High risk of biological invasion from prayer animal release in China

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Prayer animal release (PAR)—a traditional "compassion-based" religious practice of releasing captive animals into the wild to improve the karma of the releaser—has been regarded as a major anthropogenic pathway facilitating species invasions worldwide. However, comprehensive, quantitative assessments of PAR-related invasion risks, crucial for the development of mitigation strategies, are lacking. To address this knowledge gap, we conducted a literature review of the prevalence of PAR events and examined the overlap between PAR intensity across China and habitat suitability for non-native vertebrates released in these events. Our results revealed that 63% of the areas with high PAR intensity in China were also suitable for non-native vertebrate establishment, a degree of overlap that was greater than expected by chance. In addition, field surveys in China detected higher richness of non-native fishes at PAR sites than at non-PAR sites. These findings imply an overall high risk of biological invasions associated with PARs. We recommend interdisciplinary cooperation among scientists, religious groups, and government agencies to effectively manage PARs and reduce the associated bioinvasion risk.

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Prayer animal release (PAR)—or *fangsheng* in Chinese, *hōjō* in Japanese, and *tshe thar* in Tibetan—is a popular ritual practice common in Asia, with a long history of Buddhist and Taoist influences (Shiu and Stokes 2008; Awoyemi *et al.* 2012; Liu *et al.* 2012). The earliest known PAR event was recorded in *Liezi*, a famous Taoist publication of the fifth century BCE (Graham 1960). Buddhist writing and teachings promote PARs as a means of gaining spiritual merit and karma (Agoramoorthy and Hsu 2005; Shiu and Stokes 2008; Liu *et al.* 2012), which partly accounts for why the ritual is so widespread. In an era of rapid globalization, PAR events are currently no longer limited to Asia, having become increasingly popular in the Americas, Europe, and Oceania (Awoyemi *et al.* 2012; Liu *et al.* 2012; Magellan 2019).

In modern PAR activities, certain taxa are more commonly released than others. For example, fishes and gastropods are often used in PAR ceremonies because more individuals can be released in a single event due to their low per-unit cost, which results in greater overall perceived gains in karma (Liu *et al.* 2013). Vertebrate taxa such as turtles and birds are also popular in PAR ceremonies because turtles symbolize longevity in the Chinese culture and birds are considered charismatic, making for more impressive PAR events (Shiu and Stokes 2008; Khudamrongsawat *et al.* 2019).

The number of animals involved in PAR events is staggering (Awoyemi *et al.* 2012). For example, the Buddhist China Preserve Life Association reported that more than 20 million animals—the vast majority of which were small aquatic species—were released in at least 300 ceremonies conducted in 2008 alone (Awoyemi *et al.* 2012). In Phnom Penh, Cambodia, an estimated 688,675 birds are purchased annually in local markets for the purposes of ceremonial releases (Gilbert *et al.* 2012). Similarly, in Hong Kong, China, approximately 680,000–1,050,000 birds are associated with PARs each year (Chan 2006).

Although PAR is a compassion-based religious practice with deep respect for the environment and living beings, PAR events result in the release of many non-native species, largely due to a lack of ecological awareness. Consequently, PARs have been identified as one of the most important anthropogenic pathways of biological invasions (Liu *et al.* 2012), posing

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threats to biodiversity, economic well-being, and public health (Blackburn *et al.* 2019; Diagne *et al.* 2021; Zhang *et al.* 2022). For example, the establishment of several of the most notorious invasive species, such as the red-eared slider (*Trachemys scripta elegans*) and American bullfrog (*Lithobates catesbeianus*) in China (Liu *et al.* 2012, 2013), Asian swamp eel (*Amphipnous cuchia*) and silver carp (*Hypophthalmichthys molitrix*) in the US (Nico *et al.* 2011), and white-crested laughingthrush (*Garrulax leucolophus*) in Singapore (Corlett 2010), is thought to be associated with PAR activities. In addition, 6% of birds sold for ceremonial release in Taiwan were exotic species, most of which were mynas (*Acridotheres tristis*, *Acridotheres javanicus*, and *Acridotheres fuscus*) (Severinghaus and Chi 1999). Given the serious risks that PARs pose to the environment and to biodiversity, conservation organizations (eg the Society for Conservation Biology, SCB) have called for immediate actions to curb the likely adverse effects of PARs. Such actions include educating particular religious groups about the risks involved with PARs, enforcing regulations and laws, providing alternatives to PARs, and monitoring of biodiversity at PAR sites (Agoramoorthy and Hsu 2005; Awoyemi *et al.* 2012, 2016; Magellan 2019). Although the potential ecological and environmental issues caused by PARs are disconcerting to academics and the general public alike, the potential risk of PAR-related species invasions has never been fully evaluated. Filling this knowledge gap is critical for developing effective anti-invasive species policies and management approaches (Magellan 2019).

