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Global impacts of invasive species on the tipping points of shallow lakes

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Abstract

There is growing acknowledgement that human-induced change can push ecosystems beyond tipping points, resulting in the dramatic and sudden loss of vital ecosystem services. Invasive non-native species (INNS) are spreading rapidly due to anthropogenic activities and climate change and can drive changes to ecosystem functioning by altering abiotic conditions and restructuring native communities. Shallow lake ecosystems are especially vulnerable to perturbation from INNS as they can exist in two alternative stable states: either clear water with an abundance of vegetation or turbid, unvegetated and dominated by phytoplankton. Through a global meta-analysis of studies observing the effects of INNS on recipient lake ecosystems, we found that certain INNS drive significant changes in the abundance of key taxa and conditions that govern the balance of alternative equilibria in shallow lakes. Invasive fish and crustaceans demonstrated effects likely to lead to early ecosystem collapse to a turbid state and delay ecosystem recovery. Invasive molluscs presented opposite effects, which may delay ecosystem collapse and encourage ecosystem recovery. Our results demonstrate that INNS could significantly alter the tipping points of ecosystem collapse and recovery, and that not all invasive species may initiate system collapse. Our results provide guidance for managers of invaded shallow lake ecosystems, which provide diverse services including sanitation, potable water supply, industrial cooling, aquaculture and recreational resources. Moreover, our approach could be applied to identify key potential drivers of change in other crucial ecosystems which demonstrate alternative equilibria, such as coral reefs and kelp forests.

KEYWORDS
ecosystem services, invasive species, lake, meta-analysis, tipping points

1 | INTRODUCTION

Invasive non-native species (INNS) can alter ecosystem functioning and structure, affecting native biota (e.g. density, distribution, species richness, abundance and biomass of other species) and abiotic conditions (e.g. nutrient availability, physical habitat structure, light levels and the flow of materials) (Charles & Dukes, 2007; Essl et al., 2020). Aquatic systems are particularly vulnerable to the establishment of INNS, due to a history of disturbance through intense anthropogenic exploitation of rivers, lakes and coastal areas for aquaculture,

recreation, canal construction, discharge of ballast waters and sport fisheries (Gallardo & Aldridge, 2013, 2018; Kolar & Lodge, 2002; Ricciardi et al., 2000). As successful INNS often constitute new functional components in the recipient community, their ecological impacts propagate throughout the food web, often triggering trophic cascades (Strayer, 2010). The capabilities of INNS to propagate changes in invaded systems have led them to often be characterized as ecosystem engineers (Crooks, 2002; Sousa et al., 2009). The ability of INNS to influence the functionality of ecosystems suggests that their establishment could have implications for the alternative equilibria model for shallow lakes (Scheffer et al., 1993a).

It has become increasingly clear that complex dynamical systems, from ecosystems to financial markets to the climate, have tipping points at which a sudden shift to a contrasting state may occur (Scheffer et al., 2009). The concept of alternative equilibria explains the phenomenon where a shallow lake can exist in one of two alternative stable states: clear with a high abundance of submerged vegetation or turbid with few submerged plants (Scheffer et al., 1993a) (Figure 1a) with the alternative equilibria stabilized by a number of reinforcing mechanisms (Scheffer et al., 1993b). As a consequence of this reinforcement, once a system becomes turbid, it subsequently resists restoration efforts (Scheffer & Van Nes, 2007). For example, in turbid states with high phytoplankton biomass and suspended sediments, the buffering effects of bottom-rooting macrophytes are lost and restoration to a clear water state requires extensive reductions in nutrients or turbidity.

In shallow lake ecosystems, the level of the critical threshold, or tipping point, is thought to be driven by three basic assumptions: (1) Turbidity increases with the nutrient level as a result of phytoplankton growth; (2) vegetation reduces turbidity and (3) vegetation disappears when a critical turbidity is exceeded (Scheffer et al., 1993b). This can be illustrated by a simple graphical model, initially presented by Scheffer et al. (1993) (Figure 1b). Equilibrium turbidity can be demonstrated by two different functions of the nutrient level in both vegetation dominated and unvegetated states. Above the threshold of critical turbidity, vegetation will be absent, and therefore the upper equilibria line applies. Below the critical turbidity threshold, where vegetation can survive, the lower equilibria line applies. This simple model intuitively demonstrates the existence of alternative equilibria and how a system may demonstrate hysteresis and catastrophic transitions (tipping points). Steady nutrient enrichment of a system will cause it to progress along the lower limit line, until the critical threshold is reached, at which point vegetation disappears, and the system jumps a higher level of turbidity. For a system to revert to a clear water state, it must reach the alternative tipping point at which phytoplankton growth is limited enough to allow vegetation to establish and dominate.

The theory of alternative stable states remains a central concept for the study and understanding of shallow lake systems (Carpenter et al., 2020; Dakos et al., 2019; Schallenberg, 2020). While the effects of INNS on shallow lakes are widely documented, there has been no attempt to systematically appraise the likely outcome of multiple taxonomic or functional groups on the recipient ecosystem.

