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United States amphibian imports pose a disease risk to salamanders despite Lacey Act regulations

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Batrachochytrium salamandrivorans (*Bsal*), one of two fungal pathogens that cause the deadly amphibian disease chytridiomycosis, is a major impending threat to salamander biodiversity in North America, where it is not yet known to occur. In the United States, a 2016 wildlife trade policy restricted trade in 20 salamander genera in attempts to prevent *Bsal* introduction. However, little comprehensive data is available to evaluate the impact of this policy action. Here we collate a dataset of United States amphibian imports from 1999 to 2021 using Law Enforcement Management Information System (LEMIS) data and show that reported legal trade in the targeted taxa was effectively reduced by the ban. Unfortunately, amphibian trade into the United States continues to risk *Bsal* introduction given that other species and genera now known to carry *Bsal* are still traded in large quantities (millions of live individuals annually). Additional policy responses focused on *Bsal* carrier taxa, especially frogs in the genus *Rana*, could help mitigate the impact of *Bsal* on North American salamanders.

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The emerging infectious disease chytridiomycosis has devastated amphibian populations globally[1]. The disease is caused by two closely-related fungal pathogens, *Batrachochytrium dendrobatidis* (*Bd*) and *Batrachochytrium salamandrivorans* (*Bsal*). First described in 1998[2], *Bd* has been implicated in the decline of hundreds of amphibian species, including the presumed extinction of over 90[3,4] (but see debate regarding the true extent of disease-driven declines[5]). *Bd* has a broad host range and is capable of infecting members of all three amphibian orders[6], but population-level impacts of *Bd* outbreaks have been mostly concentrated in frogs (order Anura)[3,4]. By contrast, *Bsal*, which was only recognized as a distinct species in 2013[7], has caused declines in western European salamander populations. Notably, the fire salamander (*Salamandra salamandra*) has experienced mass die-offs and local extirpations from *Bsal*[4,7,8]. While *Bsal* was historically understood to exclusively infect salamanders (order Caudata)[9], we now know it is also capable of infecting anurans, suggesting that frogs could act as important vectors of the fungus[8,10,11]. *Bsal* is thought to be endemic to Asia, and while some Asian amphibians may therefore act as aclinical *Bsal* reservoir hosts due to long-term coexistence with the pathogen[9], movement of *Bsal* into novel geographic regions is expected to expose largely naïve amphibian populations that could become imperiled by disease.

The global wildlife trade is a primary mechanism for the international spread of *Batrachochytrium* species[9,12–16]. *Bd* has been detected on amphibians in diverse trade endpoints, including pet stores, food markets, and scientific/zoological institutions, reflecting high demand for frogs in these settings[13,17,18]. Similarly, the international trade in salamanders sourced from Asia has been implicated as an important pathway for *Bsal* spread[9], and *Bsal* has been detected on animals in pet stores and captive collections in Europe[9,10,19,20]. *Bsal*'s high virulence and broad host range suggest there may be serious impacts on salamanders globally should it continue to spread via wildlife trade on a scale similar to *Bd*[9,21–23].

Amphibian conservationists have been particularly worried about the consequences of *Bsal* introduction to the United States given the country's salamander biodiversity. The United States hosts nearly 30% of all salamander species globally[21], and prospective laboratory studies on native amphibians indicate that numerous species are susceptible to lethal *Bsal* infection[24–26]. In light of its large pool of *Bsal*-susceptible salamander species, the robust amphibian trade into the United States raises serious concerns. The live amphibian trade into the country numbers in the millions of individuals annually[13,27,28], and an analysis focused specifically on potential *Bsal* carrier species estimated that ~750,000 of these individuals entered the United States in the five-year period between 2010 and 2014[21].

Thankfully, there has been policy action in the United States aimed at mitigating the threat of *Bsal* introduction. In 2016, the United States Fish and Wildlife Service (USFWS) published an interim rule listing 201 salamander species from 20 genera under the Lacey Act as injurious wildlife, effectively prohibiting their importation into the United States[29]. Ostensibly, this policy has been a success: in the years since the Lacey Act intervention, survey efforts have not detected *Bsal* in captive[30] or wild amphibians[31,32] in the United States. However, this encouraging news is tempered by the fact that numerous amphibians not considered in the interim rule have since been found to be capable of hosting *Bsal*, including notable anuran genera such as *Alytes*, *Bombina, Hyla*, and *Rana*[8,10,26,33]. As a consequence, the importation of potential *Bsal* carrier species into the United States likely continues, with little published data quantifying changes in the amphibian trade following the 2016 Lacey Act interim rule.

Here we collate and clean a comprehensive dataset spanning two decades of amphibian imports into the United States to evaluate trends in amphibian trade, with a focus on species potentially driving the global spread of *Bsal*. More specifically, this multi-decade dataset allows us to address multiple questions of conservation interest: (1) How has the overall magnitude of amphibian imports into the United States changed over time? (2) From which countries do United States amphibian imports originate, and are these countries known to have *Bsal*? (3) Which United States ports do amphibian imports flow into? (4) Did the 2016 Lacey Act interim rule effectively restrict trade in the listed species? (5) What is the magnitude of trade in species and genera not currently listed as injurious in the United States that may nevertheless serve as *Bsal* carriers? Collectively, our results demonstrate how the global amphibian trade continues to generate opportunities for *Bsal* invasion into the United States.

Results

General trends in live amphibian imports into the United States. From 1999 to 2021, the live amphibian trade into the United States totaled 85.82 million individuals, an average of 3.73 million individuals annually (Fig. 1). 31.28 million of these live amphibian individuals (36.4%) were declared as originating from the wild. Despite the fact that the live amphibian trade has declined during this timeframe (Poisson GLM $\beta = -0.039$, $SE = 0.00002$), in the post-Lacey Act period (i.e., 2016–2021) there were still, on average, 2.85 million live amphibians imported annually (Fig. 1). The trade in live amphibians is accompanied by a robust trade in amphibian legs and meat: our dataset indicates 2.76 million kg of amphibian legs/meat entered the United States annually from 1999 to 2021. Over 90% of the total amphibian leg and meat trade in this time period (58.17 million kg) derived solely from one species, the American bullfrog (*Rana catesbeiana*).