Here, we attempted to address this knowledge gap by focusing on PARs in China, the country where such events are most frequently reported (Appendix S1: Figure S1). We used a null model approach to evaluate PAR-related invasion risk by testing whether the spatial overlap between PAR intensity (as a proxy for propagule pressure) and habitat suitability for the establishment of non-native vertebrates (amphibians, reptiles, mammals, birds, and freshwater fishes) is significantly greater than would be expected by chance. We focused on vertebrates because they account for the majority of animals released in PARs (Appendix S1: Figure S1). Furthermore, we conducted field surveys to provide empirical evidence of PAR-related invasions by testing whether non-native fish richness is higher at PAR sites than at non-PAR sites when controlling for covariates and confounders. Finally, we strongly recommend cooperation among scientists, religious groups, and government agencies in efforts to mitigate the adverse effects of PARs.

Methods

Data collection

To gather information about PAR events, we conducted a thorough search of both peer-reviewed and gray literature in the Web of Science and Scopus databases. Using an original application programming interface, we also collected PAR information from publicly available databases, news reports, and other online resources (see Appendix S1: Panel S1 for details). For each PAR event, after eliminating duplicate records, we extracted the following information: animal taxonomic group, number of individual animals, associated financial cost, and locality (Figure 1a; Appendix S1: Figure S1).

Propagule pressure

Propagule pressure is a key determinant of the successful establishment of non-native species, but it is often difficult to ascertain the exact number of individuals involved in introduction events. To overcome this deficiency, proxy variables are commonly used to estimate propagule pressure (Lockwood *et al.* 2009). Given that the exact number of individual animals released during each PAR event was unknown, we estimated propagule pressure via three proxy variables: (i) the frequency of PAR events, (ii) the financial cost of PAR events, and (iii) the spatial density of religious temples. As the frequency and cost of PAR events were available only at the provincial level, we converted these two variables into grid-level data at a resolution of 1 km using the epicenter approach described by Early *et al.* (2016). Additional methodological details, including how the spatial distribution of religious temples (Appendix S1: Figure S2) was derived, are provided in Appendix S1: Panel S1.

Habitat suitability

To quantify the habitat suitability for non-native vertebrate establishment throughout China, we used a species distribution model (SDM): a widely accepted ecological niche-based tool to evaluate the probability of non-native species establishment (Bellard *et al.* 2013). Given that most of the species in PARs are described by common names rather than by scientific names (Liu *et al.* 2013), we constructed SDMs using three nested pools of non-native vertebrate species. The first pool (n = 29 species)—our most conservative approach—consisted of only those vertebrates that were clearly identified to the species level in PAR records. Because religious followers may release vertebrate species that are available for purchase in local markets or pet shops (Liu *et al.* 2013), the second pool (n = 736 species) consisted of all non-native vertebrates in China sold as food items or pets in local markets and online shops, as identified through a comprehensive literature search. The third pool (n = 1722 species) consisted of all non-native vertebrates that have been introduced to China, including Taiwan, Hong Kong, and Macao, which were identified via an intensive online-to-offline data collection effort. We converted the continuous SDM outputs into species presence/absence maps and then evaluated the potential habitat suitability for establishment of non-native species involved in PARs by estimating the predicted richness of non-native species.