The alternative equilibrium model provides an established and well-understood framework against which ecosystem-level outcomes can be mapped. We believe that due to the outsized effects INNS can have on an ecosystem, they may act to alter the rate at which tipping points are reached by directly or indirectly affecting interactions between the drivers of the alternative equilibria model illustrated in Figure1a. This study presents the results of a comprehensive global meta-analysis of studies which report the effect of INNS on recipient freshwater ecosystems. The meta-analysis does not focus on comparing studies reporting the impacts of INNS on the tipping points of freshwater ecosystems but considers all relevant studies reporting impacts of INNS on freshwater ecosystems. This approach allowed us to quantify the relevant ecosystem effects of key taxonomic groups of INNS which are central to the model of alternative equilibria. Through calculating the effect sizes of different taxonomic groups of INNS (fish, molluscs, plants and crustaceans) on key components of the alternative equilibria model, we can effectively evaluate how certain INNS may affect tipping points in shallow lake ecosystems.

2 | Methods

2.1 | Data acquisition

Data were collated from a publicly available dataset regarding the global ecological impacts of INNS on freshwater environments (Gallardo et al., 2016), and brought up to date through the collation of additional data gathered by Tang (2020) such that all available published data were collated up until 30 December 2019. In total, Tang (2020), identified 51 additional studies published since Gallardo et al. (2016). Both authors implemented identical literature search methodologies, inclusion criteria and data collation (see Supplementary Methods).

All studies included in this dataset share three key characteristics. First, all studies focused on taxa, including all animals and plants (including phytoplankton), which spend at least one stage of their life cycle in freshwater. Second, only studies which quantitatively compared control and experimental treatments were included. For example, studies comparing a number of water bodies which have been invaded (experimental) against sites which remained uninvaded (control); waterbodies before (control) and after (experimental) the arrival of INNS; field studies manipulating habitats through the removal of INNS or using enclosures to prevent the entrance of INNS; and before–after eradication settings which studied the recovery of a system after eradication of an INNS, in which case 'before eradication' is considered treatment and 'after eradication' the control. Third, only studies which reported measurements of the mean, variability around the mean and the number of replicates were included. For additional information regarding study inclusion criteria, please see the Supplementary Methods and the methods outlined in Gallardo et al. (2016) and Tang (2020). The full list of studies included in this analysis is shown in Table S1.
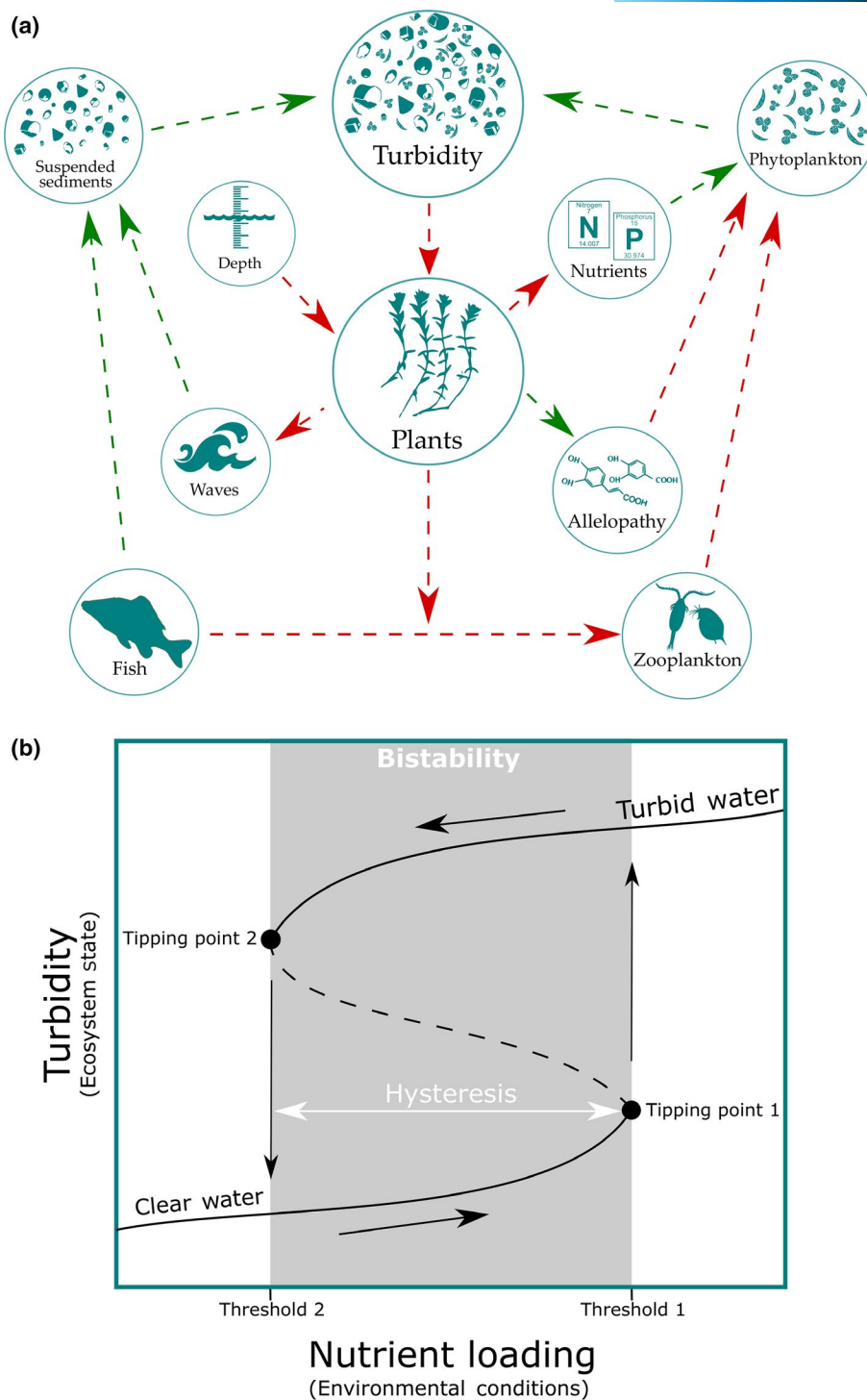
FIGURE 1 Interactions and tipping points which govern the alternative stable states of shallow lake ecosystems. (a) Main feedback loops thought to be responsible for alternative equilibria in shallow lakes. Green arrows indicate positive effects, red arrows negative effects. (b) Tipping points mark the discontinuous changes in ecosystem state. The black solid lines represent the stable equilibria. The dashed line represents the border between the basins of attraction between the two stable states. The lower solid line indicates a clear water state. Plants can only exist on the lower line, until Threshold 1 is reached. Threshold 1 represents the critical turbidity level of the system. As nutrient loads increase, turbidity follows the lower solid line until the line crosses Threshold 1. At this point (Tipping point 1), the equilibrium disappears, and the system's turbidity moves abruptly to the upper, unvegetated and phytoplankton dominated, stable state. In order for a system to return to the lower line, nutrients must be reduced to a much lower level, where the system crosses Threshold 2 (Tipping point 2), or turbidity must be substantially reduced. The difference between the tipping points marks the hysteresis in the system

