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Decision-making under uncertainty for species introductions into ecological networks

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Statement of authorship

L.B.V., K.A.P, and L.E.D. designed the research, L.B.V. wrote the code and performed the modeling, H.L. checked the code, L.B.V, K.A.P., M.T.H., A.K., A.J.S., H.L., and L.E.D. performed the literature review and wrote the paper.

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Abstract

Ecological communities are increasingly subject to natural and human-induced additions of species, as species shift their ranges under climate change, are introduced for conservation, and are unintentionally moved by humans. As such, decisions about how to manage ecosystems subject to species introductions and considering multiple management objectives need to be made. However, the impacts of gaining new species on ecological communities are difficult to predict due to uncertainty in introduced species characteristics, the novel interactions that will be produced by that species, and the recipient ecosystem structure. Drawing on ecological and conservation decision theory, we synthesize literature into a conceptual framework for species introduction decision-making based on ecological networks in high uncertainty contexts. We demonstrate the application of this framework to a theoretical decision surrounding assisted migration considering both biodiversity and ecosystem service objectives. We show that this framework can be used to evaluate trade-offs between outcomes, predict worst-case scenarios, suggest when one should collect additional data, and allow for improving knowledge of the system over time.

Main Text

Introduction

Ecological communities are increasingly subject to natural and human-induced additions of species (Seebens et al. 2017). Additions occur as species shift their ranges under climate change (Wallingford et al. 2020), species are unintentionally spread by humans (Blackburn et al. 2011; David et al. 2017; Fantle-Lepczyk et al. 2022; Seebens et al. 2017), and species are intentionally introduced for conservation (Corlett 2016; Peterson & Bode 2020), restoration (Bullock et al. 2011), biocontrol (Begg et al. 2017), or to provide ecosystem services (Pejchar & Mooney 2009). Species that then become invasive tend to negatively impact biodiversity of the recipient ecosystem (Crystal-Ornelas & Lockwood 2020; David et al. 2017; Mollot et al. 2017) and have negative economic impacts (Bradshaw et al. 2016; Fantle-Lepczyk et al. 2022; Hanley & Roberts 2019; Matsuzaki & Kadoya 2015; Pejchar & Mooney 2009). For example, species introductions can also degrade ecosystem services, such as the spiny water flea (*Bythotrephes longimanus*) invasion in Lake Mendota, USA (Walsh et al. 2016), which reduced recreational opportunities. In contrast, species introduced for restoration or conservation are expected to have neutral or positive impacts on net biodiversity (Bullock et al. 2011; Corlett 2016) and, in some cases, are introduced explicitly to support ecosystem services. For example, the western honeybee (*Apis mellifera*) has been introduced around the world to support honey production and crop pollination (Geslin et al. 2017; Moritz et al. 2005). Given this range of potential impacts from introduced species and often incomplete data on species and ecosystems, a theoretically grounded framework for assessing risk and making decisions related to species introductions under uncertainty is necessary to meet conservation goals and avoid unintended outcomes. Using ecological forecasting to develop theory in applied management contexts has been identified as a key frontier and opportunity (Dietz et al. 2018, Adams et al. 2020, Lewis et al. 2022) but has not received sufficient attention in the context of introduced species and ecosystem management decision-making.

Predicting the consequences of species introductions for biodiversity and ecosystem services poses a challenge because species interact in complex networks and introduced species form new interactions in the recipient ecosystem (Jackson et al. 2017; Pantel et al. 2017; Peterson & Bode 2020, Peterson et al. 2021). The addition of a new species can alter the abundance of the species it directly interacts with, but also indirectly impact other species through the species interaction network in the recipient ecosystem (David et al. 2017; Frost et al. 2019; Galiana et al. 2014; Romanuk et al. 2017; Wootton 2002). For example, predators introduced into aquatic ecosystems tend to reduce the abundance of benthic invertebrate and zooplankton prey, thus allowing phytoplankton populations to increase (Gallardo et al. 2016). Such indirect effects can potentially cause cascading extinctions or loss of ecosystem services within the recipient ecosystem (e.g., see Peterson & Bode 2020; Walsh et al. 2016). Due to interactions that form, the success and effects of a species introduction can depend on both the properties of the recipient ecosystem (e.g., biodiversity, connectance, whether the system has been previously disturbed) and the introduced species (e.g., generality or trophic level) (David et al. 2017; Frost et al. 2019; Traveset & Richardson 2014). Consequently, prediction of introduction impacts ideally requires information about species interactions within the recipient ecosystem (i.e., ecological network structure), as well as plausible ways that the introduced species might interact with these resident species (Windsor et al. 2022).

The process of predicting the impacts of an introduced species on a recipient ecosystem involves many sources of uncertainty. First, the exact species entering new ecosystems is not always known, such as for unintentional introductions (Fournier et al. 2019; Pyšek & Richardson 2010; Seebens et al. 2016). Second, even when the identity of the introduced species is known before an introduction (e.g., for assisted migration, IUCN 2013), the novel interactions between that species and resident species have often never been observed before, and therefore must be predicted and carry uncertainty (Kamenova et al. 2017). Third, uncertainty over the interaction network structure of the recipient ecosystem is common, due to the challenges of collecting this data (Aufderheide et al. 2013; Berlow et al. 1999). Prior work has argued that such uncertainty in ecosystem structure precludes predicting the impacts of a disturbance on the populations of specific species within an ecosystem (Yodzis 1988; Novak et al. 2011). However, recent work in food web theory has suggested that prediction in real ecosystems is feasible (Aufderheide et al. 2013; Iles & Novak 2016; Mougi 2017) and, in a growing number of cases, predictions from dynamic models have aligned with observational and experimental data (Berlow et al. 2009; Boit et al. 2012; Jonsson et al. 2018). Despite the challenges of forecasting under uncertainty, forecasting the impacts of species additions can provide useful information for testing ecological theory (e.g., by revealing the extent to which assumptions about the underlying system are correct, Dietze et al. 2017). Forecasting can also aid with decision-making, by, for example, generating a range of potential outcomes under uncertainty to reveal trade-offs between objectives and potential worst-case scenarios (Adams et al. 2020; Polasky et al. 2011).

In response to these needs and challenges, we synthesize literature from several subdisciplines (e.g., invasion ecology, food web theory, conservation decision science) into a framework for decision-making related to species introductions under uncertainty and multiple management objectives. The framework combines an ecological network perspective with concepts from decision science and consists of 6 steps (Fig. 1): 1) identify management objectives and translate them to outcome metrics of interest, 2) identify or predict the introduced species, 3) predict the interactions of the introduced species with species and ecosystem services in the recipient ecosystem, 4) predict the population dynamics after species introduction, 5) evaluate trade-offs of management alternatives under uncertainty, and 6) test and explore predictions to improve future decision-making. For each step, we first review existing quantitative methods for prediction when appropriate. We then demonstrate how these steps can be synthesized by applying our framework to a case of decision-making for assisted migration with the dual goals of preserving biodiversity and providing ecosystem services. Throughout, we highlight sources of uncertainty and suggest how this uncertainty can be carried through the prediction process. With our application, we show that this framework can be used to reveal important trade-offs among objectives and worst-case scenarios, suggest cases in which more data should be collected before making a decision, and allow for testing of ecological theory and improving knowledge of the system over time.

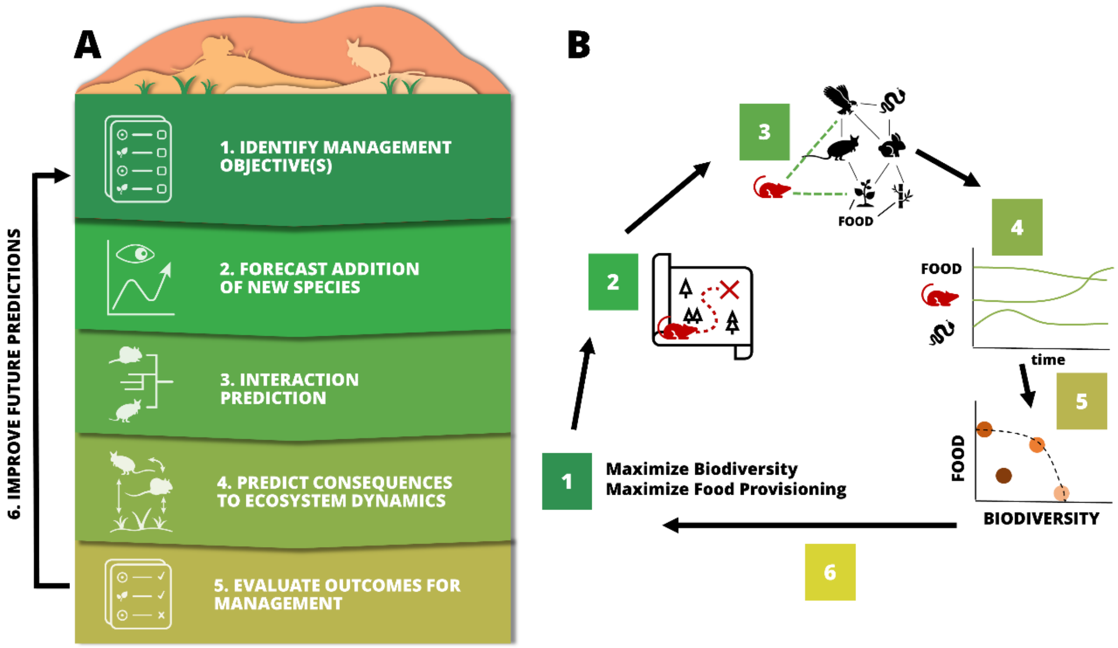

Figure 1. Our six-step framework for assessing risk and aiding decision-making for species introductions under uncertainty. This diagram demonstrates the six steps in the framework that we outline and apply in this Synthesis. Panel A shows the six steps. Panel B shows a stylized example of applying the six steps: 1) identify management objectives and translate them to outcome metrics of interest, 2) identify the introduced species, 3) predict the interactions of the introduced species with species in the recipient ecosystem, 4) predict the population dynamics after species introduction, 5) evaluate trade-offs of management alternatives based on management objectives under uncertainty, and 6) test and explore predictions to improve future decision-making.