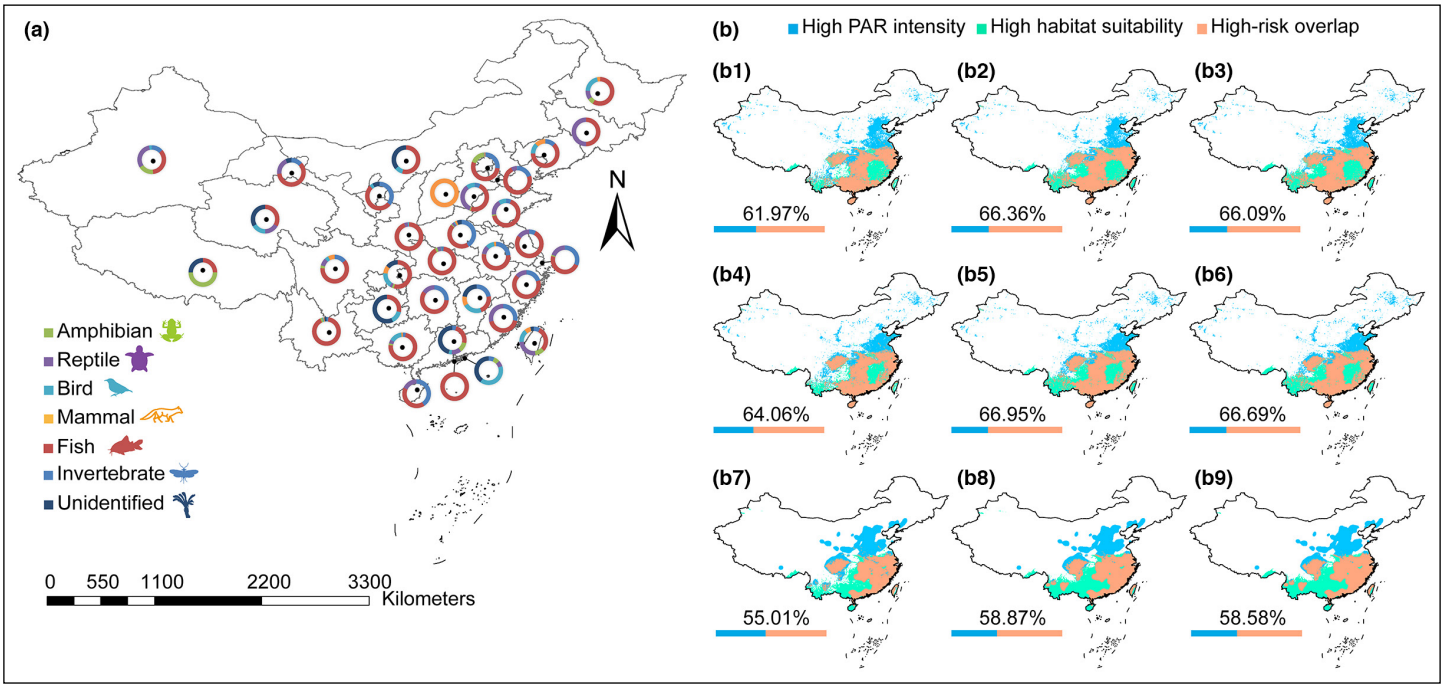

Figure 1. (a) Taxonomic composition of organisms involved in prayer animal release (PAR) in provinces across China and (b) the risk of non-native vertebrate establishment based on analysis of the overlap between the highest (top 20%) PAR intensity (b1–b3: frequency of PAR events; b4–b6: cost of PAR events; b7–b9: religious temple density) and habitat suitability (b1, b4, b7: non-native vertebrates directly identified in PAR events [first pool]; b2, b5, b8: traded non-native vertebrates [second pool]; b3, b6, b9: all non-native vertebrates introduced to China [third pool]). Silhouettes freely obtained from the "islide" plug-in (https://www.islide.cc).

Additional details about SDM construction are provided in Appendix S1: Panel S1.