In this analysis, species were merged into appropriate taxonomic groups as to best reflect the taxonomic categories presented in the model of alternative equilibria (Scheffer et al., 1993b) (Table S2). By doing so, it is recognized that both species-level data and information pertaining to the trophic level of certain organisms would be omitted from the analysis. By following this approach, we lose the ability to identify certain native species which may be particularly affected by the arrival of INNS, and equally, we cannot identify specific INNS which may have an outsized effect on the abundance of certain native species. However, as this analysis is focused on assessing the impact of INNS on the established model of alternative equilibria at the ecosystem level, as outlined by Scheffer et al. (1993), it was appropriate to group native species and INNS based upon the taxonomic categories outlined in the model.

The biotic response variables were filtered to contain only abundance-related data (comprising changes in density, biomass and coverage metrics of native species), as opposed to species richness data, as it is the changes in the abundance of key taxa within an ecosystem, such as the overall abundance of fish, plants, phytoplankton or zooplankton, which are most likely to alter the relationships between the key drivers of the alternative equilibria model (Figure 1a). For example, the total abundance of phytoplankton will likely have a larger impact on turbidity than the diversity of species within the phytoplankton community. Additionally, in the meta-analysis conducted by Gallardo et al. (2016), with which this study shares the majority of observations, they found no general evidence for a decrease in species diversity in invaded habitats. Due to the availability of data, the only abiotic variable included in this study was nutrients. Therefore, all response variables reported in this study refer to changes in the abundance of a native taxon or nutrient levels as a result of the introduction of a certain taxon of INNS. The final dataset contains 418 observations across 101 studies for 54 unique INNS.

2.2 | Data analysis

The Hedges' g effect size, also known as standardized mean difference (SMD), and variance was calculated for each observation (418 observations). Calculation of the SMD allows for the standardization of the multiple abundance metrics used across the studies included in the meta-analysis (Gallardo et al., 2016). The SMD estimates the standardized difference in the response variable (i.e. the change in abundance of native taxa or nutrients) as a result of the presence of INNS, by comparing experimental and control treatments for each observation. The SMD also weighs cases by their sample size and the inverse of their variance and was calculated as follows:

$$SMD = \frac{(X_E - X_C)}{J} S$$

where X denotes the mean value of the response variable being abundance or nutrients in treatment (X_E) and control (X_C) groups; S is the pooled standard deviation of the two groups; and J is a weighting

factor based on the number of replicates in the treatment and control groups. J was calculated as:

$$J = \left(1 - \frac{3}{4(X_E + X_C) - 9}\right)$$

SMD is unitless and ranges from $-\infty$ to $+\infty$. The magnitude of SMD can be interpreted as follows: ≤ 0.2 is considered a small effect, $0.2 \leq |SMD| \geq 0.5$ is a medium effect; $0.5 \leq |SMD| \geq 0.8$ a large effect; and ≥ 1.0 is a very large effect (Anton et al., 2019).