Framework linking ecological theory to decisions under great uncertainty

<u>Step 1: Identify management objectives for multispecies conservation</u>

Clarifying objectives is a key first step in any structured decision-making process (Game et al. 2013; Martin et al. 2009), including for multi-species management. Conservation and management of multiple interacting species can involve a range of objectives (Mace 2014; Nicholson & Possingham 2006; Xiao et al. 2019) chosen by stakeholders. While conservation generally focuses on preventing extinctions, more specific objectives can be defined within that overarching aim (Nicholson & Possingham 2006). In a multi-species context, these objectives can include minimizing the likelihood of extinctions of certain high-risk species (e.g., umbrella species) or all species (reviewed in Nicholson & Possingham 2006) and maximizing the number of extant, interacting species (McDonald-Madden et al. 2016).

Management aims may also be related to ecosystem services, for example, improving carbon sequestration or water quality while minimizing the chance of species extinctions (Polasky et al. 2012), or even include factors such as social equity (Halpern et al. 2013). Management can meet multiple goals simultaneously (Dee et al. 2017b; Xiao et al. 2018). However, managing for the goals of biodiversity and ecosystem services can lead to trade-offs, depending on the ecological context and ecosystem services considered (Dee et al. 2017a; Polasky et al. 2012; Reyers et al. 2012; Xiao et al. 2018; Xiao et al. 2019). In a coastal food web, for example, the management strategies that best provide ecosystem services (e.g., shoreline protection, food production from fisheries) and best protect species (species richness of interacting species) were more aligned when basal species provided ecosystem services (Xiao et al. 2018). Further, during restoration, trade-offs can emerge between ecosystem service and conservation goals when non-native species can outperform native species in the provisioning of certain services (Bullock et al. 2011).

Step 2: Identify or forecast species that are being introduced into an ecosystem

The next step is to identify potential introduced species. In this step, a species might be chosen to be intentionally introduced (or reintroduced) to progress a management objective. Conversely, the management objective might seek to prevent an unintentional species introduction with negative impacts (i.e., invasion) or maintain biodiversity under future shifts in species distributions with climate change. We consider each of these cases and ways to choose or predict which species will be introduced.

Intentional introductions or reintroductions

Increasingly, species are being reintroduced into an ecosystem from which they were lost or introduced for the first time to address conservation goals, such as via assisted migration (Richardson et al. 2009), restoration (Ewel & Putz 2004), or augmentation of habitat and resources for native species (Severns & Warren 2008). Choosing a species for introduction depends on both the management goals and the habitat into which a species will be introduced. For example, species can be introduced to degraded habitats within and slightly beyond their current ranges to increase species richness and catalyze community regeneration (Ewel & Putz 2004; Seddon 2010). Non-native species are also often introduced to a novel system for ecosystem service benefits (i.e., agriculture, aquaculture, or pest control). Species introduced for this purpose might be selected based on their known ecosystem service benefit, or traits that indicate their potential to provide a service (e.g., tree size or persistence of leaves for regulating services). Non-native species also often have a proclivity to persist with climate and land use change, more so than native species, which can ensure service resilience to change (Schlaepfer et al. 2011). For example, non-native African honeybees (*Apis mellifera cutellate*) were found to provide pollination services in forest fragments in Amazonia, Brazil, where native pollinators no longer could (Dick 2001).

Another motivation for species introduction is moving a threatened species. Assisted migrations (also called conservation translocations or managed relocations) involve assisted colonization outside the native range of a species to reduce the chance of extinction (IUCN 2013; Richardson et al. 2009; Thomas 2011). Species chosen for assisted migration will often be rare or threatened and require the identification of suitable habitat and resources for monitoring (Griffith et al. 1989; Richardson et al. 2009). While more may be known about species interactions in the case of an intentional introduction, these situations still present challenges in identifying impacts of species introduction, which are explored in the remainder of this framework.

Unintentional introductions

Predicting the arrival of non-native species remains a major challenge in invasion ecology (Pyšek and Richardson 2010; Seebens et al. 2016). With increasingly globalized trade, methods for assessing the likelihood of species introduction via human transportation networks have been developed; global trade traffic, for instance, can help predict species spread (Drake & Lodge 2004). Similarly, models predict introductions of non-native marine species using global shipping intensities, environmental variables, and species occurrence data (Seebens et al. 2016). Others determine areas of introduction risk by using species distribution models (Bellard et al. 2013, but see Liu et al. 2020) or matching “climate envelopes” to identify suitable areas for introduction (Bomford et al. 2009; Pertierra et al. 2017).

Species traits, such as those related to foraging, reproductive strategy, or dispersal ability, can also be used to assess which non-native species might be introduced into an ecosystem, as well as if that species is likely to have negative effects (i.e., become invasive) (Carboni et al. 2016; Catford et al. 2019; Mathakutha et al. 2019; Milbau &

Nijs 2004; van Kleunen et al. 2010). Existing trait frameworks compare the ecological profile of known invasive species with the ecological profiles of other species to predict their capacity to become future invaders (Fournier et al. 2019). Identifying potential invasive species might be used to plan for worse-case scenarios for unintentional introductions, as in the systematic process of horizon scanning by experts (Roy et al. 2014). Improved understanding of species mechanisms of introduction, establishment, and spread, as well as growing databases on species ecological traits (e.g., TRY, Kattge et al. 2020) make this approach increasingly feasible (Nunez-Mir et al. 2019).

Species range shifts

Shifts in historic ranges of plant and animal species due to global climate change will result in species introductions into new communities (Lurgi et al. 2012; Walther 2010). However, predicted shifts vary considerably depending on the model used to forecast range shifts. Mechanistic species distribution models, for example, can be used to identify outcomes of shifts in climatic constraints for a species' range by mapping a species' fundamental niche based on physiological information (i.e., morphological, physiological, phenological, and behavioral traits) onto the multivariate environmental space (Chuine et al. 2010; Guisan & Zimmermann 2000; Kearney & Porter 2009). Further constraining predicted distributions by incorporating species' interactions with competitors and enemies (i.e., by computing the realized niche, Vandermeer 1972, see Grainger et al. 2019; Wisz et al. 2013) is less common, but can improve the realism of these models (Lany et al. 2020; Ovaskainen et al. 2016; Pollack et al. 2014; Staniczenko et al. 2017). Finally, predicting changes in species' ranges depends on the climate change scenario considered, and uncertainty increases with time in even the most high resolution climate forecasts (Lawler et al. 2006).

Step 3: Predict which resident species will interact with the newly introduced species

After a focal introduced species has been identified, our next step is to predict how this species will interact with existing species in the recipient ecosystem and impact existing or new ecosystem services. In some cases, interaction partners of introduced species can be anticipated based on observations in similar ecosystems, or if the species is being reintroduced. For example, effects of fouling from invasive zebra mussels (D*reissena polymorpha*) on native mussel populations were consistent and thus potentially predictable across locations (Ricciardi 2003). However, observations of analogous interactions might not be available when a species introduction will produce novel interactions (Corlett 2016). In these cases, predictions of likely interactions of an introduced species can be elicited from experts (e.g., Peterson et al. 2021) or produced by quantitative methods (Kamenova et al. 2017). We review options for the latter (summarized in Fig. 2).

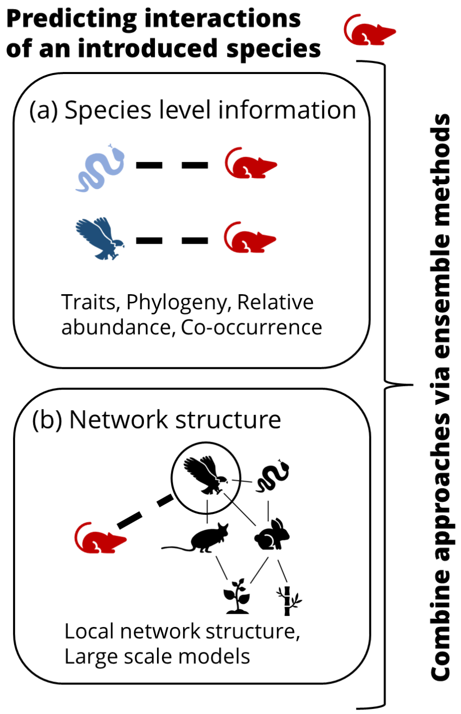

Figure 2. Approaches to predict novel interactions. Various sources of information can be used to predict the novel interactions of an introduced species. (a) Species level information about the introduced species and resident species such as traits or phylogeny can be used. In addition, one can use information based on (b) the recipient network structure. Findings within both ecology (Terry & Lewis 2020) and network science (Ghasemian et al. 2020) demonstrate that ensemble methods, or combining predictions across multiple methods, can perform better at predicting missing interactions than any single method alone, which offers a potential avenue for future work. Interaction prediction can also be performed for an entire regional species pool to produce a metaweb (Morales-Castilla et al. 2015; Gravel et al. 2013, but see Ohlmann 2019).