Spatial overlap between PAR intensity and habitat suitability

We evaluated the degree of spatial overlap between areas with high propagule pressure (based on the three proxies: PAR frequency, PAR cost, and temple density) and habitat suitability (predicted richness of established non-native species using the three pools) across China. Following the approach described by Early *et al.* (2016), we defined areas with high propagule pressure as grids in the top 20th percentile of PAR intensity and defined areas with high habitat suitability as grids in the top 20th percentile of predicted richness of non-native vertebrates. We then assessed the proportion of these grids that overlapped (Figure 1b). We also generated 999 null distributions of both high PAR intensity and high habitat suitability areas, respectively. Then, we applied a Mann-Whitney U test to determine whether the observed spatial overlap between high PAR intensity and high habitat suitability was significantly greater than the null expectation (Appendix S1: Figure S4). To assess the robustness of our findings, we conducted additional analyses based on different thresholds (ie top 10% and 30%) for defining high-risk areas, SDM predictions derived from occurrence data excluding invaded areas of China, and SDM predictions using different presence probability thresholds, as well as separate analyses for each taxonomic group (Appendix S1: Panel S1; Figures S5 and S6).

Field evidence

Given that our literature review showed that fish ranked as the most frequently released taxon in PARs, from July to October for the years 2020 and 2021, we conducted freshwater fish surveys in Guangdong, the province in China in which the most money was spent on PARs. In addition, during the field survey, we also conducted interviews with participants in PARs to determine which non-native fish species were released at nine PAR sites in the trunk (main stem) and tributaries of the Pearl River (Figure 2a). Finally, to assess wild populations of non-native fishes, we conducted fish surveys at the same PAR sites and at nine randomly selected non-release sites in the same river branch with similar hydrologic conditions (see Appendix S1: Panel S1 for details). Considering that the observed difference in non-native fish richness between PAR and non-PAR sites may be influenced by other human activities, we constructed a linear mixed-effects model (LMM) to explore the relationship between the presence of PAR events (independent variable) and the richness of non-native fishes (dependent variable), controlling for the human footprint, which reflects general anthropogenic influences on non-native species invasions. Because there might be similarity in the prevalence of release activities and fish distributions in the same trunk and tributary of the Pearl River, we also included the identity of trunks and tributaries as a random factor to control for potential spatial pseudoreplication.