Meta-analysis was conducted using the metaphor package for R (Viechtbauer, 2010). We assessed the effect size of each taxonomic group of INNS (crustaceans, plants, fish and molluscs) (Table S1) on each environmental response variable (abundance of benthic invertebrates, plants, fish, phytoplankton, zooplankton and nutrients) by building a separate mixed-effect model for each combination of response variable and taxonomic group of INNS. Mixed-effects models used the study reference and invasive species name as random factors to account for the effect of multiple observations of an exotic species within a study and across multiple studies. Model results were considered significant if their 95% CI intervals did not overlap with zero, and p values were $\leq .05$. All models used the rma.mv function, which calculates statistical significance based upon a Wald-type test. Effect sizes were only calculated where there were ≥ 5 cases capturing the effect of an invasive taxa on a single response variable (Gallardo et al., 2016). A significantly positive value for SMD represents a positive effect on the response variable, that is, an increase in the abundance of a native taxa or nutrients as a result of the presence of an INNS. Whereas a significantly negative SMD value implies a negative effect on the response variable. However, a significantly positive or negative SMD value does not correspond directly to a positive or negative impact on the equilibria of ecosystem tipping points, and this is interpreted through applying the magnitude of the positive or negative effect sizes to the model of alternative equilibria (Figure 1a).

We did not calculate effect sizes for interactions where the taxonomic group of INNS was the same as the taxonomic group of the response variable, for example, the effect of invasive plant species on existing plant species' abundance. This was done as, for the purposes of this study, we focused on the effect of INNS on the overall abundances of certain taxa. Studies which reported changes in the abundance of existing taxonomic groups did not provide data for the subsequent total abundance of that taxonomic group in the system. For example, although an invasive plant may lead to a decline in native plant abundance, the overall abundance of plants in the system may have increased. The absence of this data unfortunately precludes our ability to identify any potential buffering of effects arising from the presence of native species of the same taxonomic group as the invader.

2.3 | Publication bias

Publication bias refers to the selective publication of articles finding significant effects over those which find non-significant effects.

Publication bias could distort the results of this meta-analysis as it could lead to an overestimate of the effects of invasive species on the aquatic environment. As noted by Anton et al. (2019), regtest and trim-fill functions are not implemented in the metafor package for mixed-effects models (Viechtbauer, 2010). Publication bias was therefore evaluated using Egger's regression test (Egger et al., 1997), running models which included the standard error of the effect sizes (as the square root of the variance) as a moderator (Viechtbauer & Cheung, 2010). Potential publication bias was determined when the intercept of the model was significantly different from zero ($p \leq .05$). The data were then examined for potential outliers, which were defined as effect sizes with standardized residual values exceeding the absolute value of three (Viechtbauer & Cheung, 2010) using the rstandard function in R. Potential outliers were removed to adjust for potential publication bias. Adjusting for publication bias did not change the outcome of the analyses. The need to adjust for publication bias would have been confirmed when the significance of the random-effects model, with the study reference as a random factor, changed before and after the removal of potential outliers (Table S3). The sensitivity analysis illustrated that the findings are robust against publication bias.

To avoid the majority of literature review pitfalls outlined by Haddaway et al. (2020), this study attempted to present a focused scope, robustly calculate standardized effect sizes, implement appropriate mixed-effects modelling, assess publication bias using Egger's regression test and maintain transparency regarding methodology, raw data, and analytical code (Haddaway et al., 2020).

3 | RESULTS

Data were systematically compiled from 418 observations across 101 studies for 54 unique INNS. The results of the overall analyses indicate that the arrival of invasive fish, crustaceans and molluscs is likely to have a significant negative effect on the abundance of certain taxa and nutrients which are central to the maintenance of states within alternative equilibria (Figures 2 and 3). However, invasive plants did not have a significant impact on the abundance of any taxa or nutrients (Figures 2 and 3).