The live amphibian trade into the United States is dominated by members of the order Anura. Anurans represented >80% of the live imported amphibians in every year studied, rising to >99% of individuals in the post-Lacey Act period (Fig. 1).

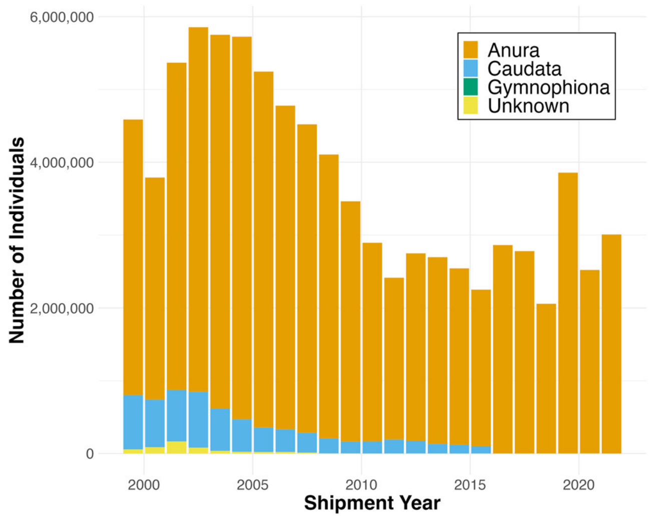

Fig. 1 Live amphibian imports to the United States from 1999–2021 by taxonomic order. This figure shows only LEMIS import data for live amphibian shipments that were recorded in terms of numbers of individuals. Colors indicate the amphibian taxonomic order, and the ordering of categories within each stacked bar corresponds to ordering in the legend. Note that caecilians (order Gymnophiona) represent an extremely small portion (<1%) of live amphibian imports annually.

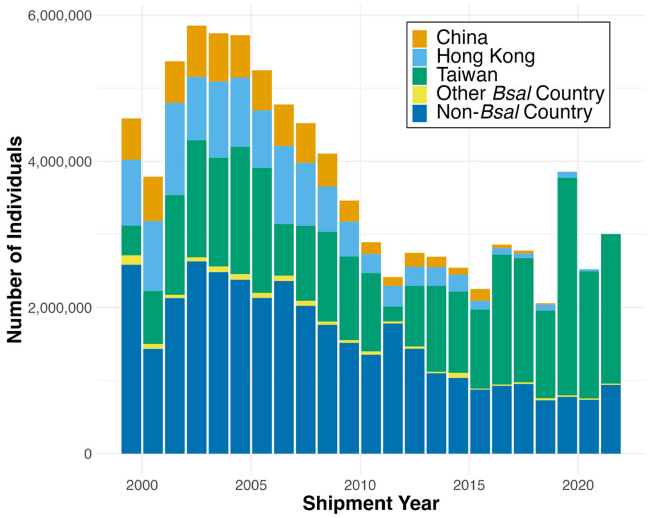

Fig. 2 Live amphibian imports to the United States from 1999–2021 by country of origin. This figure shows only LEMIS import data for live amphibian shipments that were recorded in terms of numbers of individuals. Colors indicate the country of origin, and the ordering of categories within each stacked bar corresponds to ordering in the legend. We specifically highlight the 10 countries that are known to host wild, *Bsal*-positive amphibians, but, for simplicity of presentation, seven of these countries (Belgium, Germany, Japan, The Netherlands, Spain, Thailand, and Vietnam) have been combined into an "Other *Bsal* Country" category.

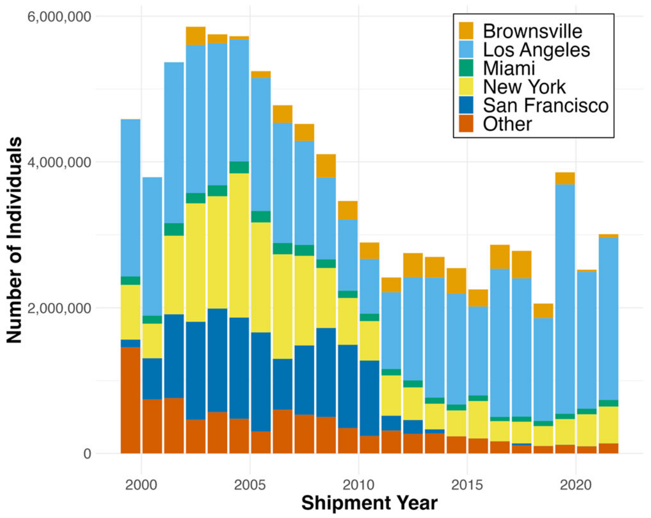

Fig. 3 Live amphibian imports to the United States from 1999–2021 by port of entry. This figure shows only LEMIS import data for live amphibian shipments that were recorded in terms of numbers of individuals. Colors indicate the United States port of entry, highlighting the five most common ports of entry for live amphibians, and the ordering of categories within each stacked bar corresponds to ordering in the legend.

Caudates always represented <20% of individuals imported annually, with this number dropping to <1% in the years from 2016 to 2021 (Fig. 1). Members of Gymnophiona represented <1% of live amphibian individuals traded in every year studied (Fig. 1).

Amphibians imported to the United States were primarily exported from countries in Asia and Latin America. Nearly one-half (48.5%) of all live amphibians imported to the United States from 1999 to 2021 originated from just two Asian exporters: Taiwan (30.04 million individuals; 35.0%) and Hong Kong (11.57 million individuals; 13.5%). Ecuador, Singapore, and China round out the top five amphibian exporters to the United States during this time period. Further, >50% of all live amphibian individuals imported annually into the United States originated from countries that are known to host wild amphibians infected with *Bsal*, with the exception of the years 1999, 2011, and 2012 (Fig. 2). In 2016 and all subsequent years, >64% of all live imported amphibian individuals have originated from *Bsal*-positive countries (Fig. 2). Taiwan, a *Bsal*-positive country, emerges as a particularly important amphibian exporter to the United States: in the post-Lacey Act period, Taiwan is the point of origin for >58% of live amphibians imported each year (Fig. 2). We further note that if we consider all wildlife imports to the United States from 2000 to 2014 (using the full Eskew et al.[34,35] dataset), Taiwan is only responsible for the export of ~4.3% of live individuals. Thus, Taiwan appears to play a disproportionate role in the amphibian trade specifically.