When the data are available, we suggest using quantitative methods that predict novel interactions based on information about the introduced and resident species, such as traits, phylogenies, or relative abundance, and properties of the recipient ecological network structure (e.g., see Desjardins-Proulx et al. 2017; Terry & Lewis 2020). Past work predicting ecological interactions has been motivated at least partially by the specific problem of predicting interactions of introduced species (e.g., Morales-Castilla et al. 2015; Bartomeus et al. 2016). For example, Pearse and Altermatt (2013) leverage phylogeny to predict interactions between native and non-native species. Predicting the interactions (e.g., links) made by new species (e.g., nodes) joining a network (or "network forecasting") is also a more generic problem with applicability to various scientific domains, such as for protein interaction networks or social networks (Rohr et al. 2016). Approaches for interaction prediction from other quantitative fields are increasingly being applied to ecological networks (e.g., see Desjardins-Proulx et al. 2017; Pichler et al. 2020; Terry & Lewis 2020), with further opportunities to do so.

Introduced and resident species traits

A common approach for predicting interactions between two species is matching their traits, as traits allow or prevent interactions (Bartomeus et al. 2016; Eklöf et al. 2013; Reide et al. 2011). Particularly successful approaches have used machine learning methods to predict unknown species interactions based on databases of known species interactions and associated species traits (e.g., Desjardins-Proulx et al. 2017; Laigle et al. 2018; Pichler et al. 2020). For example, body size is highly predictive of trophic interactions, as predators tend to be larger than prey (Brose et al. 2006; Gravel et al. 2013). Species traits can also be used to identify "forbidden links," those interactions that are known not to occur due to a fundamental mismatch between potential interaction partners (Jordano et al. 2003; Morales-Castilla et al. 2015). For example, one species' jaw must be able to effectively fit and chew another species for a feeding interaction to occur, with mismatches between predator gape size and prey body size limiting potential interactions (Eklöf et al. 2013). Species' phylogenetic relationships can be used as proxies for unknown traits, as species tend to choose new interaction partners that are phylogenetically similar to their existing partners (Elmasri et al. 2020; Morales-Castilla et al 2015; Pearse & Altermatt 2013, Pearse & Altermatt 2015).

Resident species relative abundance

Species relative abundance constrains the likelihood and magnitude of realized interactions, when interactions are possible (Bartomeus et al. 2016; Canard et al. 2014; Morales-Castilla et al. 2015; Pomeranz et al. 2019). If two species are known to co-occur in a habitat, encounters and subsequent interactions are more probable when each species has a high abundance. Two rare species are unlikely to encounter one another and, therefore, are less likely to interact (Bartomeus et al. 2016; Canard et al. 2014). A reasonable prediction therefore is that an introduced species is unlikely to interact with a rare species in the recipient ecosystem, as introduced species often enter ecosystems at low abundances (Hansen et al. 2013; Peterson & Bode 2020). However, this prediction might hold better for generalist introduced species (Canard et al. 2014) or miss consequential interactions between an introduced species and a rare species in the recipient ecosystem (Vázquez et al. 2007).

Local and global structure of the recipient network

Understanding the structure of the recipient ecological network structure can also aid in prediction of interactions between an introduced species and resident species (e.g., as in Dalla Riva & Stouffer 2016; Seo & Hutchinson 2018; Stock et al. 2017; Terry & Lewis 2020). One approach estimates species-level latent traits based on the observed network structure that can be used to make future interaction predictions (e.g., as in Rohr et al. 2010; Rohr et al. 2016). Additionally, various methods take advantage of local network structure to predict interactions (Dalla Riva & Stouffer 2016; Desjardins-Proulx et al. 2017; Rohr et al. 2016). For example, a species such as a generalist consumer with high degree centrality (a metric from network theory based on the number of interactions a species has) in the recipient network might be more likely to interact with the introduced species than another species with lower centrality (Rohr et al. 2016). Potential interactions can also be inferred by fitting models of network structure to partially observed networks, such as group-based models (Allesina & Pascual 2009; Sander et al. 2015) or probabilistic food web models (Williams et al. 2010).

The output of the approaches discussed in Step 3 is a set of plausible ecological network structures for an ecosystem after a species introduction based on adding high probability novel interactions of the introduced species to the recipient network.

Step 4: Predict introduced species establishment success and consequences for resident species population dynamics and ecosystem services

Using the networks produced in Step 3, the next step is to predict whether the species will establish and, if so, how this introduction will impact metrics relevant to each management objective. If the introduced species establishes, it can impact resident species' abundances and biomasses (David et al. 2017) as well as directly or indirectly impact ecosystem services (Walsh et al. 2016). When these impacts are significant and negative the species is considered invasive (Iannone et al. 2020).

Previous theoretical work has identified properties of recipient network structure (e.g., connectance) and introduced species (e.g., generality) that impact species ability to establish and magnitude of impacts (Frost et al. 2019; Hui et al. 2016), sometimes in combination (Baiser et al. 2010; Galiana et al. 2014; Lurgi et al. 2014; Romanuk et al. 2009; Romanuk et al. 2017; Valdovinos et al. 2018). Increasing data collection and further theoretical studies might produce predictive relationships between introduced species and recipient ecosystem characteristics and magnitude of impacts in terms of common management objectives. In our theoretical example, we expand on previous work considering biodiversity outcomes by also considering management objectives related to ecosystem services and impacts under multi-species introductions.

One common approach to produce predictions of introduction success and impacts is using dynamic models, which are systems of equations that track the change in species populations or biomasses over time under the influence of their interaction partners. This family of models include the Lotka-Volterra framework (Lotka 1925; Volterra 1926), bioenergetic consumer-resource models (Williams & Martinez 2004; Yodzis & Innes 1992) such as the Allometric Trophic Network model (Berlow et al. 2009; Brose et al. 2006) (See SI Box 1), and other models developed for specific types of systems (e.g., Valdovinos et al. 2013 for plant-pollinator networks and Christensen & Walters 2004 for exploited aquatic ecosystems). Dynamic models have been used to predict the consequences of species invasions (Baiser et al. 2010; Lurgi 2014; Romanuk et al. 2009; Romanuk et al. 2017; Valdovinos et al. 2018) and intentional introductions (Baker et al. 2019; Peterson & Bode 2020; Peterson et al. 2021). Different dynamic models make different assumptions about systems and thus have advantages and limitations. So, a challenge is deciding what level of complexity is appropriate for a model and what reasonable ranges of parameters should be explored to match a real-world system (Cao et al. 2017; Geary et al. 2020; Martin et al. 2018; Spence et al. 2017). Ensemble techniques in which outcomes are evaluated from several dynamic models or different parameterizations of the same model can be a useful way to account for this uncertainty (Geary et al. 2020; Peterson & Bode 2020; Peterson et al. 2021; Spence et al. 2017).

Although not commonly done, dynamic models can also be used to forecast changes in ecosystem services following a species introduction (Fig. 3). If ecosystem services are included as nodes in an ecological network, one can map the populations or biomasses of connected species to the strength of that service (Dee et al. 2017a). A challenge, however, is specifying the dynamic relationships between species and services (Dee et al 2017; Rieb et al. 2017).

Step 4 produces predictions for how plausible changes in network structure after a species introduction will impact the populations or overall biomasses of species in the recipient network and ecosystem services.

Step 5: Evaluate consequences for multiple management objectives and their trade-offs under uncertainty

Predictions of a range of potential impacts to population dynamics using the quantitative techniques in Step 4 can feed into a structured decision-making process. Structured decision-making is a framework used in conservation to facilitate logical and transparent decision-making by incorporating the values, objectives, and knowledge of stakeholders (Addison et al. 2013; Conroy & Peterson 2013; Gregory et al. 2012), including from local communities and indigenous groups (Rudd et al. 2021). Intentional species introductions are expensive endeavors and assisted migrations may be unappealing due to the risk of failure or risks to resident species. Similarly, interventions to prevent unintentional species introductions carry high management costs and risks of damages to public perception (Diagne et al. 2021). Comparing management alternatives and taking uncertainty in predictions into account before acting can increase the likelihood that interventions meet management goals and avoid unintended consequences (Polasky et al. 2011).