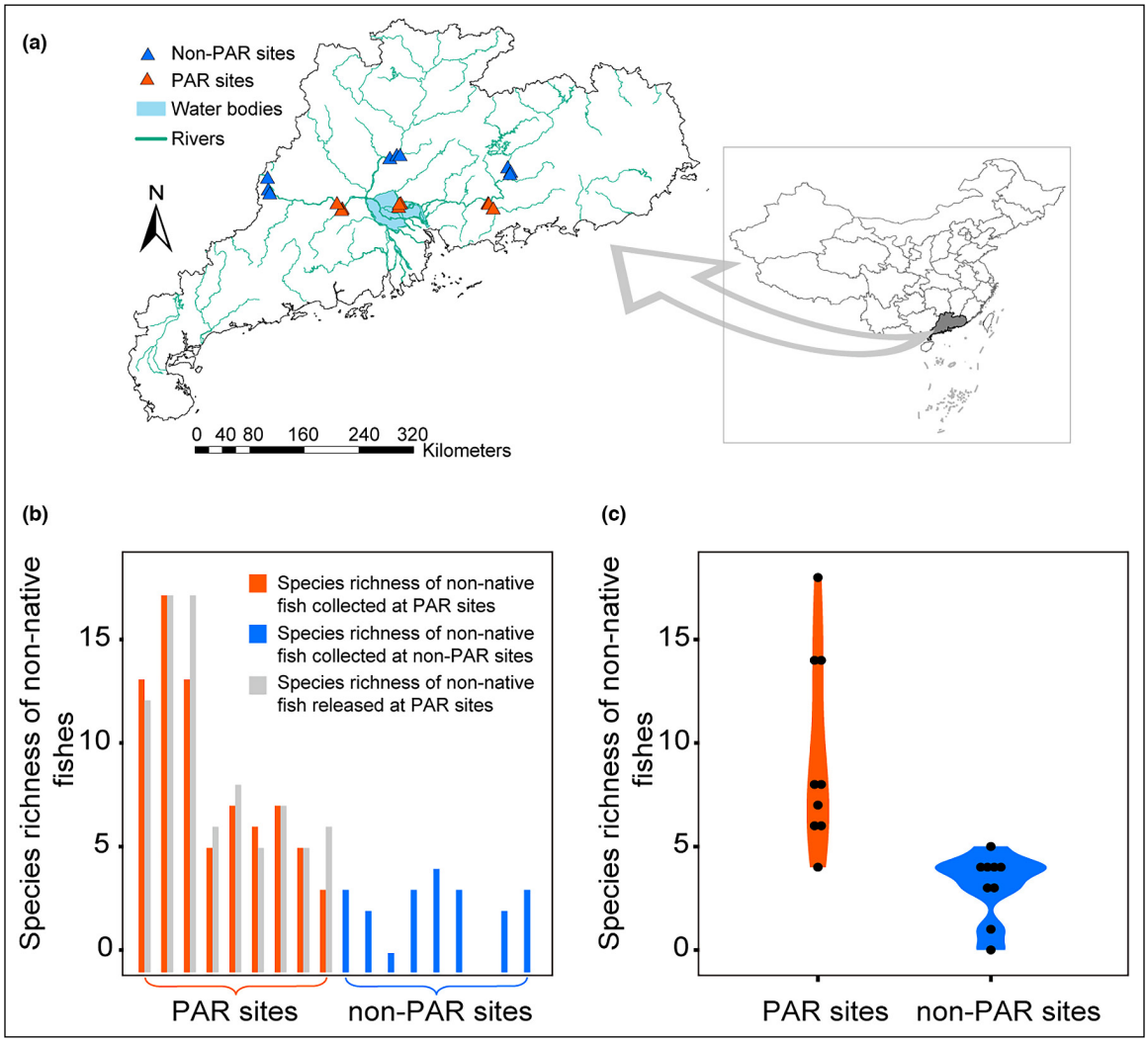

Figure 2. Field surveys of non-native fishes in China's Guangdong province at PAR and non-PAR sites. (a) Red and blue triangles represent PAR and non-PAR sites, respectively. (b) Non-native fish richness at PAR sites (red bars) and non-PAR sites (blue bars); light gray bars indicate the richness of non-native fishes released in PAR activities. (c) Violin plot comparing species richness of non-native fishes at PAR (red) and non-PAR (blue) sites.

Results

We identified at least 9912 PAR events from 1950 to 2021 in 28 countries across all continents except Antarctica (Appendix S1: Figure S1). More than half of the countries in which a PAR event occurred are located in southern and eastern Asia (57%, 16 out of 28), with these countries accounting for 99% (9845 out of 9912) of the global PAR events in our database. We recorded a total of 9730 PAR events across China, most of which were distributed in the southern provinces of Hainan (n = 2010 events), Zhejiang (n = 1500 events), and Shanghai (n = 993 events) (Figure 1a; Appendix S1: Figure S1). The total cost spent on PAR events was approximately ¥152,909,757 (~US$22 million), with the highest amounts spent in the provinces of Guangdong (¥57,905,935 [~US$8 million]), Shanghai (¥33,498,654 [~US$5 million]), and Hainan (¥24,896,199 [~US$4 million]) (Appendix S1: Figure S2). Our search also revealed a total of 38,663 Buddhist and Taoist temples in China, which were primarily distributed in the southern and eastern parts of the country (Appendix S1: Figure S2).

From more than 700 common names provided in PAR records, we identified 29 non-native vertebrate species used in PAR events in China, including one amphibian species, one reptile species, four bird species, and 23 freshwater fish species. Of the 736 non-native vertebrate species available for sale as food items in local markets or as pets in stores, 43 were amphibians, 225 were reptiles, 97 were mammals, 150 were birds, and 221 were freshwater fishes. From 1950 to 2021, a total of 1722 non-native vertebrates were introduced into China, including 94 amphibians, 518 reptiles, 239 mammals, 455 birds, and 416 freshwater fishes. For all SDMs, both measures of predictive power (area under the curve [AUC] and the true skill statistic [TSS]) revealed good model performance (mean ± standard error [SE], AUC: $0.955 \pm 3.51 \times 10^{-5}$, TSS: $0.833 \pm 7.51 \times 10^{-5}$). SDMs across the three non-native species pools consistently predicted that most areas in southern China exhibited high habitat suitability for non-native vertebrate

establishment, especially the middle–lower reaches of the Yangtze, Pearl, and Yarlung Zangbo rivers (Appendix S1: Figure S3).