Although live amphibians imported to the United States flow into over 40 unique ports of entry, the majority concentrate in relatively few major ports nationwide. From 1999 to 2021, the top five United States ports of entry for live amphibians have been Los Angeles (39.11 million individuals; 45.6%), New York (17.97 million individuals; 20.9%), San Francisco (12.88 million individuals; 15.0%), Brownsville (4.34 million individuals; 5.1%), and Miami (2.51 million individuals; 2.9%). Since the year 2000, these five ports alone have accounted for >80% of all live amphibians imported annually into the United States (Fig. 3). In the post-Lacey Act period, Los Angeles has been the port of entry for >68% of all live amphibians imported annually (Fig. 3). These amphibian import patterns largely mirror the wildlife trade more generally. Over the 2000 to 2014 period for which we have comprehensive data on the overall wildlife trade[34,35], Los Angeles was the port of entry for nearly 50% of live individuals, while New York and Miami accounted for ~14% and ~13% of individuals, respectively.

Impact of the Lacey Act interim rule on amphibian imports. Of the 20 caudate genera listed under the 2016 Lacey Act interim rule, 17 were shipped live into the United States at some point during the study period (Fig. 4a). Import of these genera averaged 255,011 live individuals per year, and there was a decrease in trade over time even before the Lacey Act interim rule was announced (Poisson GLM $\beta = -0.167$, $SE = 0.0001$; model estimated decrease of 40,890 individuals per year on average). However, the implementation of the interim rule clearly coincided with a decrease in the trade of listed genera. In 2016, the year in which the Lacey Act interim rule was implemented, only 1058 individuals from these genera were imported, and in the 2017–2021 time period <200 individuals were imported annually (Fig. 4b). Moreover, the metadata regarding these recent shipments indicates that the vast majority were treated as expected given the Lacey Act interim rule: the only shipments containing Lacey Act genera that were actually cleared for entry to the United States from 2017 to 2021 (as opposed to refused) were declared as being traded for scientific purposes with the exception of a single *Cynops pyrrhogaster* individual that was traded for "personal" purposes and was reported as cleared for entry in 2017.

A formal impact evaluation analysis also indicated that the Lacey Act interim rule depressed the trade of listed species. While this model detected a trend of decreasing trade volume over time during the pre-intervention period (1999–2015; Poisson GLM $\beta = -0.136$, $SE = 0.0001$), there was nevertheless an immediate decrease in trade volume attributable to the

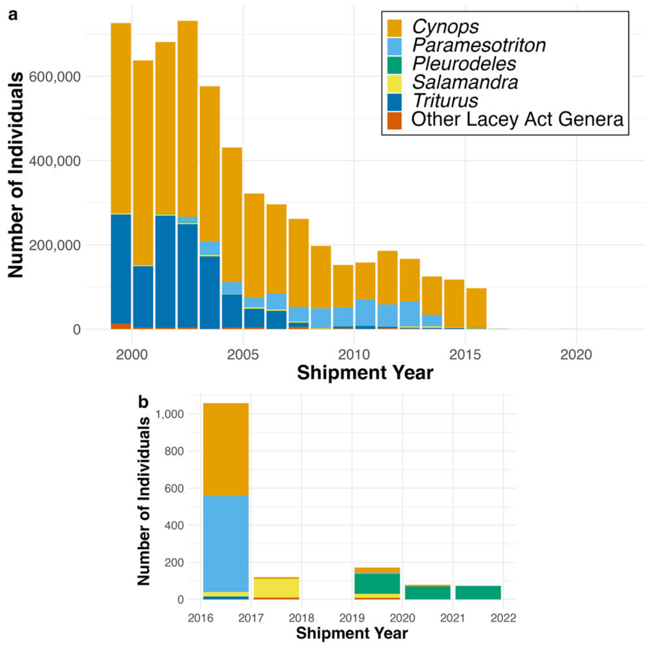

Fig. 4 Live amphibian imports to the United States from 1999–2021 of genera listed under the 2016 Lacey Act interim rule. This figure shows only LEMIS import data for live amphibian shipments that were recorded in terms of numbers of individuals. Data are shown for both (**a**) the full 1999–2021 timeline and (**b**) the 2016–2021 period corresponding to the year of the Lacey Act interim rule and subsequent years (note difference in *y*-axis scales). Colors indicate the amphibian genera, and the ordering of categories within each stacked bar corresponds to ordering in the legend.

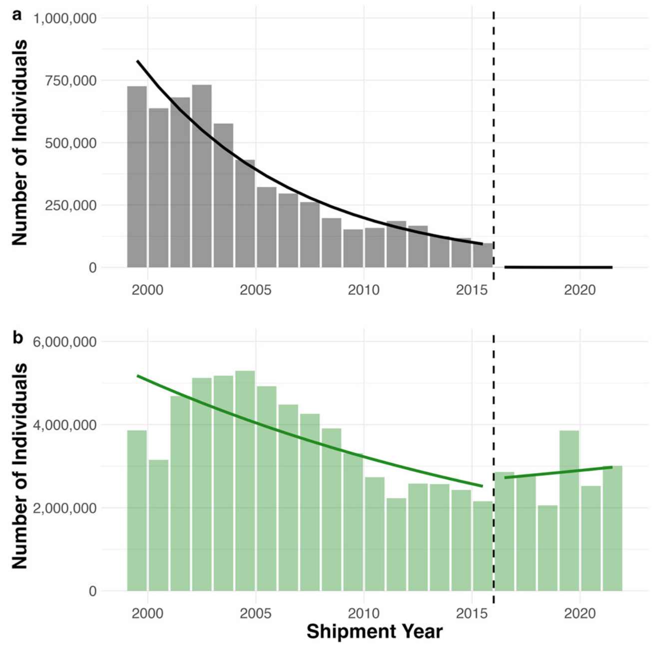

Fig. 5 Impact evaluation analysis applied to live amphibian imports to the United States from 1999–2021. This figure and analysis only considered LEMIS import data for live amphibian shipments that were recorded in terms of numbers of individuals. For impact evaluation modeling, data were split into (**a**) genera listed by the 2016 Lacey Act interim rule and (**b**) non-listed amphibian taxa (note difference in *y*-axis scales). Underlying data in (**a**) is identical to Fig. 4a. The vertical dashed line represents the timing of the focal intervention (the Lacey Act interim rule). Solid lines represent model predictions of trade trends before and after the intervention.