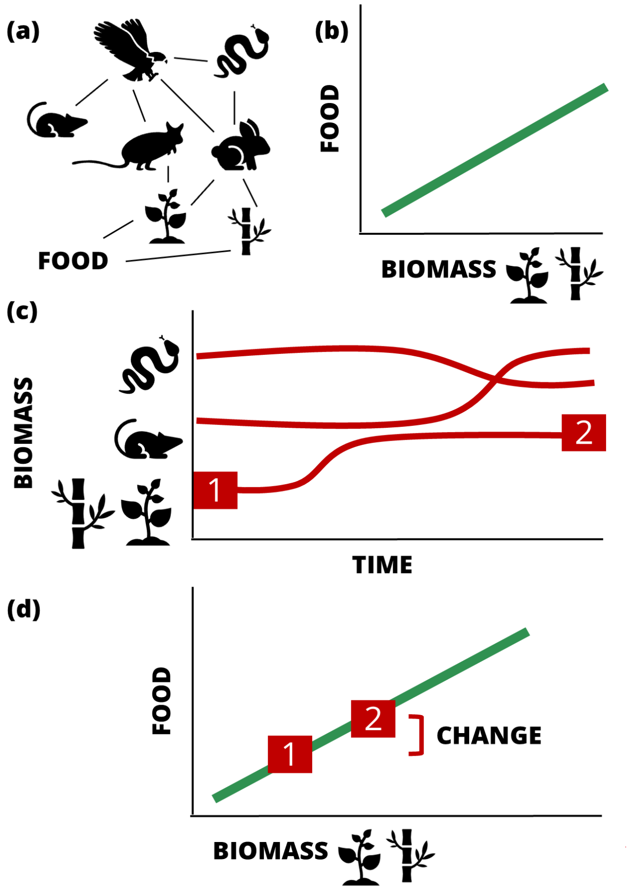

Figure 3. Predicting the change in ecosystem services using dynamic models. Ecosystem services (e.g., food production) can be incorporated into dynamic simulations by (a) including the ecosystem service node in the recipient ecosystem network by identifying which species contribute to that service and (b) fixing a relationship between

the total biomass of the ecosystem service providing species and the amount of the ecosystem service. In our demonstration we chose a simple linear relationship with slope 0.5 that might be characteristic of a provisioning service. Then, (c) the population dynamics for all species are simulated and (d) the change in total biomass of the ecosystem service providing species can be used to estimate the change in ecosystem service amount under population dynamics.

There are many tools for evaluating and comparing alternative management actions to support structured decision-making including optimization and multi-criteria decision analysis (Lester et al. 2013; Polasky et al. 2011; White et al. 2012). The most appropriate approach will depend on the decision context, like whether there are multiple or single objectives, one-time or sequential decisions, and whether outcomes can be expressed in monetary terms. For example, putting some objectives such as the benefits of conserving species and reducing extinction risk in monetary terms is unethical. In these cases, options like cost effectiveness analysis may be preferable approaches and have been used in a variety of contexts (e.g., Gerbert et al. 2018; Joseph et al. 2009). When multiple objectives are important and may pose trade-offs, other techniques like multi-criteria decision analyses or trade-off analyses can be considered (Halpern et al. 2013; Lester et al. 2013; Polasky et al. 2008). Similarly, there are a suite of tools for analyzing decisions under uncertainty and imperfect information (Canessa et al. 2015; Marescot et al. 2013; Memarzadeh & Boettiger 2018; Moore & Runge 2012; Polasky et al. 2011).

Step 6: Improve future predictions

After a decision is made, the system can be monitored to test and explore predictions and update future predictions using an adaptive management approach (Parma et al. 1998; Walters 1986; Williams 2011; Williams & Brown 2018). In adaptive management, the system is monitored after an action is taken (e.g., an introduction has occurred) to update model assumptions and therefore future management recommendations (Williams 2011;Williams & Brown 2018). The same monitoring data can be used to assess the accuracy of predictions from ecological forecasts and allow for improvement of ecological theory (Lewis et al. 2022). As systems are monitored over time, time series datasets are produced, opening opportunities for further refinement of models for ecological forecasting by applying approaches such as empirical dynamic modeling (Daugaard et al. 2022; Johnson et al. 2021, Ye et al. 2015). Monitoring systems to test and improve predictions after structured decision making thus provides an opportunity to iterate between forward and reverse engineering of dynamic models for ecosystems (Martin et al. 2018).

Demonstrating our framework

We demonstrate the application of this framework via a hypothetical example of assisted migration involving a decision in a data-poor context of whether to introduce two threatened species into an existing ecosystem. Rather than analyzing a specific system, we chose to use common theoretical approaches for modeling ecosystems to provide a general illustration of how the framework can produce actionable insights. We chose to investigate a scenario in which one of the introduced species occupies an intermediate trophic level and the other is a top predator. We therefore have four choices of management alternatives – to introduce: neither species, both species, only the intermediate species, or only the top predator species.

Application of Step 1: Define objectives

First, we define our management objectives: to maximize the amount of each introduced species, to maximize the recipient ecosystem's biodiversity, and to ensure the continuity of an ecosystem service supported by the recipient ecosystem. For each, we define quantitative metrics that can be predicted after the species introduction using simulations: the final biomass of the intermediate species, the final biomass of the top predator species, the fraction of resident species remaining in the ecosystem, and the final ecosystem service amount under different introduction alternatives.

Application of Step 2: Identify introduced species

In this hypothetical example of assisted migration, we do not need to forecast which species will be introduced because the species have been chosen intentionally due to their threatened status, and likely compatibility with the recipient ecosystem. For example, in a multi-species assisted migration project in Western Australia, the endangered Shark Bay bandicoot (*Perameles bougainville*) was selected to be translocated to an island refuge just beyond its current distribution (Peterson et al. 2021).

Application of Step 3: Predict interactions

We next predict how the introduced species will interact with species in the recipient ecosystem and contribute to ecosystem services. We follow the modeling approach for simulating species introductions used in Romanuk et al. (2009), Romanuk et al. (2017), and Lurgi et al. (2014). We generate 37 biologically plausible networks representing the recipient ecosystem using the niche model (see SI Box 1; Williams &

Martinez 2000). For demonstration purposes, we explore a case in which there is considerable uncertainty in the interactions of the two introduced species with species in the recipient network. We assume the intermediate species has a niche parameter between 0.4 and 0.6 and that the top predator has a niche parameter between 0.8 and 1 (SI Fig. 12). We generate 5 evenly spaced possible niche parameters for each of the two introduced species in these respective ranges. For each possible niche parameter, we explore a small, medium, and large feeding range as well as a low, middle, and high center of the feeding range (i.e. 5x3x3 = 45 possible niche model parameter sets for each introduced species, see SI Box 1; Williams & Martinez 2000).

We predict interactions of the introduced species based on the niche model rules, so the introduced species eats resident species falling into its feeding range and is eaten by those resident species whose feeding ranges it falls into (see SI Box 1 for details). This produces 45 possible interaction networks shortly after introduction for each of the 37 networks for each of the two alternatives in which species are introduced into each network alone. When species are introduced together, rather than considering 5 evenly spaced niche model parameters for the two species, we consider possibilities based on only 3 each (i.e., 3x3x3=27 niche model parameter sets for each introduced species, reducing the simulations per network to 27^2=729 rather than 45^2=2,025, and the overall computational time from the order of days to hours).

In total, we consider 30,340 total network structures shortly after introduction (45 for the intermediate species, 45 for the top predator species, 729 for both species, and 1 without an introduction, for each of the 37 networks, SI Table 1). For prediction in real-world contexts, one could use species trait data from the recipient ecosystem to establish a relationship between species traits (e.g., body size) and niche parameter values (e.g., as in Gravel et al. 2013, and see Rohr et al. 2016 for a similar approach based on relating traits to latent matching and centrality parameters).

We assume that all basal species (those with only predators and no prey) in the ecosystem directly contribute to a hypothetical ecosystem service of interest; such a relationship might be reflective of services provided by plants, such as carbon storage and sequestration, forage production for livestock, or riverbank stabilization (Calvo-Rodriguez et al. 2017; Zhao et al. 2020). We also assume that neither of the introduced species directly contributes to the basal-provided ecosystem service considered (Mace et al. 2012). We also investigated how results would change if the ecosystem service was provided by a single basal species (i.e., that provides a specialized function), rather than all basal species.

Application of Step 4: Simulate dynamics and consequences of new interactions

Next, we predict the impact of introducing species on population dynamics using the Allometric Trophic Network model (Martinez 2020; Williams & Martinez 2004; Yodzis & Innes 1992). To facilitate decision making under uncertainty, we suggest that outcomes from a wide range of feasible dynamic models are evaluated. In our demonstration, we include within the scope of feasible models Allometric Trophic Network models parameterized with the species interaction network structures produced from Step 3 and with reasonable parameter values based on empirical measurements (see SI Box 1; Brose et al. 2005; Brose et al. 2006; Romanuk et al. 2009; Yodzis & Innes 1992). This is a simplifying choice, and outcomes from additional dynamic models (e.g., Lotka-Volterra models or other parameterizations of the Allometric Trophic Network model) could also be considered simultaneously. We run dynamics for 2000 timesteps after the system has reached equilibrium under the four alternatives.