Invasive crustaceans (Table S1) had a significant negative effect on zooplankton abundance (SMD = -0.74 ± 0.69 [mean effect size $\pm$ 95% CI], $p = .035$) and plant abundance (SMD = -1.4 ± 0.83, $p < .001$). Non-significant effects of invasive crustaceans were observed for phytoplankton (SMD = 0.36 ± 0.63, $p = .254$), nutrients abundance (SMD = -0.54 ± 0.95, $p = .264$) and on benthic invertebrate abundance (SMD = -0.34 ± 0.54, $p = .222$). There were insufficient data to calculate effect sizes for invasive crustacean impacts on fish abundances.
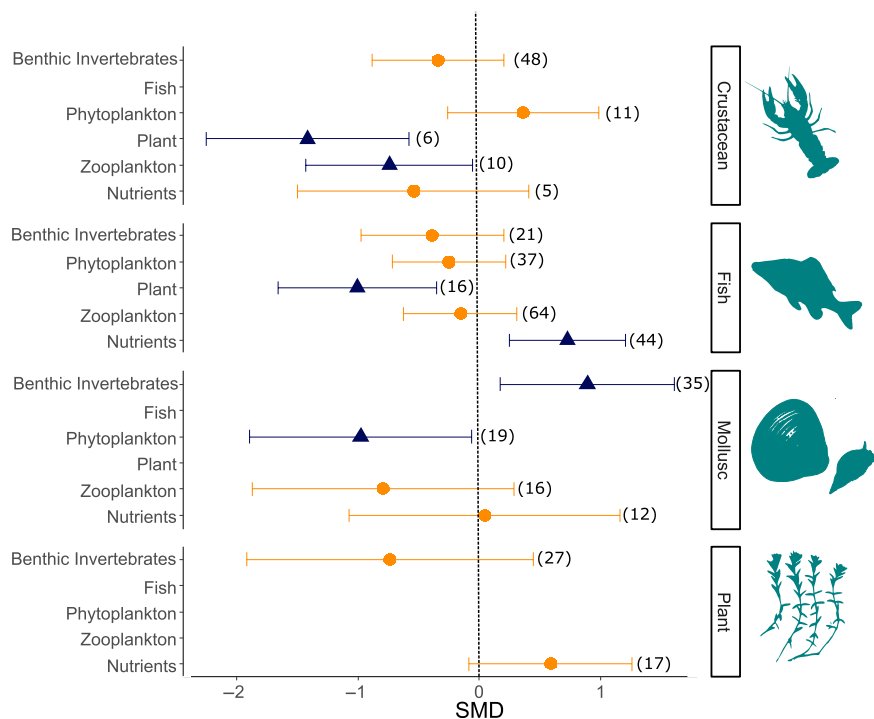
FIGURE 2 Mean effect size (standard mean deviation ± 95% CI) of invasive species on response variables that drive alternative stable states in shallow lakes. Effect size (SMD) indicates an increase (SMD >0) or a decrease (SMD <0) in abundance or the response variable. The dotted vertical line indicates where SMD = 0. The bars represent the 95% CI, significant effects (blue bars, triangle points) are observed when they do not overlap zero. Non-significant effects are denoted by yellow bars and circular points. Numbers in brackets denote the number of observations used to calculate the SMD. Blank interactions are a result of <5 observations being available to calculate the SMD. A positive or negative SMD value alone does not directly indicate the likelihood of a favourable or unfavourable regime shift. In order to understand the impact of the calculated effect sizes on regime shifts, the SMD values were applied to the established model of alternative equilibria, illustrated in Figure 3
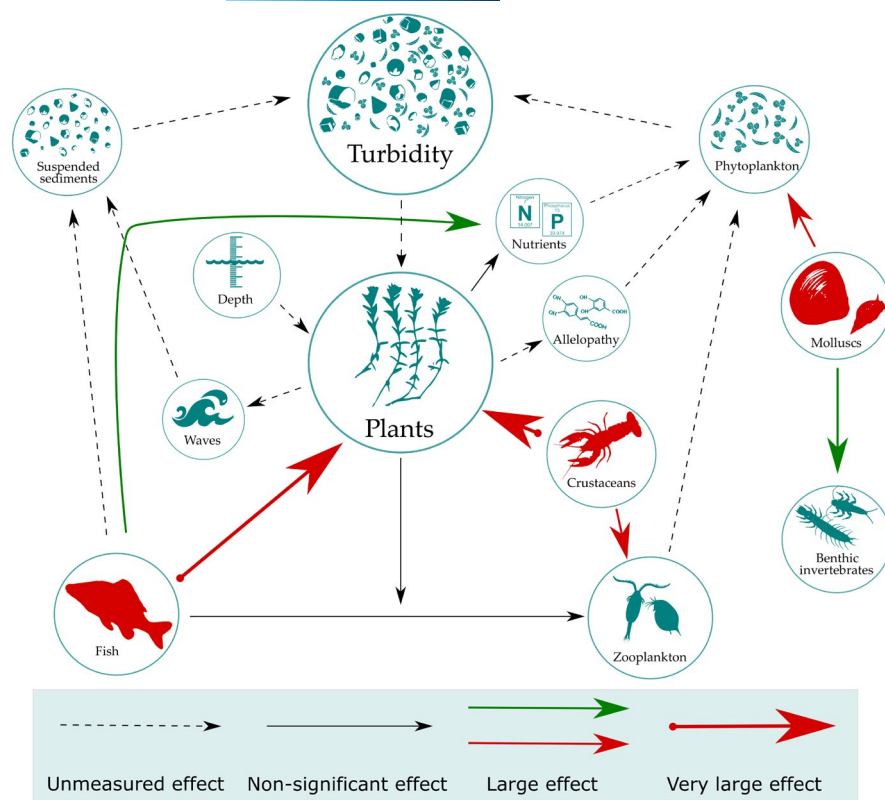
FIGURE 3 Interactions between significant invasive species effects on the dynamics of alternative equilibria in shallow lakes. The size and shape of the arrows indicate the effect size (SMD) of the invasive taxa on the abundance of relevant reponse variables. Red arrows indicate negative effects (SMD <0) and green arrows indicate positive effects (SMD >0). The size of the effect is determined by the value of the SMD, and can be interpreted as follows: ≤0.2 is considered a small effect, 0.2≤|SMD|≥0.5 is a medium effect; 0.5≤|SMD|≥0.8 a large effect; and ≥1.0 is a very large effect (Anton et al., 2019). Unmeasured effects capture the interactions within the system which were not directly measured in the studies available for meta analysis. Non-significant effect arrows indicate where the SMD ± 95% CI overlaps with zero