intervention (Poisson GLM $\beta = -4.655$, SE $= 0.032$) as well as a further decline in the time trend post-intervention (Poisson GLM $\beta = -0.577$, SE $= 0.022$; Fig. 5a). In contrast to the salamander taxa that were subject to the Lacey Act interim rule, non-listed amphibian species showed an immediate increase in trade volume post-intervention (Poisson GLM $\beta = 0.124$, SE $= 0.001$) as well as an increase in the temporal trend (Poisson GLM $\beta = 0.063$, SE $= 0.0001$) such that the model projected increasing trade volumes over time in the post-intervention period for these species (Fig. 5b).

Imports of *Bsal* carrier species and genera. Our review of the literature identified 91 *Bsal* carrier species spanning 44 genera and two amphibian orders (Anura and Caudata; Supplementary Data 1). We found a modest trade in these specific species in the post-Lacey Act period. Throughout the 1999 to 2021 time period, 30 known *Bsal* carrier species have been imported to the United States, but the data indicate that <600 live individuals of these species have been traded annually since 2016 (<150 live individuals annually from 2017 to 2021; Fig. 6). However, examination of live trade in the genera that are known to carry *Bsal* paints a vastly different picture. Imports of these genera have averaged 2.43 million live individuals annually in the post-Lacey Act period (Fig. 7a). Put differently, >80% of the United States' live amphibian imports annually from 2016 to 2021 (represented in full in Fig. 1) derives from amphibian genera that have members known to host *Bsal*. This trade is dominated by the genus *Rana*, which represents >96% of the live trade in known *Bsal* carrier genera every year from 2016 to 2021 (Fig. 7a). The only other genus to represent >1% of annual *Bsal* carrier genera trade over this time period was the genus *Bombina* in the years 2016–2018 (Fig. 7a). In the post-Lacey Act period, over 70% of these individuals annually have their point of origin in Taiwan (Fig. 7b), and over 70% annually are imported to the United States via the port of Los Angeles (Fig. 7c).

Discussion

We collated and analyzed what is, to our knowledge, the longest comprehensive dataset of amphibian trade flows into the United States, and we evaluated this trade with respect to the potential for introduction of the amphibian pathogen *Bsal*. Our results show that while conservation policy has effectively reduced the legal trade in some known *Bsal* carrier species, other potential *Bsal* carrier taxa are still imported in large numbers, representing a continued threat to salamanders in the United States and North America more broadly[21–23,36]. These specific, conservation-relevant findings are embedded within the broader context of the overall United States amphibian trade that our dataset documents, and having this curated resource openly available will facilitate future amphibian trade research.

Our analyses illustrate that the live amphibian trade into the United States is substantial and largely composed of anurans. Despite there being a negative trend in the number of live amphibians entering the United States between 1999 and 2021, the most recent six years of data indicate that nearly three million live amphibians still enter the country annually, the vast majority (>99%) being anurans. These results align with other work suggesting the relative dominance of the anuran trade both in the United States and globally[36,37]. The prevalence of anurans in the amphibian trade along with their potential to carry *Bsal* requires us to reconsider the true magnitude of *Bsal* importation risk to the United States, as we discuss in more detail below.

The trade data also reveal that relatively few ports of entry concentrate amphibian flows entering the United States, an

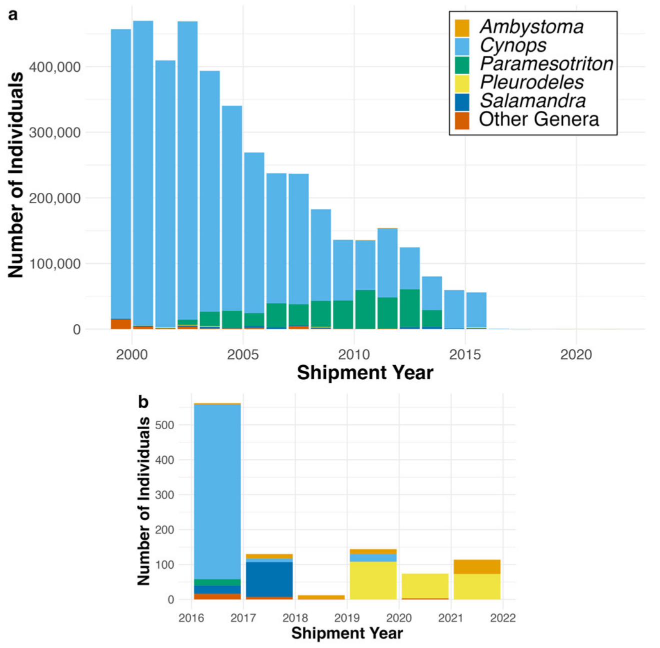

Fig. 6 Live amphibian imports to the United States from 1999–2021 of known *Bsal* carrier species. This figure shows only LEMIS import data for live amphibian shipments that were recorded in terms of numbers of individuals. The LEMIS data were filtered to only those species we recorded as known *Bsal* carriers ($n = 30$ species in the LEMIS dataset). Data are shown for both (**a**) the full 1999–2021 timeline and (**b**) the 2016–2021 period corresponding to the year of the Lacey Act interim rule and subsequent years (note difference in *y*-axis scales). For visual simplicity, colors indicate the amphibian genera to which these species belong, and the ordering of categories within each stacked bar corresponds to ordering in the legend.

observation that could help guide effective allocation of disease surveillance and biosecurity effort[38]. In particular, Los Angeles and New York represent the two most common ports for live amphibians to enter the United States in the post-Lacey Act period. As others have emphasized[21], Los Angeles is especially important as a potential entry point for *Bsal* to the United States: the majority of live individuals belonging to *Bsal* carrier genera that entered the country in the post-Lacey Act period did so through this port. Los Angeles County also has a large number of pet-related businesses that could act as dispersal hubs, distributing infected animals across the landscape[22,38].