To track the consequences for ecosystem services, we assume that there is a linear relationship between the total biomass of the ecosystem service providing species and the amount of the ecosystem service provided (Fig. 3). For example, the nitrogen transport amount in a system might be linearly linked to the population abundance of specific bird species (Gaston et al. 2018). However, we recognize that contributions to ecosystem service may not always increase linearly or positively with a species' biomass or abundance (see Dee et al. 2019), and the framework allows for more complex functional forms linking the biomasses of species to the amount of an ecosystem service provided. The output of Step 4 is the final biomasses for each species and final ecosystem service amount after running population dynamics for each of the plausible network structures.

<u>Application of Step 5: Assess trade-offs under uncertainty and identify strategies that avoid worst-case scenarios</u>

Finally, we compare the four alternative actions based on the indicators of our objectives from Step 1. We illustrate Step 5 by applying trade-off analyses from economic decision theory, which is gaining use in conservation (Lester et al. 2013; Polasky et al. 2008), to evaluate the four alternatives given uncertainty over the introduced species niche model parameters and the recipient network structure. Trade-off analysis is a technique for transparent decision-making between management options under multiple objectives. Trade-off analysis identifies Pareto-optimal planning options (i.e., the efficiency frontier), or those in which no objective can be improved without decreasing another. Importantly, trade-off analysis also reveals suboptimal options (see Box 1 for details on Trade-off analysis).

Box 1. A summary of trade-off analysis and Pareto-optimality

Conservation often involves multiple, sometimes competing, management objectives. Trade-off analysis is a technique for transparent decision-making for multiple objectives (Cabral et al. 2016; Lester et al. 2013; Posalsky et al. 2008; White et al. 2012). The application of trade-off analysis involves mapping projected outcomes for each objective that will arise from a particular set of management actions onto an *n*-dimensional space, where each of the axes measures the amount of a particular objective in any relevant unit for that objective (well-defined market values in monetary terms are not necessary; see Polasky et al. 2008). For example, trade-off analysis has previously been applied in marine spatial planning that aims to achieve fisheries yield, energy production, and recreation in the form of whale watching (White et al. 2012) and for balancing trade-offs among social equity, conservation, and economic yield (Halpern et al. 2013).

Trade-off analysis generates a “cloud” of outcomes in the multidimensional space created by metrics corresponding to multiple management objectives, where each point represents the level of an objective (e.g., service amount or population size of a threatened species) provided under a given management option. The shape of the ensuing cloud of management outcomes provides three important insights for elucidating and evaluating potential trade-offs (de Groot et al. 2010). First, it defines the range of best possible planning options – known as the efficiency frontier – where the Pareto-optimal alternatives lie on the outer perimeter of the cloud of outcomes. Pareto-optimal alternatives are those in which no objective can be improved without decreasing another. Therefore, the efficiency frontier represents the best possible outcomes for objectives given multiple management alternatives. However, which outcome on the efficiency frontier is best ultimately depends on how stakeholders weigh and value the different objectives. Second, trade-off analysis identifies suboptimal options, which are all the points interior to the efficiency frontier. Finally, it visualizes interactions among objectives (i.e., do inherent trade-offs exist or not?). The process of visualizing and communicating outcomes from different management alternatives can help surface underlying conflicts amongst decision makers, facilitate deliberations, and help find common ground.

Recent work has demonstrated that trade-off analysis for conservation decision-making can also incorporate uncertainty in outcomes (Cabral et al. 2016). Cabral et al. (2016) show how exposing uncertainty in trade-off analysis can reveal cases in which risk averse decision-makers might choose a more certain suboptimal strategy over an uncertain Pareto-optimal one.

In our case, we assess trade-offs arising from our species’ introduction management alternatives between: the final biomass of the intermediate species, the final biomass of the top predator species, the fraction of resident species remaining in the ecosystem, and the final ecosystem service amount. We use the mean outcomes across simulations within each network to identify suboptimal and Pareto-optimal strategies and plot a plausible efficiency frontier based on each pair of metrics (Fig. 4).

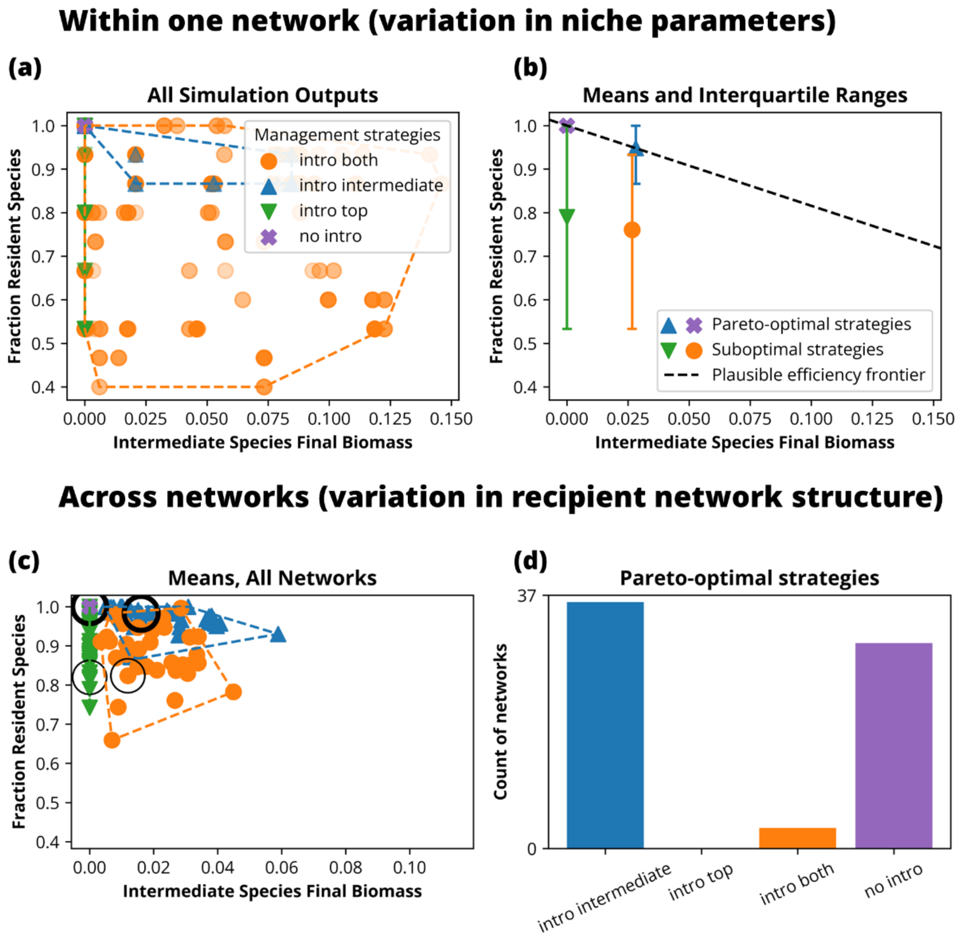

Figure 4. The process used for constructing summary trade-off plots shown in Fig. 5. The first row (subplots a and b) shows the trade-offs for a single network between one pair of metrics, the intermediate species final biomass vs. the fraction resident species remaining. These trade-offs are evaluated for a single network for four management options: introducing both species, introducing just the intermediate species, introducing just the top species, and no introduction. In subplot (a) the full range of simulation outcomes for this single network are plotted for the pair of metrics, with uncertainty due to variation in niche model parameters of the introduced species. In subplot (b), only the mean results for this network are plotted for each management option, along with the interquartile ranges. Pareto-optimal and suboptimal management options are calculated

based on these means for the pair of metrics, and a plausible efficiency frontier is plotted. In the second row (subplots c and d), the mean outcomes are plotted for all 37 of the networks that we evaluated for these two metrics, with uncertainty due to recipient network structure. The outcomes for the network shown in subplots (a) and (b) are circled for demonstration and the Pareto-optimal strategies are bolded. In subplot (d) the Pareto-optimal strategies are counted across the networks evaluated, to demonstrate how variation in recipient network structure impacts the optimal decisions for this pair of metrics. A full set of trade-off plots showing all two-way metric combinations for an example network is provided in the Supporting Information (SI Fig. 5 and SI Fig. 6).

We also compare this approach to a less conservative approach to decision-making based on the median outcome metrics and to a highly conservative approach to decision-making under uncertainty based on the worst possible, rather than mean, outcomes under each management alternative (i.e., using the maxi-min objective, see Polasky et al. 2011).

Application of Step 6: Testing predicted outcomes

Given the results of the trade-off analysis and relative weighting of objectives, we assume a decision would be made to introduce both threatened species. After this introduction, data could be collected on the final biomasses of the introduced species and impacts to the ecosystem services and biodiversity of the recipient ecosystem. These values could be compared to the range of predicted outcomes to evaluate the applicability of the assumptions used for predictive modeling.

Results

Choosing the best strategy balancing multiple objectives

Our results provide general heuristics that can guide conservation decision-making under high uncertainty in recipient network structure and the interactions of the introduced species by considering Pareto-optimal strategies in aggregate across all plausible networks (as shown in Fig. 5).