When defining the top 20% of grids as the high-risk threshold, we determined that approximately 63% (range: 55.01–66.95%) of the areas with high PAR intensity in China were simultaneously suitable for non-native species establishment (Figure 1b): a degree of overlap significantly greater than would be expected by chance (Mann-Whitney U test: $z = -5.17$, $P < 0.001$; Appendix S1: Figure S4). These high establishment risk areas were primarily concentrated in southern and eastern China, including the provinces of Guangdong, Fujian, Zhejiang, Shanghai, Jiangsu, Hunan, Yunnan, and Anhui. We obtained similar results based on (i) different non-native vertebrate pools used to predict habitat suitability, (ii) different variables used to quantify PAR intensity, (iii) different percentiles (10% and 30%) used to define high-risk areas, (iv) different SDM predictions derived from occurrence data across the non-native species' entire ranges or excluding invaded areas of China, and (v) different presence probability thresholds in the SDMs (Figure 1b; Appendix S1: Figure S5). In addition, separate analyses for each of the five vertebrate groups yielded similar spatial patterns (Appendix S1: Figure S6). Some provinces, such as Yunnan, Guizhou, Guangxi, and Jiangxi, were characterized as being highly suitable for non-native vertebrate establishment despite having relatively low PAR-related introduction intensities. In contrast, some administrative units, such as Shandong, Hebei, Tianjin, and Beijing, had high PAR intensities but relatively low risk of non-native establishment.

During field surveys, we observed 24 non-native fish species released at PAR sites, with the majority (95.8%, 22 out of 24) having established wild populations (Figure 2b). Indeed, richness of non-native fishes was three times as high at PAR sites (mean ± standard deviation [SD] = 9.4 ± 4.7) than at non-PAR sites (mean ± SD = 3.1 ± 1.6) (Figure 2c). After accounting for the human footprint associated with each sampling site (LMM analyses: estimate = 0.108, $P = 0.107$), there was still significant correlation between PAR events and non-native fish richness (estimate = 2.996, $P = 0.008$), providing further evidence of PAR-induced bioinvasion risk. Species-accumulation curves of freshwater fish richness showed that our sampling effort was adequate to obtain robust results (Appendix S1: Figure S7).

Discussion

High bioinvasion risk associated with PARs in China

To our knowledge, this study provides the first quantitative evaluation of the establishment risk of non-native vertebrates related to PAR activities. Our results showed that the spatial overlap between areas with high PAR-related propagule pressure and areas with high habitat suitability for non-native vertebrate establishment was significantly greater than would be expected by chance, indicating an overall high risk of establishment after the release of non-native vertebrates during these rituals. The results of sensitivity analyses based on different proxies for propagule pressure and habitat suitability produced similar results, demonstrating the robustness of our findings to data uncertainties.

We detected a strong relationship between the introduction and subsequent establishment of non-native species via PAR in China. One potential explanation is that the three surrogates of PAR intensity (PAR frequency, PAR cost, and temple density) are higher in southern China, where there are also large expanses of suitable habitat for the establishment of non-native vertebrates. Moreover, previous studies have reported that PARs commonly occur in remote areas far from human disturbance, because religious followers often believe that natural sites are more beneficial to the released animals (Wasserman *et al.* 2019; Campbell *et al.* 2021). Our study therefore could serve as a decision tool, with a detailed map of areas and a list of non-native vertebrates with high PAR-related invasion risk, which could help inform management strategies to mitigate and minimize further introductions of invasive species through the PAR pathway (Magellan 2019).