In addition, the data provide information on the country of origin of amphibian imports to the United States. Other work has suggested that United States amphibian imports are becoming increasingly spatially consolidated, with imported animals coming from fewer exporting countries over time[38]. Our data are consistent with this observation given that a single exporting country, Taiwan, has sourced the majority of live amphibian imports each year since 2016. This finding is particularly troubling given that wild Taiwanese amphibians are known to be infected with *Bsal*[39]. However, interpretation of these import patterns requires some caution given that the country of origin listed in the LEMIS wildlife trade data we analyze may, in some cases, erroneously report a country of re-export rather than the shipment's true country of origin[38]. Nonetheless, like information on common ports of entry, the best available data on country of origin for amphibian imports could be used to prioritize disease surveillance efforts by allowing investigators to target imported amphibian shipments from high-risk *Bsal* areas for pathogen screening. Alternatively, there may be opportunities for productive bilateral cooperation on more comprehensive programs that screen amphibians for *Bsal* at both the country of export and the United States port of entry.

A primary aim of our analyses was to evaluate the impact of the 2016 Lacey Act interim rule on trade in the species listed therein. We found that the Lacey Act action appears to have been highly effective in reducing legal trade in the targeted species[36]. Since 2016, the data suggest that only a few hundred of these individuals have entered the country in total, nearly all intended for scientific purposes. Given the frequent failure of the conservation community in translating scientific understanding to real-world solutions[40], the 2016 Lacey Act interim rule should be commended as a tangible conservation success. The interim rule was implemented quickly relative to the discovery of *Bsal*[28], and the scope of the action was far-reaching, given information available at the time. The apparent efficacy of the Lacey Act interim rule is tempered by a few caveats, however. First, it is challenging to establish a causal link between the interim rule's implementation and trade declines in listed species. While we argue it is reasonable to attribute the trade reduction in listed species to the interim rule's enforcement, especially given that trade volume in non-listed amphibians actually increased following the rule (Fig. 5b), it is possible that trade in listed species was influenced by other confounding factors we do not account for. Second, in other wildlife trade contexts, shipment declarations and trade data sources may contain purposeful misreporting that conceals the true geographic origin, source (i.e., captive-bred vs. wild-caught), or even species of the shipment in question[28,41–44], perhaps especially when such misreporting helps the shipment to evade trade controls. As such, there is no way to guarantee that injurious species listed in the interim rule have not been imported by declaring fraudulent taxonomic information. Third, our data does not account for the potential illegal, undocumented trade in Lacey Act listed species. The illegal wildlife trade is inherently difficult to characterize[45,46], but it remains a possible avenue for *Bsal* introduction to the United States despite the apparent success of Lacey Act enforcement. In fact, we might expect illegal trade frequency to increase for listed *Bsal* carrier species given that trade regulations (such as trade bans) can inflate prices and drive trade underground in cases where consumer demand remains high[47].

Setting aside potential problems with comprehensive enforcement of the 2016 Lacey Act interim rule, the most obvious issue with the current regulation is simply that the rule was written with incomplete information on *Bsal* host range. As a result, import of potentially injurious taxa to the United States continues. Of particular concern is continued trade of seven anuran genera now known to carry *Bsal*: *Alytes*, *Anaxyrus*, *Bombina*, *Hyla*, *Osteopilus*, *Rana*, and *Scaphiopus* (Supplementary Data 1). While previous analyses have highlighted the potential *Bsal* introduction risk associated with *Bombina*, a *Bsal* carrier genus popular in the pet trade and native to Eurasia[16,36], they have not fully addressed issues related to the genus *Rana*. The American bullfrog (*R. catesbeiana)* is one of the most heavily-traded species within the genus as it is farmed for the food trade in countries throughout North America, South America, and Asia[48], and the species is thought to have played a major role in the global spread of *Bd*[13–15,49,50]. Preliminary data indicates the American bullfrog may be resistant to *Bsal*[26], but other members of *Rana* appear to be capable of carrying the pathogen in laboratory[26] and field settings[33] (although we note that others have interpreted some of these findings with caution[36]). In sum, the current evidence base, which has been generated by independent research groups, suggests that at least some members of *Rana* are susceptible to *Bsal*, and further investigations are urgently needed to more comprehensively assess the *Bsal* carrier status of various *Rana* species,