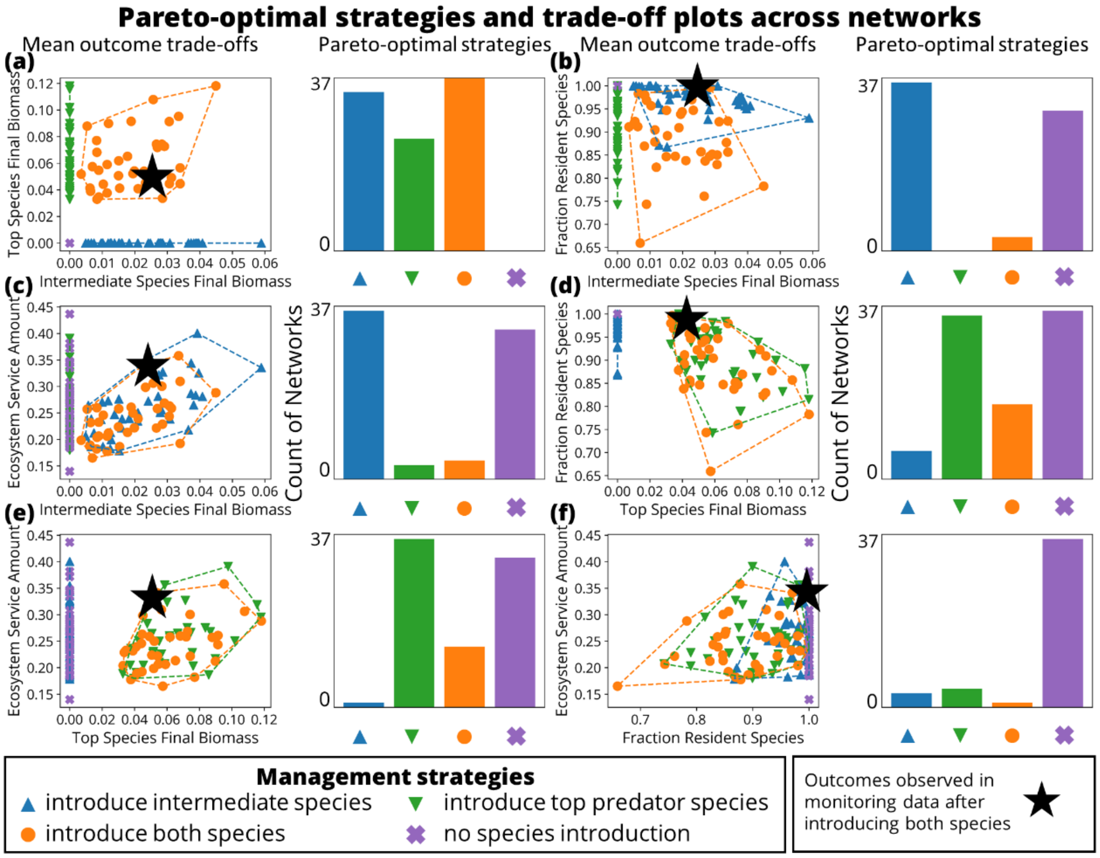

Figure 5. Trade-off plots for every pair of outcome metrics across the 37 networks and four management strategies evaluated. The means in outcome metrics across simulation runs are used to summarize for the management alternatives involving introductions (the process of constructing these plots is shown in Fig. 4). The counts of Pareto-optimal management strategies across networks are tallied to the right of each summary plot for each pair of metrics to elucidate trends in results across different recipient ecosystem network structures. After a decision is made, in this case to introduce both species, the outcomes for the metrics observed from monitoring data can be compared to the mean outcomes from the simulations to potentially adjust and improve future predictions for the ecosystem (Step 6). To illustrate Step 6, we include example outcomes observed from monitoring data as stars.

Any introduction option involves risk to resident species biodiversity and ecosystem services compared to no introduction (Fig. 6b, 6c, 6e). The introduced top predator species generally establishes with a higher mean final biomass than the introduced intermediate species across networks (in alignment with previous results, e.g., Galiana et al. 2014; Romanuk et al. 2009) and has on average more negative and more variable impacts on the ecosystem service amount (Fig 6). If the ecosystem service is assumed to be provided by only one basal species rather than all basal species, the top predator introduction still tends to have a more negative impact to services; however, across management options there is more variability in whether the ecosystem service amount increases or decreases after an introduction (or, shows directional indeterminacy, see Yodzis 1988, Fig. 6f). Occasional positive impacts to ecosystem services were due to indirect effects from the introduction in which intermediate species decreased in biomass after an introduction, thus reducing pressure on basal species and allowing basal species biomass to increase (SI Fig. 2). These results are laid out in detail in SI Box 2.

Considering trade-offs between the final biomasses of both introduced species, all three of the introduction alternatives are often Pareto-optimal across the networks, with introducing both species being Pareto-optimal the most often (Fig. 5a). However, in order to maximize resident species biodiversity and ecosystem service values, introducing just one species or none tends to be favorable (Fig. 5b, 5c, 5d, 5e). Finally, if we only consider the outcomes for resident species biodiversity and ecosystem service values, refraining from introducing either species tends to be a Pareto-optimal strategy for reducing risk to resident biodiversity and ecosystem services (Fig. 5f).

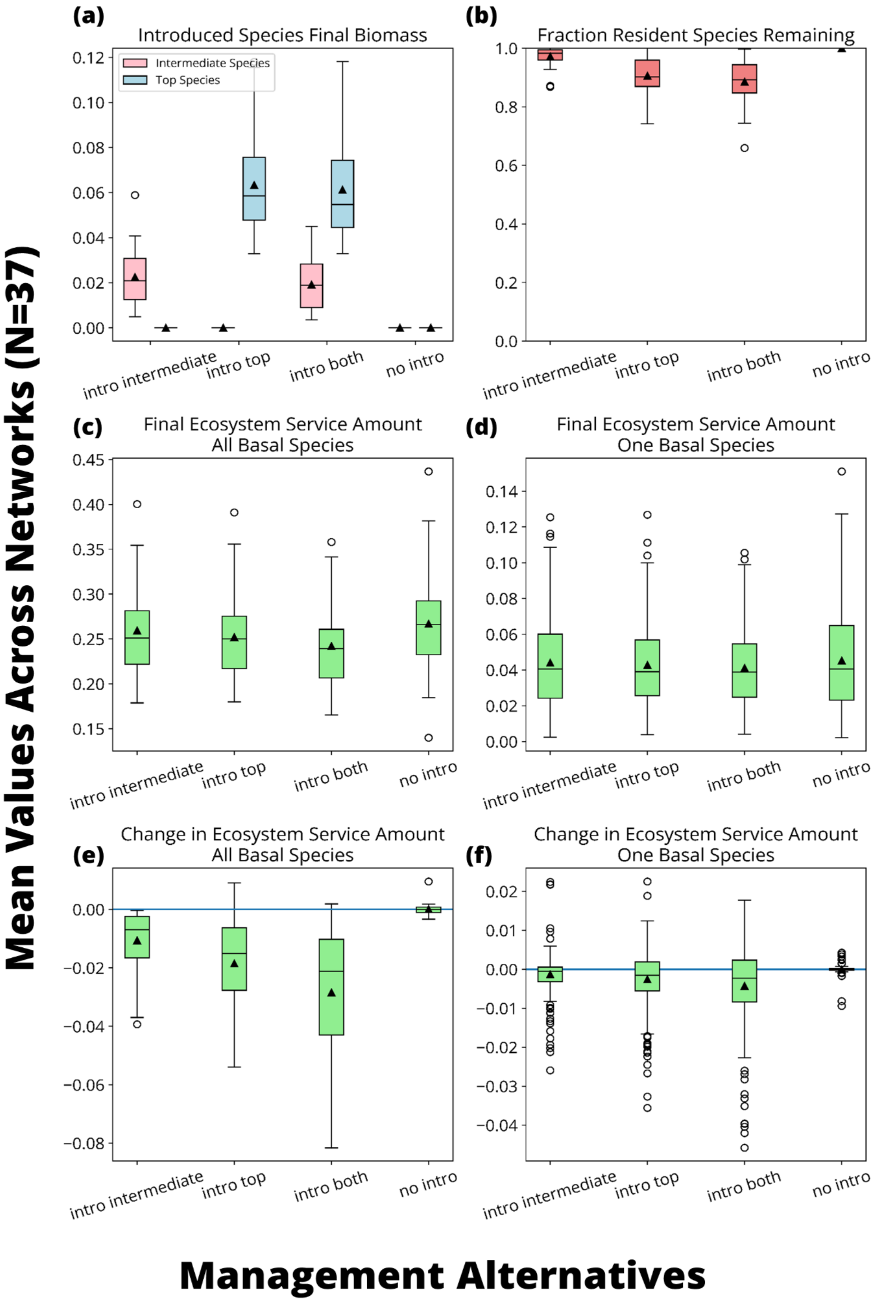

Figure 6. Results for the four metrics corresponding to management objectives under four management alternatives. Results for the four metrics (a: Intermediate Species Final Biomass & Top Species Final Biomass, b: Fraction Resident Species Remaining, c: Final Ecosystem Service Amount) evaluated in the trade-off plots are

summarized across the 37 networks for each of the four management alternatives to show general patterns across networks as well as between-network variability in outcomes. For the three management alternatives involving introductions the mean results used in the trade-off plots are summarized (median results are shown in SI Fig. 3). Aggregate results are also shown in subplot (d) for if the ecosystem service was presumed to be provided by one basal species rather than all basal species. To produce the results shown in subplot (d), for each network, the final ecosystem service amount was calculated assuming the ecosystem service was provided by each basal species in the network rather than all basal species (one data point per management alternative, network, and basal species in that network). Subplot (e) shows the change in final ecosystem service amount after an introduction under each management alternative and subplot (f) summarizes this same value when the ecosystem service is provided by a single basal species in the network. One outlier network with a large change in ecosystem service amount was removed from subplot (e) for clarity (full subplot shown in SI Fig. 7).