Our field surveys provided additional support for the modeling results, as established non-native species were more common around PAR sites than non-PAR sites, a finding consistent with the results of a previous study demonstrating that the establishment of the American bullfrog in Yunnan province was positively related to the frequency of release events (Liu *et al.* 2012). The field data also align with previous speculation that PAR events were likely a major factor in the establishment of several non-native fish species in lakes and rivers in Guangdong province, including mrigal carp (*Cirrhinus mrigala*), redbelly tilapia (*Coptodon zillii*), and Nile tilapia (*Oreochromis niloticus*) (Wei *et al.* 2019).

Related management in China

In light of the widespread nature of PAR events and the associated risk of biological invasions, scientists and conservation organizations (including SCB) have proposed a series of recommendations for reducing risks associated with PARs. These recommendations include: increasing ecological and environmental education targeted at particular religious groups (such as Buddhist and Taoist groups, which are more likely to conduct PARs than others), religious followers, and the public; promoting enforcement of existing laws and regulations; providing practical alternatives to PAR activities; and monitoring PAR sites (Awoyemi *et al.* 2016; Magellan 2019). Putting these recommendations into practice will require effective and dedicated collaboration among scientists, religious groups, and government agencies (Figure 3).

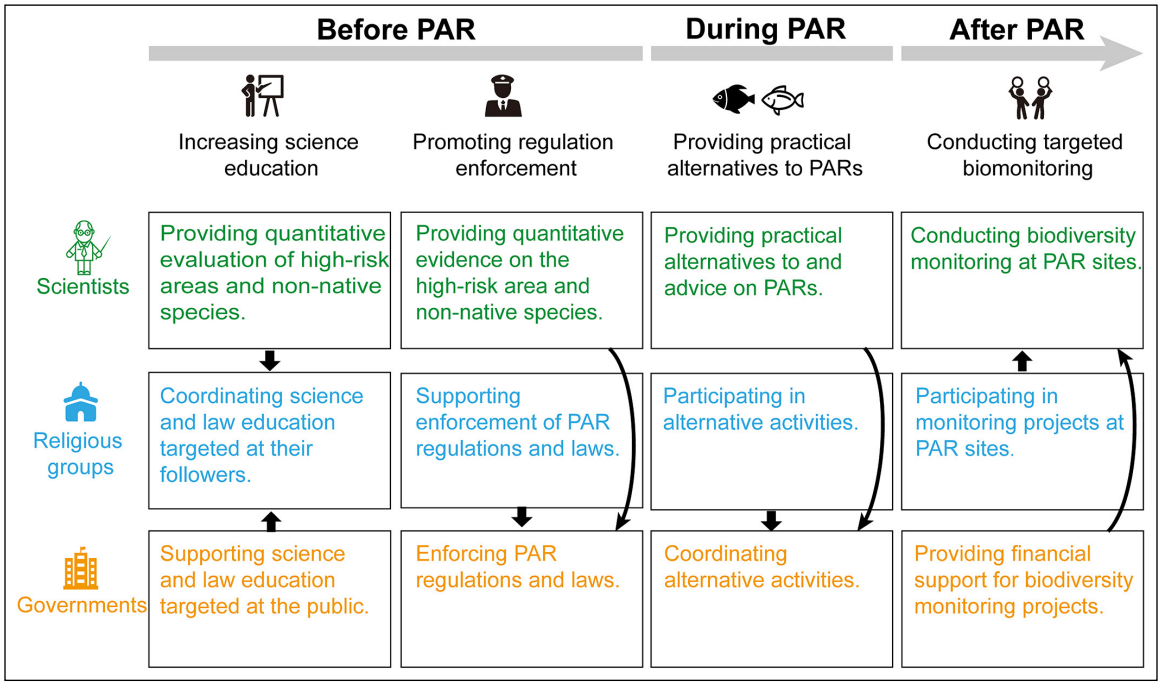

Figure 3. Illustration of a representative collaborative framework among scientists, religious groups, and government agencies aimed at mitigating the adverse effects of PAR-related biological invasions on native species and ecological systems. Silhouettes freely obtained from the "islide" plug-in (https://www.islide.cc).