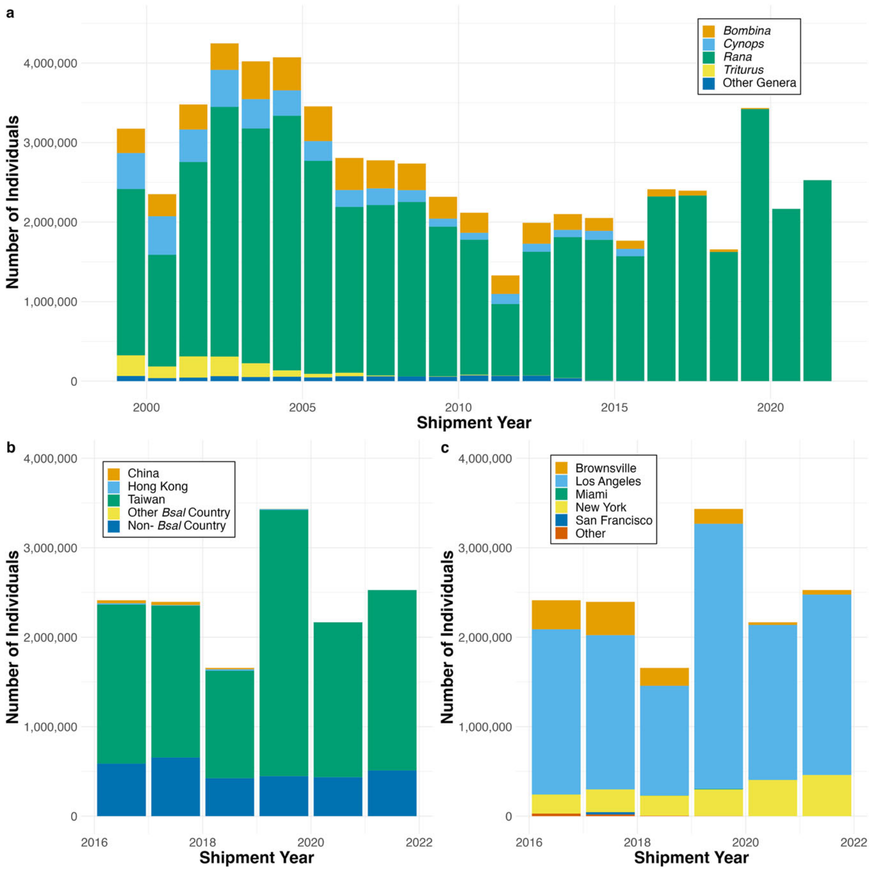

Fig. 7 Live amphibian imports to the United States from 1999–2021 of known *Bsal* carrier genera. This figure shows only LEMIS import data for live amphibian shipments that were recorded in terms of numbers of individuals. The LEMIS data were filtered to only those genera we recorded as containing known *Bsal* carrier species ($n = 33$ genera in the LEMIS dataset). In (**a**) the full 1999–2021 timeline is shown. Colors in (**a**) indicate the amphibian genera, and the ordering of categories within each stacked bar corresponds to ordering in the legend. Panels (**b**) and (**c**) depict the 2016–2021 period corresponding to the year of and years following the Lacey Act interim rule (note difference in *y*-axis scales), with (**b**) highlighting the country of origin for *Bsal* carrier genera and (**c**) highlighting the United States port of entry for *Bsal* carrier genera.

including the American bullfrog. If any *Rana* species commonly harbor *Bsal* this would be a critical concern for the amphibian conservation community given the broad distribution of many of these frogs and their popularity in the wildlife trade.

A multi-pronged approach is necessary to help mitigate the threat of *Bsal* introduction to and spread within the United States. First, although large-scale surveillance efforts have thus far failed to detect *Bsal* in captive or wild amphibians in the United States[30–32], ongoing disease surveillance in multiple settings (i.e., in the field and along multiple nodes of the amphibian trade network) is imperative to ensure early detection and potential control of the pathogen is possible[23,36]. Despite the considerable logistical, economic, and political challenges, there is actually broad public support for biosecurity measures aimed at reducing wildlife disease risks within the herpetological trade[51], and in the case of fungal pathogens of plants, border biosecurity has proven effective at slowing the rate of novel pathogen arrival[52]. Hence, biosecurity in the form of widespread amphibian disease surveillance at ports of entry would boost the likelihood of detecting invasive pathogens like *Bsal* before they are able to spread among native biota[16,28]. Further, this strategy is likely more cost-effective than field surveillance to detect *Bsal* in the wild, and it could be made even more comprehensive if exporting countries also engage in disease testing at the point of origin (although not all exporting nations may have the capacity to do so[29]). Disease surveillance may be most feasible and effective if it is targeted towards known *Bsal* carrier species, and, in the wildlife trade context, if it focuses on major ports for amphibian entry (e.g., Los Angeles) and shipments coming from countries with a robust amphibian trade and known *Bsal* endemism (e.g., Taiwan).

In addition to increased disease surveillance and border biosecurity, amphibians within the United States stand to benefit from further policy responses that could reduce the probability of *Bsal* introduction, given that prevention of introduction is arguably the most effective lever available for reducing ultimate disease impact[23,53,54]. Most obviously, current scientific knowledge regarding *Bsal*'s host range could be used to update the 2016 Lacey Act interim rule[16,36], supporting the intended purpose of that initial listing action. It is now clear that the regulations governing amphibian trade in the United States are based on incomplete information and do not account for the full set of species that should be considered injurious as a consequence of their *Bsal* host status. Any of the *Bsal* carrier species or genera recovered in our literature search are potential candidates for listing. However, the genus *Rana* is arguably of most importance given the substantial volume of trade in that genus, especially if additional *Rana* species are found to be capable of carrying *Bsal*. Stronger trade restrictions might even adopt a precautionary principle regarding amphibian imports to the United States. For example, in the amphibian trade context more generally, where trade itself can lead to overexploitation and species endangerment, there have been calls for whitelisting policies built on the premise that all species should be granted trade protections until it can be demonstrated that their trade is sustainable[37]. Translated to the wildlife disease setting, this might look like a policy that preemptively restricts trade until it can be shown that an amphibian species is unlikely to serve as a host for *Bsal*.

Wildlife trade bans are not without controversy, however, as some argue that such strict measures have the potential to run counter to conservation goals by driving trade in listed species into underground, illegal markets where effective disease monitoring would become even more difficult[48,55]. An alternative approach is to work with stakeholders to encourage the "clean trade" or "healthy trade" of pathogen-free animals without completely regulating away the legal trade in particular amphibian species[11,26,54,56]. For example, healthy trade policies could establish required disease testing and pathogen-free certification programs for amphibians in the pet trade, and despite the additional burden of such monitoring, amphibian business owners and hobbyists might view the benefits of disease-free animals as worth the cost[54,56]. Indeed, initial survey work indicates that businesses involved in the amphibian trade are aware of disease threats to amphibians, are interested in obtaining certified pathogen-free animals, and generally believe that businesses do have a role to play in reducing disease risks within the amphibian trade network[48,56]. While these findings are encouraging, it is also true that few amphibian businesses currently engage in pathogen testing[56], suggesting that additional resources or incentives may be needed to establish the biosecurity practices that would help ensure a healthy amphibian trade. More broadly, it is unlikely that completely voluntary implementation of healthy trade practices would be sufficient to ensure that *Bsal* is not introduced to the United States[29]. Instead, federal or multi-national planning and implementation of such a program, crafted in close collaboration with amphibian business owners and hobbyists, may provide a better safeguard against an amphibian biodiversity crisis in North America[26]. Within the United States, a national healthy trade program would be particularly valuable should gaps remain in the Lacey Act's regulation of trade in amphibian species known to be susceptible to *Bsal*.