We also explore results using medians of the outcome metrics (SI Fig. 3), which is a less conservative approach, as rare, extreme negative outcomes from introductions have less impact on the Pareto-optimal strategies. The primary difference in these results is that introducing neither species is Pareto-optimal less often. Finally, we also consider a decision-making context using the more conservative maxi-min criteria (Fig. 7). Under the maxi-min objective, decision-makers choose the alternative with the best worst outcome (see SI Fig. 4, Polasky et al. 2011). Using the maxi-min decision criteria, the results generally suggest that it is best to pursue no introduction due to the risks of negative impacts to resident biodiversity and ecosystem services.

Sensitivity of results to uncertainty identifies when more information is needed

Producing a range of outcomes under uncertainty also allows us to identify when results are most sensitive to uncertainty in the recipient network structure and interactions of the introduced species. This could suggest when it is most important to collect more data to resolve uncertainty in assessment of management options. Not all 37 network structures produce the same results for Pareto-optimal strategies considering each pair of metrics (Fig. 5). Notably, the top predator, introduced independently or together with the intermediate species, shows more between-network variability in establishment success and impacts (Fig. 6a, 6b, 6e). This sensitivity suggests that it may be more important to resolve recipient network structure when evaluating risks for a top predator introduction.

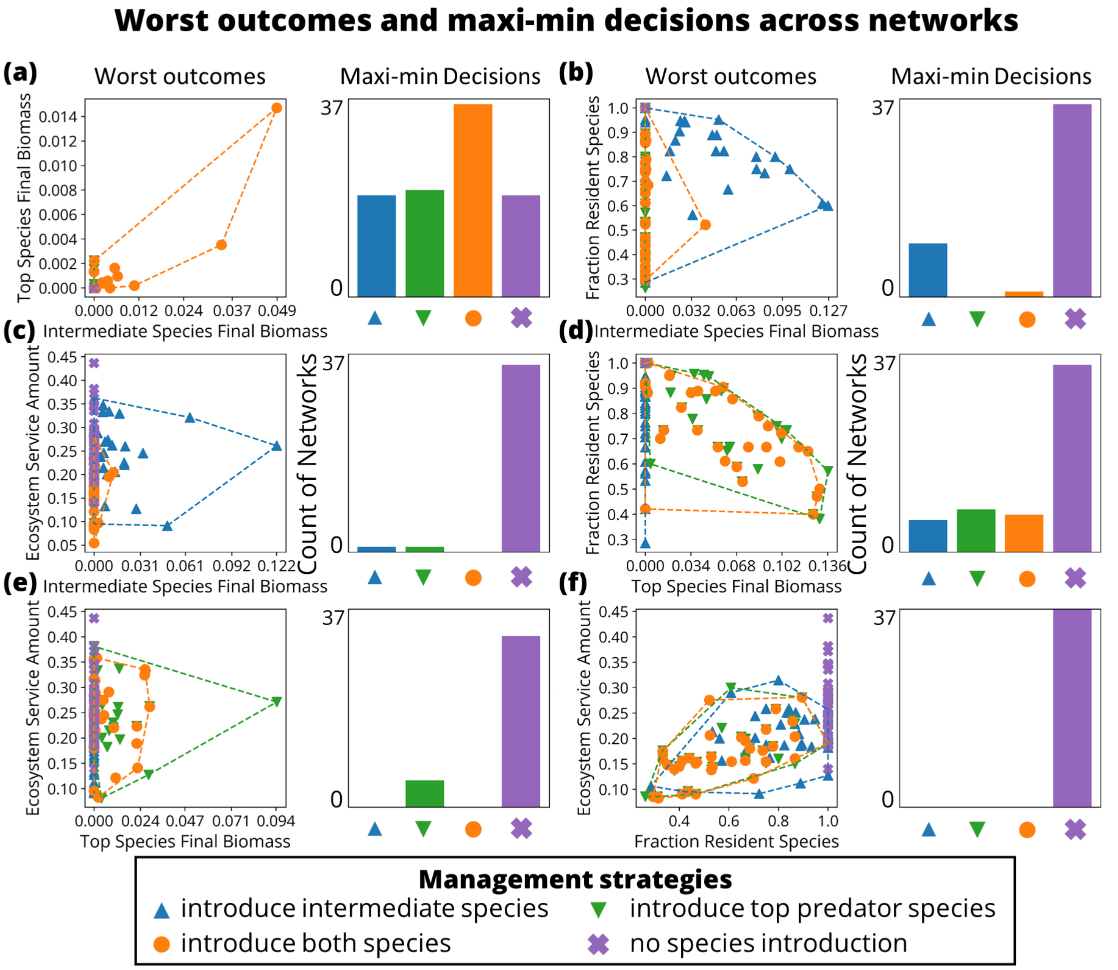

Figure 7. Worst-case plots for every pair of outcome metrics across the 37 networks and four management strategies evaluated. We compute the worst outcome by normalizing the range of the axes to [0,1] and measuring the Euclidean distance of each outcome to the origin. Outcomes closest to the origin are considered the worst and maxi-min decisions are the options with worst outcomes furthest from the origin. The counts of maxi-min decisions are tallied in summary plots to the right of the plots for each pair of metrics to elucidate trends across different network structures characterizing the recipient ecosystem.

For ecosystem services, the importance of reducing uncertainty in the recipient network structure depends on the assumptions about how species provide services (Fig. 6c, 6d, 6e, 6f). When all basal species provide a service the results are more directionally consistent than when one basal species provides a service (Fig. 6e, 6f). One species providing a service might realistically be the case for some regulating or provisioning services (e.g., for rare species, see Dee et al. 2019), and in these cases reducing uncertainty in network structure would be more important before decision-making.

Additionally, we observed within-network variability in results based on the uncertainty in plausible niche parameters, and thus the novel interactions, of the introduced species (Fig. 8). The final introduced species biomasses showed more within-network variability than the other metrics. The intermediate species showed more within-network variability in establishment success than the top predator species (Fig. 8a), while the top predator species showed more within-network variability in impact to resident species biodiversity and ecosystem services than the intermediate species (Fig. 7b, 7c). The impact to ecosystem services had higher within-network variability when the ecosystem service was provided by one basal species rather than all basal species (Fig. 8d).

Monitoring the system and improving future predictions

Examples of true outcomes after choosing to introduce two species are visualized on the plots in Fig. 5. In an adaptive management approach, we can use these observed outcomes to adjust assumptions for future decision making, for example by putting more weight on the network structures that produced predictions closer to the observed outcomes when summarizing simulation results. With the observed outcomes displayed in Fig. 5, we might now assume that there is less risk to resident species biodiversity and basal-provided ecosystem services under species introductions than previously thought. If one observes that outcomes are outside of the range of predictions for the management option chosen, then the underlying modeling assumptions must be revisited for future decision-making. Other models could be compared to see if they provide predictions that align with observations (e.g., providing an opportunity to test ecological theory as in Lewis et al. 2022) or, once sufficient time series data is collected, dynamic models could be reverse engineered (Martin et al. 2018).

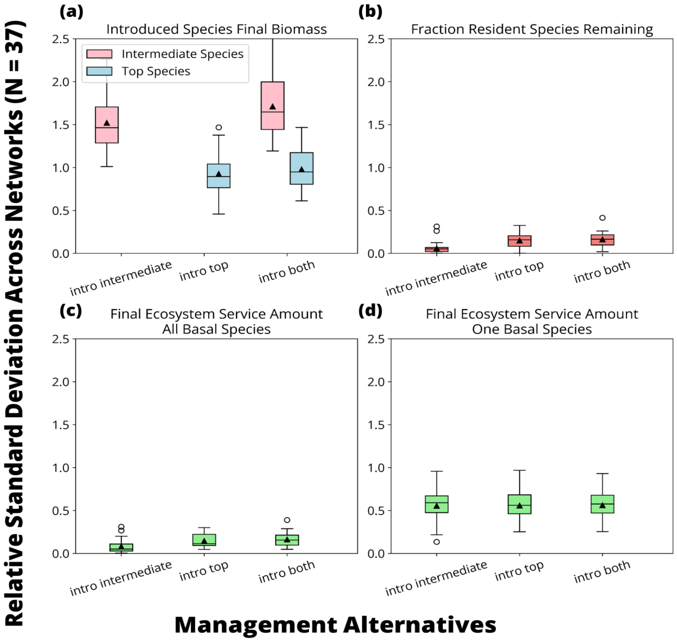

Figure 8. Relative standard deviation of results within each network across uncertainty in introduced species niche model parameters. The relative standard deviation in results across simulations within a network for each of the four metrics used in the trade-off plots (a: Intermediate Species Final Biomass & Top Species Final Biomass, b: Fraction Resident Species Remaining, c: Final Ecosystem Service Amount) and three management alternatives involving introductions are summarized across the 37 networks to reveal general patterns related to within-network variability in outcomes. Higher relative standard deviations indicate that the results for this metric across simulations within a network are more spread out from the mean. In subplot (d), the relative standard deviation is also shown for when a single basal species provides the ecosystem service.