Invasive fish (Table S1) had a significant positive effect on nutrient abundance (SMD = 0.73 ± 0.48, p = .003) and a negative impact on plant abundance (SMD = −1.01 ± 0.66, p = .003). Non-significant effects were found for abundances of benthic invertebrate (SMD = −0.39 ± 0.59, p = .196), phytoplankton (SMD = −0.25 ± 0.47, p = .297) and zooplankton (SMD = −0.15 ± 0.47, p = .517).

Invasive molluscs (Table S1) had a significant positive effect on the abundance of benthic invertebrates (SMD = 0.89 ± 0.72, p = .015) and a negative effect on phytoplankton abundance (SMD = −0.98 ± 0.92, p = .037). Non-significant effects were calculated for abundance of zooplankton (SMD = −0.79 ± 1.08, p = .150) and nutrients (SMD = 0.05 ± 1.12, p = .935). There were insufficient data to calculate the effects of invasive molluscs on fish or plant abundances.

Invasive plants (Table S1) had non-significant negative effects on abundance of benthic invertebrates (SMD = −0.74 ± 1.18, p = .222) and nutrients (SMD = 0.59 ± 0.68, p = .088). There were insufficient data to calculate effect sizes of invasive plants on phytoplankton, zooplankton and fish abundances.

4 | DISCUSSION

4.1 | The effects of invasive species on the dynamics of alternative equilibria

Figure 3 illustrates how the effects revealed through the meta-analysis map onto the dynamic system which governs the alternative equilibria of shallow lakes. Invasive fish had two large and synergistic effects on recipient ecosystems, with a large positive effect

on nutrient abundance and a very large negative effect on plant abundance. Both of these effects have the consequence of pushing a system towards maintaining a turbid state. Reduced plant abundance may lead to increased wave action and suspension of sediments while increasing nutrient availability for phytoplankton and relieving potential allelopathic pressures on phytoplankton growth. The positive effect on nutrient abundance associated with invasive fish could be associated directly with factors such as disturbance-related release of benthic phosphorus (Adámek & Maršálek, 2013), or indirectly such as through foraging-related reductions in plant abundance (Miller & Provenza, 2007).

Crustaceans had a similarly synergistic effect on their invaded systems, with a large negative effect on zooplankton abundance and a very large negative effect on plant abundance, both of which can push a vegetated clear water system towards the critical turbidity threshold. The ecosystem-level effects of increased turbidity resulting from reduced plant abundance are exacerbated through simultaneous reductions in the grazing effects of zooplankton, further enabling proliferation of phytoplankton.

Systems invaded by molluscs experienced a large decline in phytoplankton abundance, and a large increase in benthic invertebrate abundance. The ability of bivalve molluscs to directly remove phytoplankton through their filter feeding activities may act to maintain a clear water state at higher nutrient levels and has the potential to push a turbid unvegetated system towards the tipping point for a clear water system. Indeed, studies of invasive zebra mussels (*Dreissena polymorpha*) in the tidal Hudson River revealed a 17-fold decrease in phytoplankton and proliferation of bottom-rooting macrophytes (Smith et al., 1998). Additionally, gastropods reduce algae

abundance and encourage macrophyte growth through actively grazing periphytic algae which compete with macrophytes for light and nutrients (Brönmark, 1989; Lodge, 1986). Increased benthic invertebrate abundance resulting from mollusc invasions is likely tied to the often-noted effects of bivalve beds which in shallow systems provide substrate in the form of shells and increased macrophyte growth, shelter from predation and food for benthic invertebrates through the enrichment of sediments with organic matter from the bivalves' faeces and pseudofaeces (Duchini et al., 2018; Strayer et al., 1998; Zhang et al., 2011). This transfer of particulate matter and nutrients from suspension in the pelagic environment to deposition into the benthic sediment, and subsequent assimilation into benthic invertebrate biomass, can push systems towards a clear water state.

In the context of a system in a clear water state, invasive molluscs could delay a tipping point to a turbid system. The ability of molluscs to supress phytoplankton biomass masks the effect of increasing eutrophication. This masking effect has been noted in studies of the invasive bivalve, *D. polymorpha* (Dzialowski & Jessie, 2009). The removal of phytoplankton results in a potential delay in a system reaching the catastrophic tipping point, shifting the threshold of stress at which the system collapse occurs to a higher stress level (Figure 4a).