Finally, captive animals that are already present in the United States and could possibly harbor *Bsal* represent a specific issue within the healthy trade paradigm that deserves special attention[36]. *Bsal* has been widely detected in amphibian collections in Europe where release of former pets has likely been a pathway for disease spread to wild animals[9,19,20,54], and our data indicate that large numbers of individuals from *Bsal* carrier genera have been imported to the United States from 1999 to 2021 for commercial purposes (suggesting many of these animals likely entered the pet trade). These animals included 5.34 million *Bombina*, 4.03 million *Cynops*, and 1.30 million *Triturus*, and we cannot ignore this stock of captive animals already present in the United States that potentially contains *Bsal*-infected individuals. Unfortunately, the general public is relatively uninformed about wildlife diseases that circulate within the amphibian trade[51], while the state of knowledge among pet owners is unclear. As such, considerable efforts should be made to educate the public and amphibian hobbyists, informing them of pathogen transmission risks and resources available for the safe surrender of unwanted pet amphibians[51]. Further, it is clear that transport of *Bsal*-infected captive amphibians has facilitated *Bsal* invasion of Europe[10]. Interestingly, while the 2016 Lacey Act interim rule initially banned interstate movement of listed species, this restriction was overturned by the United States Court of Appeals for the District of Columbia in a 2017 decision. Amending the Lacey Act to strengthen interstate travel restrictions on listed species could help minimize potential spread of *Bsal* among captive collections in the United States and/or between captive collections and the wild, but such a policy may find opposition among pet retailers, breeders, and owners.

Amphibians are the most threatened vertebrate group, with over one-third of species at risk of extinction due to multiple threats, including habitat destruction, pollution, and infectious disease[57,58]. Lessons learned from the global spread of *Bd* and *Bsal's* invasion of Europe suggest that amphibian conservation in the United States is at a critical juncture. We have the ability to proactively reduce the likelihood of, and simultaneously prepare for, a new amphibian biodiversity crisis in North America driven by disease[21–23,36]. To avert additional devastating impacts on amphibians, it is imperative that further conservation actions are taken to help mitigate the spread of *Bsal* within the United States.

Methods

Compiling and cleaning data on amphibian imports into the United States. To obtain a complete amphibian trade dataset for analysis, we cleaned and combined three smaller datasets that together gave a continuous record of amphibian imports to the United States from 1999 to 2021. All of these primary data sources contain data from the USFWS Law Enforcement Management Information System (LEMIS). LEMIS data have been widely used by researchers interested in various taxa to help understand wildlife trade that flows into or out of the United States[41,59,60], and the dataset has been praised as a model wildlife trade surveillance system given the relative specificity of information contained therein[37]. Historically, however, researchers have obtained LEMIS data through repeated Freedom of Information Act (FOIA) requests, with different groups requesting different information on different taxa over different time periods. Thus, compilation of a complete LEMIS amphibian trade dataset required substantial data collation efforts, as described here. Our first major dataset was a previously published collection of LEMIS data curated by Eskew et al.[34,35] that covers the wildlife trade, broadly considered, from 2000 to 2014. We supplemented this general wildlife trade time series with a specific FOIA request to the USFWS for LEMIS amphibian import data from 2016 to 2021. We requested and received data that largely matched the LEMIS fields and formatting described in Eskew et al.[34]. Finally, we were able to add two missing years of data, 1999 and 2015, to our time series using LEMIS data that the USFWS has recently made publicly available (https://www.fws.gov/library/collections/office-law-enforcement-importexport-data). We combined these three primary data sources by reconciling field names in all datasets to match the Eskew et al. [34,35] data. We also filtered the general wildlife trade datasets to only represent amphibian trade. For the Eskew et al.[34,35] data source, the "taxa" field allows for easy subsetting to rows with "amphibian" values. For the 1999 and 2015 LEMIS data, we used the wildlife category field to recover any rows with "Amp" or "AMP" values, indicating amphibian records. However, some rows in this dataset have no assigned wildlife category, and we didn't want to overlook potential amphibian records simply because they were not labeled as such. Therefore, we used the current amphibian taxonomy available from AmphibiaWeb (https://amphibiaweb.org/taxonomy/AWtaxonomy.html) to recover any records that were missing wildlife category data but where the listed genus matched with a known amphibian genus. During this process, we matched on currently accepted AmphibiaWeb genera and any known generic synonyms. Finally, we cleaned all datasets following the basic protocol outlined in Eskew et al.[34] (e.g., ensured field values matched with valid codes provided by the USFWS). In summary, these data cleaning steps left us with three cleaned amphibian trade datasets containing a consistent set of variables and field values.

After combining our three datasets to obtain a complete time series of amphibian imports from 1999 to 2021, we harmonized the taxonomic information contained within these records. The taxonomic information in LEMIS is subject to data entry errors but may also represent shifts in preferred nomenclature over time[34]. For example, in our full amphibian trade dataset, the American bullfrog initially appeared with the scientific name *Rana catesbeiana*, the misspelling *Rana catesbeinana*, and the synonym *Lithobates catesbeianus*. To conduct the most accurate, complete analyses, we sought to reconcile this sort of competing nomenclature. As such, we cleaned all of the taxonomic names in our dataset, with the AmphibiaWeb taxonomy serving as our reference given that AmphibiaWeb is one of the most widely used resources by amphibian biologists[61]. We first converted known synonyms to the preferred AmphibiaWeb nomenclature, where possible. At that point, comparison of the scientific names in our trade dataset to the AmphibiaWeb taxonomy alerted us to potential instances of taxonomic misspellings, which we manually corrected. Once we synonymized and cleaned all amphibian names, we were then able to add higher-level taxonomic information to the data, namely taxonomic family and order.