Discussion

Species introductions are increasing, from shifts in distributions due to climate change (Wallingford et al. 2020), intentional movement of species by humans for conservation (Peterson & Bode 2021), and invasions facilitated by human activities (David et al. 2017), posing risks for resident biodiversity (Mollot et al. 2017) and ecosystem services (Pejchar & Mooney 2009; Vilà & Hulme 2017) that are challenging to predict and mitigate. In response, we have synthesized prior work to suggest a framework for predicting and managing species introductions into existing communities of interacting species. This framework synthesizes literature from invasion biology and network ecology (e.g., Hui & Richardson 2019; Hui & Richardson 2022; Romanuk et al. 2009; Romanuk et al. 2017) with literature from conservation and management (e.g., Bullock et al. 2011; Dee et al. 2017b; Harvey et al. 2017; Tylianakis et al. 2010), describing a theoretically grounded process to assist in applied ecological decision-making (Possingham et al. 2000) under unavoidable uncertainty surrounding global change.

We demonstrate how this framework can be applied using a theoretical case study of assisted migration, yet the potential applications are much broader (Table 1). This framework could be applied in future work for other intentional species introductions, such as species introductions for biological control, restoration, agriculture, or aquaculture. It could also help inform actions to prevent unintentional species invasions by considering trade-offs between likely impacts of an invasion and the cost, effort, and potential effects of mitigation strategies. Our illustrative application of the framework produces general heuristics to guide management but also makes many assumptions, including that trophic interactions determine ecosystem dynamics (see SI Box 1) and that one does not need to consider the order of species introductions (Armstrong & Seddon 2007). Future applications of our predictive framework need not follow these assumptions, and, for instance, could use alternative techniques for novel interaction prediction (e.g., following Rohr et al. 2016) or dynamic modeling (e.g., Lotka-Volterra models, Lotka 1925; Volterra 1926), or also include predictions based on a different approach, such as neutral theory (Hubbell 2005). This framework could also be expanded and more broadly applied to additional types of disturbances such as species removals or landscape change.

Table 1. Examples of other potential applications of our framework. Case studies involving species introductions and various management objectives to illustrate other contexts in which this framework could be applied.

Decision context	Example Case	Objectives	References
Introduce a species for ecosystem services	Dung beetles are commonly introduced because they can provide a variety of ecosystem services. In New Zealand, the addition of new, non-native dung beetles to livestock farms resulted in a significant decrease of run-off and sediment in run-off following rainfall events; and dung beetles reduced the number of parasitic larvae that infect grazing animals.	Maximize ecosystem services Minimize risk to native biodiversity	Forgie et al. (2018) Brown et al. (2010) Sands & Wall (2016)
Introduce a species to maintain or restore biodiversity	Oyster reefs are considered one of the most vulnerable coastal ecosystems in the United States Atlantic and Gulf Coasts. Restoration of these ecosystems, i.e., reintroducing native oysters to areas that previously hosted them, is commonly considered as a way to both restore oyster populations and reestablish lost biodiversity. In Mosquito Lagoon, FL, United States, sites with oyster restoration showed an	Increase the population of a species in decline Maximize biodiversity (e.g., species richness)/Minimize risk to	Barber et al. (2010) Lown et al. (2021)

	increase in animal biodiversity (number of species) compared to sites without oysters.	native biodiversity	
Introduce a threatened species for conservation	Bull trout (*Salvelinus confluentus*) are threatened by warming waters and invasive lake trout (*Salvelinus namaycush*). In Glacier National Park, US, biologists are moving bull trout from their native range into lakes at higher elevations with more suitable conditions and where they no longer need to compete with invasive lake trout for food resources such as invertebrates and other fish.	Increase the population of a species in decline from climate change Minimize risk to native biodiversity	Karasov-Olson et al. (2021)
Prevent or slow future, predicted introduction of invasive species	The zebra mussel (*Dreissena polymorpha*) is an invasive species that has spread throughout United States waterways including the Great Lakes. Zebra mussels can have detrimental impacts on recipient ecosystems, including drastic decreases in zooplankton which indirectly impacts larval and juvenile fish populations. However, controlling established zebra mussel populations is costly and time consuming. There are a variety of strategies that have been deployed to slow the future spread of this mussel species, including boat inspections and bait regulations.	Minimize invasion establishment Minimize risk to native biodiversity Minimize management costs	Ashander et al. (2022) Bossenbroek et al. (2007)
Mitigate impacts of slow future, predicted introduction of species due to a range shift	Mobile fish species in marine habitats are able to evade the most severe effects of climate change by shifting their distribution when seeking suitable thermal habitats. However, this shift in their ranges can result in changes to food webs, increased competition for prey species, and present complications in managing species whose ranges shift to new jurisdictions. For example, the Atlantic Cod (*Gadus morhua*) is culturally and economically crucial species in North Atlantic fisheries, though its optimal thermal habitat is	Minimize risk to native biodiversity Minimize management costs	Kleisner et al. (2017) Selden et al. (2018) Palacios-Abrantes et al. (2020)

	shifting into waters beyond the US EEZ into Canadian jurisdiction.		

One limitation to using this framework in practice is low availability of data in many applied settings. Missing species interaction, trait, and abundance data can interfere with novel interaction prediction in Step 3 and parameterizing dynamic model simulations in Step 4. Species interaction data can be collected in a variety of ways, such as direct observation of interactions or stable isotope analysis of feces (Delmas et al. 2019; Kamenova et al. 2017; Vacher et al. 2016). Species interaction network structure can also be inferred based on patterns of species co-occurrence, though methodological limitations have been noted for this common approach, for example noting that species co-occurrence can be caused by abiotic factors unrelated to interaction (Barner et al. 2018; Blanchet et al. 2020; Connor et al. 2017; Ladau 2008). These processes are labor-intensive and further work is needed to develop methods to efficiently construct ecological networks at scale (Bohan et al. 2017; Kamenova et al. 2017; Stock et al. 2017; Terry & Lewis 2020).

Our results align with previous results (e.g., Yodzis 1988) showing that impacts of perturbations on species-level metrics, in our case ecosystem services provided by basal species, are not always directionally consistent under reasonable uncertainty in species interactions (but see Iles & Novak 2016). However, precisely predicting dynamics of an ecosystem and producing predictions useful for decision-making under uncertainty are not equivalent aims (Adams et al. 2020). Even uncertain predictions can prove useful for comparing likely realities with or without an intervention (Adams et al.

2020; Possingham et al. 2000), understanding the risks of undesirable outcomes (Adams et al. 2020; Regan et al. 2005; Tunney et al. 2017), and identifying when to collect more data before making a decision (but also see more formal Value of Information approaches, Canessa et al. 2015; Xiao et al. 2019). Here, we show that currently available tools for ecological forecasting can be used to produce a range of predictions useful for some decision-making contexts.

Species introductions provide natural experiments that can provide insights for basic ecological research (Sax et al. 2007). Further, intentional species introductions through management are happening around the world and provide underutilized opportunities for testing dynamic population models by collecting data before and after the introduction, after allowing adequate time for introduced species to potentially establish. Applying this framework provides an opportunity to test ecological theory and further investigate the fundamental predictability of ecosystem dynamics by taking advantage of applied management contexts. *A priori* predictions before decision-making allow both for more transparent consideration of trade-offs as well as development of knowledge about a system over time through adaptive management.

Our synthesis also suggests other fruitful avenues for future work. Our results demonstrate that assumptions about the novel interactions of an introduced species (e.g. approximate trophic level, generality) can influence the range of outcomes expected after introduction, and thus call for further methodological development for predicting the novel interactions of introduced species in ecosystems and theoretical investigation of how introduced species properties relate to expected biodiversity and ecosystem service outcomes. Our results also demonstrate sensitivity of results to assumptions about which species provide ecosystem services in recipient ecosystems (Fig. 6), and thus suggest further integration of ecosystem services into empirical ecological networks. While we focus on a simple linear relationship between basal species and an ecosystem service amount, future work can also further explore the potentially non-linear functional relationship between species biomass and the amounts of multiple ecosystem services provided by an ecosystem (e.g., Dee et al. 2017a; Gaston et al. 2019; Manning et al. 2018).

Conclusions

We synthesize literature into a decision-making framework for species introductions under multiple conservation objectives and uncertainty in species interactions. We show how this framework can be used to produce a range of predictions useful for decision making in a theoretical high-stakes case study of assisted migration. This framework, which combines ecological network theory with approaches from decision science, can be used to reveal trade-offs among objectives, avoid decisions that can lead to worst-case scenarios, suggest cases in which it is more important to reduce uncertainty before decision-making, and allow for continual learning about the system in a process of adaptive management.

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