Opposite to the effects of molluscs, invasive fish and crustaceans may lead to a tipping point occurring at a lower level of environmental stress, increasing the risk of ecosystem collapse. The detrimental effects of fish and crustaceans on zooplankton and plant abundance may reduce the capacity of plants to outgrow and outcompete phytoplankton for nutrients and light. This reduction in the suppressive power of plants and zooplankton on phytoplankton growth accelerates the rate at which a system reaches its tipping point and supresses its ability to maintain a clear water state (Figure 4b).

In the case of a recovering system, the effects of INNS on tipping points are reversed, with molluscs leading to an earlier recovery tipping point (Figure 4c), and fish and crustaceans resulting in a delayed tipping point (Figure 4d). What this demonstrates, especially in the case of invasive molluscs, is that under a high abundance of certain INNS a smaller decrease in environmental stress, in this case nutrients, is necessary to reach a tipping point. In the case of fish and crustaceans, due to the slower growing nature of bottom-rooting vegetation compared to phytoplankton growth, nutrients would need to be reduced to a much lower level to reach a tipping point. It is even possible that heavily affected systems, invaded by high abundances of crustaceans or fish, could reach a point at which nutrients would need to be reduced to a biologically impossible level to reach the tipping point. In this scenario, a system may lose its bistability once in a turbid state, while the invasive crustaceans and fish remain.

4.2 | Implications for management of invasive species in shallow lakes

With the global rise in the spread of INNS (Essl et al., 2020), our study highlights some of the effects that may arise as a result of their establishment in shallow lake systems. Understanding how

particular INNS can drive driving tipping points in shallow lakes could allow water resource managers to make better informed decisions. For example, the establishment of invasive molluscs in turbid systems could be leveraged as an opportunity (McLaughlan & Aldridge, 2013), triggering a management focus on reducing nutrient loads, to revert a system to a clear water state at an increased rate. Furthermore, if nutrient loads were reduced sufficiently before eradication of an invasive mollusc, the hysteresis effect could prevent a system from rebounding to a turbid state and would aid the reinstatement of native flora. In the case of invasive fish or crustacean establishment, their removal should be targeted at the earliest opportunity, as they both have the potential to accelerate the decline of a clear water state towards a turbid condition that is difficult to revert. As such, lake managers may wish to employ early detection and rapid response plans for high-risk invasive fish and crayfish.

Alternative equilibrium models in natural ecosystems focus on the key drivers behind tipping points. In reality, there are likely multiple stable states that shallow lakes can adopt (Scheffer & Van Nes, 2007). Additionally, there are nuances regarding the specific effects of a particular INNS and the potential ephemeral nature of an INNS' impact. These aspects are governed by factors such as predator–prey dynamics and dynamic shifts in prey communities. Such ecological relationships may allow species unaffected by INNS to flourish within affected trophic communities and therefore sustain an ecological trait which is critical for driving the dynamics of alternative equilibria. For example, it is unlikely that an invasion of *D. polymorpha* could indefinitely prevent a system from reverting to a turbid state. This is because the grazing pressure of *D. polymorpha* can favour phytoplankton with faster growth rates (Lucas et al., 2016), or for buoyant species which can occupy areas of the water column that do not mix with mussel beds (Lucas et al., 2016; Smith et al., 1998), or towards inedible toxic species (Vanderploeg et al., 2001). Over time, predator–prey dynamics could result in mussel mortality and reduced phytoplankton grazing pressure (Wilson, 2003). These ecosystem-level responses in community structure may explain why early stage invasions can cause dramatic, but sometimes short-lived changes of state in shallow lakes (Barbiero & Tuchman, 2004; Strayer et al., 2011; Wilson, 2003).

Although INNS are recognized as one of the greatest threats to global biodiversity, this study demonstrates that their effects on ecosystem services are not uniformly negative. While it would be unacceptable to promote selective introductions of INNS into shallow lakes, with appropriate risk assessment and consultation with relevant authorities, there may be scenarios where embracing already established INNS that provide favourable ecosystem engineering in ecologically deficient systems could be of great value.