To summarize, our collated amphibian trade dataset consisted of 90,641 records representing over 43,000 wildlife shipments from 1999 to 2021[62]. While prior work has sometimes provided longer time series of United States amphibian trade[63], these efforts have relied solely on CITES data which fail to document trade in the many species that are not listed under the CITES Appendices[37,59,60,64]. By contrast, the LEMIS dataset more fully captures trends in United States amphibian imports. As a result of our data cleaning procedures, 74.9% of our import records were assigned complete scientific names recognized by AmphibiaWeb (note that 24.3% of records were only reported to the genus level [i.e., they contain "sp." for the species field] and therefore cannot have complete scientific names). These scientific name matches represented 935 unique amphibian species. Over 94% of records were either originally assigned a generic name or had a cleaned generic name that matched with AmphibiaWeb genera.

Supplementary data collection. Our analyses also required us to gather data on the amphibian species listed under the 2016 Lacey Act interim rule, those more broadly that could serve as potential *Bsal* carriers, and the countries in which *Bsal* is known to exist in wild amphibians. A list of amphibian species and genera regulated under the Lacey Act interim rule was pulled directly from publicly available information from USFWS[29]. To gather data on *Bsal* carrier species (Supplementary Data 1), we conducted a review of the primary literature, building off previous work[36,65]. In reviewing the *Bsal* literature, we noted the amphibian species known to harbor *Bsal* infections, whether or not disease symptoms were also observed in those species, and the context in which the infection was detected (i.e., in a wild, captive, or laboratory-exposed animal). In our analyses, we were maximally conservative and considered a potential *Bsal* carrier species to be any amphibian species with a documented *Bsal* infection, irrespective of disease symptoms. Additionally, during the course of our literature review, we recorded the countries in which *Bsal* was detected in wild amphibians. Here, the status of Hong Kong deserves special note. LEMIS amphibian trade data record Hong Kong as a distinct country of origin despite the fact that Hong Kong is technically a special administrative region of China. Although we are unaware of *Bsal* detections in wild amphibians from Hong Kong specifically, *Bsal* is known from the abutting Chinese province of Guangdong[66]. As such, we consider Hong Kong as *Bsal*-positive for all relevant analyses, but report its trade exports as distinct from that of China generally, which is consistent with the presentation in the LEMIS data. Our decision here is further justified by the fact that Hong Kong is known to be among the most important amphibian exporters to the United States and transports animals infected with *Bd*[38,67]. Thus, lumping Hong Kong together with China could obscure its unique role in the amphibian trade.

Data analyses. For analysis of trends in amphibian trade over time, we focused primarily on trade involving live animals (records coded as "LIV" in the LEMIS "description" field), given these wildlife shipments are arguably the most likely to transport *Bsal* internationally[28,68]. We visualized trends in live amphibian imports over time, highlighting major divisions in the data, including amphibian order, country of origin, and port of entry. In particular, we sought to highlight trade patterns in the post-Lacey Act period from 2016 to 2021 (the Lacey Act interim rule became effective January 28, 2016, but to simplify analyses we treat the entire year as subject to the Lacey Act restrictions). We note that a shipment's path through the international trade network could generate opportunities for *Bsal* exposure and infection outside of the country of origin. However, our dataset indicated that the country of origin was identical to the country of export for the vast majority of live amphibian individuals imported to the United States (97.7%). Because our data suggest there are so few amphibian re-exports, we focused on the country of origin as the most important geographic factor affecting the potential for *Bsal* introduction to the United States. Next, we examined trade in the amphibian taxa included in the Lacey Act interim rule. Here, we chose to analyze trade data at the level of genera rather than species to be conservative: because a relatively large proportion of LEMIS records in our final dataset (24.3%) were only reported with the ambiguous species designation of "sp.", analyses at the genus level may be necessary to fully capture relevant trade patterns in key Lacey Act taxa. Finally, we highlighted trade in all known *Bsal* carrier species and the genera they belong to.

Where relevant, we statistically analyzed temporal trends in amphibian trade using generalized linear models (GLMs) with Poisson outcomes, treating yearly counts of imported live individuals ($n = 23$) as the response variable and year as a continuous explanatory variable. Further, we used a statistical framework designed for impact evaluation to understand how the Lacey Act interim rule affected the trade volume of listed species[69]. More specifically, we fit a Poisson GLM that allowed for both an immediate change in trade volume of listed species as a result of the interim rule as well as a change in trend over time. For this impact evaluation analysis, we treated annual trade counts from 2016 to 2021 as post-intervention data points. In addition to fitting this model to annual trade counts for amphibian species listed under the Lacey Act interim rule, for comparison, we conducted the same analysis on annual trade counts of non-listed species. We implemented all analyses within R version 4.1.1[70]. All data visualizations were created using 'ggplot2'[71] and 'cowplot'[72].

Reporting summary. Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Complete raw and cleaned data for this project are publicly available on GitHub at https://github.com/ecohealthalliance/amphibian_trade. Additionally, these same materials have been archived on Zenodo[62]. Supplementary Data 1 appears as the file "Bsal_infection_summary.csv" in both the GitHub and Zenodo repositories.

Code availability

All analysis scripts for this project are publicly available on the GitHub (https://github.com/ecohealthalliance/amphibian_trade) and Zenodo[62] repositories.

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Author contributions

P.J.C. and E.A.E. conceived of the idea for the paper. P.J.C., N.R., O.C.S., and E.A.E. contributed to data collection and curation. P.J.C. and E.A.E. analyzed the data and drafted the manuscript. N.R. and O.C.S. made comments and edits that shaped the final version of the paper.

Competing interests

All authors declare no competing interests.

Additional information

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