We suggest that multilateral cooperation should focus initially on developing and enforcing anti-invasive species policies and educating religious groups that conduct PAR activities. Areas with a high risk of non-native species introduction and establishment (orange areas in Figure 1b) should be considered core regions where PAR events are prohibited and where science education on the adverse effects of invasive species is strengthened; for instance, educational materials about the negative impacts of invasive species can be distributed at PAR sites. Consistent with previous work (Severinghaus and Chi 1999), our analysis found that the majority of PARs in China are not organized by temples but instead are conducted by individual followers (97.5%, 9489 out of 9730), indicating that there may be an opportunity for religious leaders to use their influence within communities to help prevent the release of non-native species. Indeed, respected eminent monks and religious groups in China have begun to instruct followers to reduce PAR-caused biological invasions. For example, the China Taoist Association proposed two long-term ecological and environmental protection plans, and explicitly called on followers to be rational and respectful of science, and avoid releasing non-native species.

Local governments in China have also realized the risks of PARs, and have issued notices and regulations explicitly prohibiting the release of non-native species during PAR events (Appendix S1: Panel S1). At the federal level, the Biosecurity Law of the People's Republic of China, enacted on April 15, 2021, emphasized that "No entity or individual may introduce, release, or discard any alien species without approval". In addition, the Amendment of Criminal Law of the People's Republic of China, enacted on March 1, 2021, also noted the illegality of introducing, releasing, or discarding non-native species.

We encourage scientists, conservation organizations, and government agencies to work together to provide religious groups with practical advice on PAR alternatives (Awoyemi *et al.* 2016), such as supplying a list of native species that can be used in ceremonies. For example, under the guidance of scientific organizations and through coordination with the local government, a large PAR ceremony took place in the Mentougou District of Beijing in March 2015, during which religious followers released thousands of native fish into the Yongding River. Likewise, as part of a PAR ceremony organized in June 2018 by the Wenshu Temple in Sichuan, ~50,000 native fish were released into a tributary of the Yangtze River.

We also call for a greater degree of biodiversity monitoring at PAR sites, a recommendation on which the Chinese Government has already begun to act. For instance, in 2022, the Chinese Ministry of Agriculture and Rural Affairs initiated a nationwide survey of non-native species. Targeted biomonitoring at hotspots for both PARs and non-native species should improve the efficiency of these efforts. If non-native species are found, immediate steps to eradicate these populations should be implemented. In addition, areas that are predicted to have relatively low habitat suitability but high propagule pressure (blue areas in Figure 1b) should also be monitored because wild populations can establish in

suboptimal habitats when propagule pressure is high (Leibold *et al.* 2004). Moreover, areas with high habitat suitability but few PARs (green areas in Figure 1b) should not be overlooked because even releases of small numbers of non-native species may lead to a high establishment probability in suitable habitats (Pyšek *et al.* 2010).

Although religious groups are a primary driver of PAR activities, which greatly contribute to the spread and establishment of non-native species in China, these groups have also been broadly recognized as supporters of global biodiversity conservation (Mcleod and Palmer 2015). Given that scientific groups, religious communities, and government agencies all share a common interest in environmental protection, we believe that cooperation among these entities will provide a unique opportunity to effectively manage PARs and reduce the spread of non-native species.

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Data Availability Statement

All data have been uploaded to the Science Data Bank (www.scidb.cn). Detailed information concerning data collection for PAR events (WebData 01) is available at: www.scidb.cn/en/detail?dataSetId=58a1ea6a89b54df29690d2fc63c34aec (doi.org/10.57760/sciencedb.07041). The database of non-native vertebrates in China (WebData 02) is available at: www.scidb.cn/en/detail?dataSetId=42fc9cc36ffe42b7a3bec215db77ed79 (doi.org/10.57760/sciencedb.07042). Data on non-native fishes recorded at PAR and non-PAR sites in Guangdong province (WebData 03) are available at: www.scidb.cn/en/detail?dataSetId=4e6401d133a5400896ed2963f1f70062 (doi.org/10.57760/sciencedb.07043).

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