4.3 | Invasive species establishment, management and changing tipping points

The importance of tipping points in explaining ecosystem change and informing ecosystem management is becoming increasingly
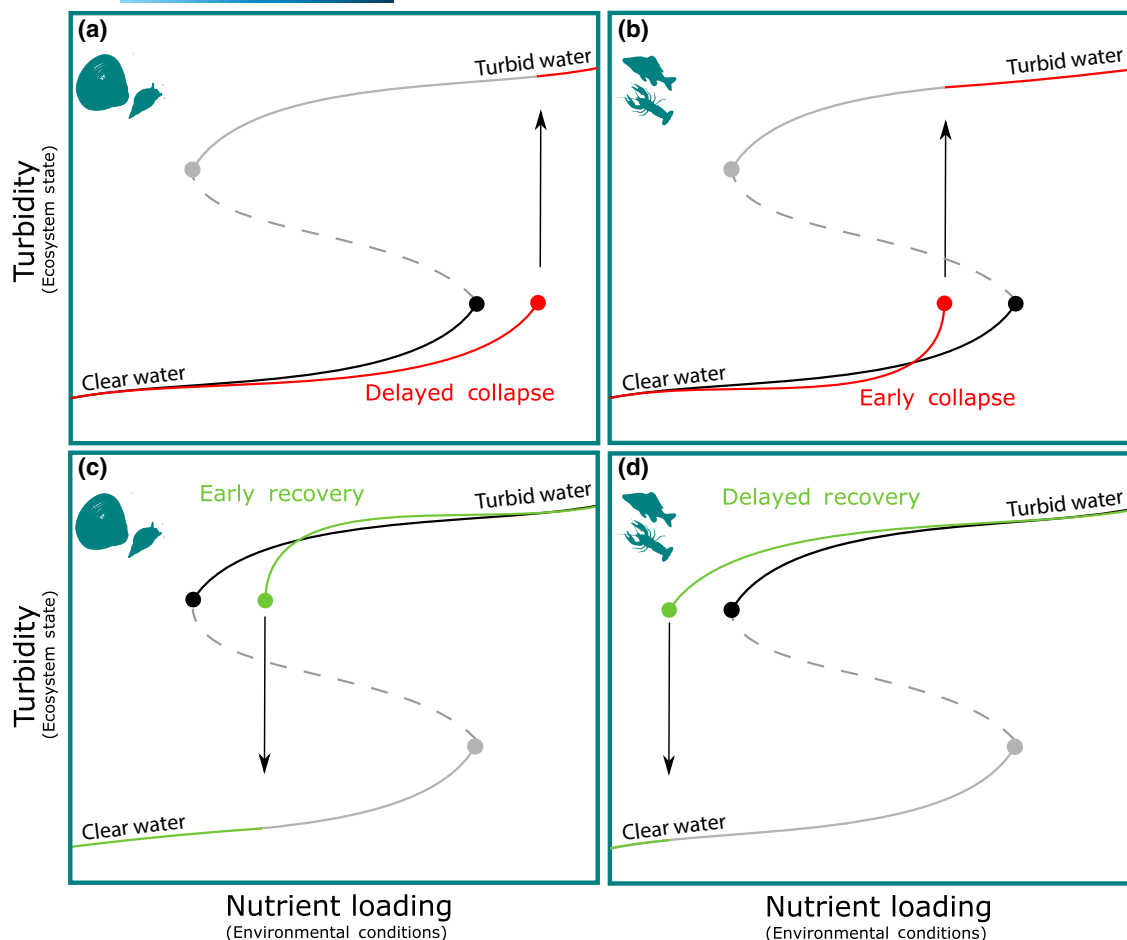
FIGURE 4 Predicted alterations of trajectories of ecosystem collapse (red solid lines) and recovery (green solid lines) as a consequence of invasive species establishment. The black and grey lines represent the two alternative stable states of a reference ecosystem containing no invasive species. The grey dashed lines indicate the unstable boundary between the two states, with circles denoting the tipping points. The coloured lines indicate the predicted trajectories of invaded systems as revealed by the meta-analysis, red lines signify collapse trajectories and green lines denote recovery trajectories. Panels (a) and (c) indicate systems with established populations of invasive molluscs. Panels (b) and (d) illustrate systems with established populations of invasive fish and/or crustaceans

recognized. Drivers such as changes in species traits within or among populations, through mechanisms of phenotypic plasticity, species sorting or evolutionary trait change, may affect an ecosystem's response to stress and therefore influence the occurrence of catastrophic tipping points (Dakos et al., 2019). We suggest that the establishment of INNS has the potential to rapidly alter the functional traits which exist in many ecosystems and may predictably alter the likelihood of a catastrophic tipping point being met. For example, invasive macrophytes have been shown to facilitate the early collapse of coral-dominated reefs, contributing to the establishment of an alternative macroalgae-dominated state (Neilson et al., 2018). Establishment of invasive sea urchins (*Centrostephanus rodgersii*) has precipitated the early collapse of Tasmanian kelp beds through overgrazing, maintaining an alternative barrens habitat (Ling & Keane, 2018). Invasion of stable desert shrublands by non-native grass species increases fire frequency, shrub mortality and soil loss, accelerating the shift to a desertified state (Ravi et al., 2009). The invasive black locust (*Robinia pseudoacacia*), a prominent and 'non-flammable'

invasive deciduous tree in American pitch pine forests, increases the ecosystem's critical threshold resistance to fire and disrupts natural cycling between alternative stable states (Dibble & Rees, 2005). We propose that employing a meta-analysis framework to quantify the effect size of INNS in ecosystems with established feedback mechanisms which drive alternative stable states will help identify how INNS may alter critical ecosystem tipping points. Outcomes can help managers prioritize resources towards high-risk INNS and can allow informed management of ecosystems towards a desirable equilibrium.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial or personal relationships which could have influenced the work reported in this paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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