1905–2005, while in CCF2, r and h are based on 11-year moving-averages. Asterisks (*) indicate that the coefficients were significant (2-tailed; P<0.05). doi:10.1371/journal.pone.0024733.t001
the 11-year moving average data for temperature and IAI produced higher CCF values compared with the analyses where annual values were used (Table 1). The close association between the 11-year moving average for temperature and IAI in China can be observed in Fig. 1A, and was well described by a linear equation with common time trend (Fig. 1A). This equation predicts that a 1°C increase in mean annual temperature corresponds to an increase of about 0.5 IAI species year−1 in China. The relationship between increasing average annual surface air temperature and establishment rate of IAI remained significant after inclusion of the annual value of imported merchandise in the regression models during 1951–2005, using either the 11-year moving average time series or simply the annual values (Table 2). Similar significant associations were noted between establishment rates of alien insect species and changes in average annual surface air temperature in the United Kingdom and the United States (Fig. 1B-C, Tables 1, 2), suggesting again that increasing establishment rates of IAI may be related to increasing ambient temperature.

**Discussion**

The discovery of newly established alien species depends on many factors such as the temporal pattern of alien introductions, relative abundance or size of the founding populations, and the sampling efforts by humans [8]. Increasing foreign trade, along with a concomitant increase in the propagule pressure of alien species, is another important determinant of species introductions [1,7,9,28].

We found significant positive associations between establishment rates of IAI and changes in mean annual surface air temperature in our three study regions over the past century. Such results suggest that rising ambient temperatures have the potential to increase establishment rates of IAI. Warmer temperatures can favor establishment of alien insects both directly and indirectly [10,29–33]. For example, warmer temperatures can provide new areas for establishment of IAI that were previously unsuitable [34], enable insects to shift their geographic range polewards [35], and to cross barriers that previously limited their natural ranges [10]. In addition, warmer temperatures can hasten insect growth and reproduction [29], improve winter survival [30], allow for greater multivoltinism [36] and higher population densities [37,38], and increase plant susceptibility and suitability to herbivorous insects [39]. Consequently, these favorable factors could lead to higher rates of establishments, shorter latent periods (i.e. time lag between introduction and discovery), and higher probabilities of population outbreaks.

Moreover, our results showed that the effects of increasing average annual surface air temperature on establishment rate were sufficiently robust to remain significant even when adjusted for changes in international trade, indicating that establishment rate of IAI can increase even when there is no increase in propagule pressure. This can occur, in part because (1) not all alien species are introduced by human activity, but rather some species arrive in new areas because of natural range expansion [33,40,41], and (2) warmer temperatures can allow more introduced species to become established.

It is important to recognize that IAI establishment rate can be influenced by factors other than propagule pressure and global warming. These other factors could include biotic traits and variation in the degree of invasiveness of the introduced species [42,43], influence of human disturbance on the invasibility of the recipient regions [43–45], and precipitation chemistry and other aspects of climate change [46,47].

**Figure 1. Associations between establishment rates of invasive alien insects and average annual surface air temperature changes during 1900–2005.** A: Mainland China; B: the United Kingdom; C: the contiguous United States. Temperature change (calculated as the deviation from the 1961–1990 mean) and establishment rate are presented as an 11-year moving average. The establishment rate (r) as a function of temperature change (h) was modeled using linear least squares regression with a common time series. The numbers in the square brackets are the regression residuals. See text for details. doi:10.1371/journal.pone.0024733.g001

In addition, increasing the effort to survey for new IAI species would be expected to result in more discoveries of new alien species. Examining this hypothesis would be valuable but is beyond the scope of the present paper. However, it should be noted that the sampling efforts in China during the 1930s–1940s, a period of general warfare, could be expected to have been lower than during...
the more peaceful years of the 1950s–1960s. However, it is interesting to note that many more IAIs were discovered in China during the in 1930s–1940s than during the 1950s–1960s (Fig. 1A). This example confirms the theoretical prediction that the expected establishment curve can increase even when both propagule pressure and survey effort remain nearly constant [8].

In conclusion, our study suggests that the increase in establishment rates of IAIs in China, the United Kingdom, and the United States during the past century can be partially explained by global warming given that warmer temperatures can facilitate bioinvasions worldwide [13,47]. Moreover, our findings suggest that the interaction between global warming and bioinvasion should be considered by plant health protection specialists and policy makers.

Supporting Information

Table S1 List of invasive alien insects and their first-recorded dates of establishment in mainland China during 1900–2005 (inclusive).

Table S2 List of invasive and noninvasive alien insects and their first-recorded dates of establishment in the United Kingdom during 1900–2005 (inclusive).

Table S3 List of invasive and noninvasive alien scolytines and their first-recorded dates of establishment in the contiguous United States during 1900–2005 (inclusive).

Table S4 Minimum and maximum values for the response and explanatory variables used in the present study by country.

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Author Contributions

Conceived and designed the experiments: DH RZ. Performed the experiments: DH. Analyzed the data: DH. Contributed reagents/materials/analysis tools: DH RAH. Wrote the paper: DH RZ RAH.

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