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Reducing uncertainty in species management: forecasting secondary spread with expert opinion and mechanistic models

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Abstract. Predicting the spatial and temporal dynamics of invasive species is critical for successful management intervention, yet substantial uncertainty exists about how species will interact with human pathways when introduced to new ecosystems. We demonstrate a novel approach for quantifying uncertainty when predicting the uptake, movement, and establishment of invasive species by combining mechanistic modeling of the spread process with expert opinion of the demographic factors that govern species performance. We demonstrate the utility of this approach using a case study involving the transfer potential of nonindigenous species (NIS) in the Laurentian Great Lakes basin (GLB). A survey using structured expert judgment was completed by 24 North American taxonomic experts, covering 60 species of NIS established in the GLB. Experts estimated species-specific demographic parameters describing population growth and establishment potential, which were incorporated into an existing mechanistic model of human-mediated spread via ballast water with species-specific spread rates (number of ports or lakes invaded/year) as outputs. Expert judgments within each group varied widely, indicating that generalizable rates of spread across taxa are unlikely and highlighting the value of cross-taxon comparisons. Most species were predicted to establish throughout the GLB within 10 yr, assuming status quo management conditions. Sensitivity analysis for expert performance-based weighting demonstrated that most model outputs were insensitive to weighting (<1% difference over baseline) and shows the robustness of the joint model. Overall, the joint expert opinion and predictive modeling method demonstrates a novel means of handling sparse data when forecasting invasion dynamics. Divergent estimates resulted in a range of likely spread rates, but improved upon traditional best-guess approaches. Incorporating joint methods into ecological decision-making frameworks has clear implications for invasive species management but may also inform other ecological scenarios where data are scarce and conservation action is urgent.

Key words: ballast water; ecological management; expert judgment; Great Lakes; invasive species; mathematical modeling; population dynamics; prediction.

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Introduction

Forecasting the performance of nonindigenous species (NIS) in novel ecosystems is fundamental for making sound ecosystem management decisions. In principle, identifying the species most likely to establish and spread allows prevention and control programs to confront invasions based on the greatest perceived risk to native species and ecosystems. However, in practice, decisions are challenging due to the high degree of epistemic and stochastic uncertainty surrounding all aspects of the invasion process (Mack et al. 2000, Ricciardi et al. 2011), including how invasive species will interact with human pathways (Essl et al. 2015). The relevance of human pathways in mediating invasions was identified early in the field of invasion biology (Elton 1958) and has become increasingly recognized with globalization (Sala et al. 2000, Butchart et al. 2010, Padayachee et al. 2017). Human pathways, particularly those linked with transport and commerce, therefore present a critical avenue for monitoring, prevention, and control (Lodge et al. 2006, 2016, Wilson, et al. 2009). Despite evidence that "shoot first, ask later" tactics are often the best way to prevent the establishment of new invaders (Bax et al. 2001), many management decisions have demonstrated complacency to newly discovered species in the absence of scientific knowledge (Simberloff 2003). To navigate this impasse, methods for increasing the accuracy of forecasting are needed and would ultimately result in more deliberate and effective prevention management decisions.

In addition to propagule pressure (Jeschke and Strayer 2008), there are two main mechanisms that strongly dictate invasion success—the ability to establish reproducing populations from small initial population sizes and the rate of population growth (Williamson and Fitter 1996, Blackburn et al. 2015). These two factors also influence natural dispersal and, importantly, dictate how a species may spread across landscapes if it has the opportunity to interact with human pathways. Gaining a better understanding of the magnitude of each of these factors is critical in forecasting the extent to which invasion dynamics might manifest in a new environment. For example, poor ability to establish at a small introduced population size coupled with a generally slow population growth rate is more likely to result in patchy establishment success, slow rates of secondary spread, and generally reduced potential to interact with human pathways. Conversely, high establishment success following introduction and a high population growth rate should result in more opportunity to interact with human pathways and the potential rapid and accelerating movement of the new invader throughout suitable habitat. By disentangling the processes through which these two factors dictate species performance in a novel environment, including their potential to interact with human pathways, the relative risk of spread is more likely to be quantifiable.

Using models to explore complex system dynamics and unobservable phenomena is common in ecology and can help make informed management decisions under a series of simplifying conditions (Hilborn and Mangel 1997, Irwin et al. 2011). Models have been critical tools to gain a better understanding of key invasion processes, such as the relationship between initial population size and population establishment (i.e., the risk–release relationship; Leung et al. 2004, Wonham et al. 2013), the importance of Allee effects in introduced populations (Kanarek et al. 2013), and the likelihood of achieving a desired management outcome, such as population suppression (Tsehaye et al. 2013). However, while models provide a sound representation of the mechanisms underlying the invasion process, their forecasting accuracy is often limited by a lack of species- and site-specific information, which can lead to tenuous assumptions about system dynamics. For example, forecasting models may assume similar demographic rates in native and introduced populations, expect historical rates of spread to reflect future rates of spread (Peterson and Vieglais 2001), and assume that species impacts are independent of trophic conditions in the introduced range (Ricciardi et al. 2013, Jeschke et al. 2014). These choices can have important consequences on the projected vs. realized ecological dynamics of invasive species and the allocation of management resources, illustrating the need to capture the uncertainty associated with invasions using structured and quantitative methods.

One approach for capturing uncertainty involves the use of expert-elicitation methods, which have been used to derive key information from experts in many fields of study (e.g., engineering intervention, geological exploration, Burgman 2005; or climate change, Morgan et al. 2001, Bamber and Aspinall 2013). Expert judgment is not intended to be a substitute for data obtained through experimental or other scientific means, but rather provides a useful method to allow conclusions to be drawn in situations where there are little to no data available (Cooke 1991). The use of elicited expert information has, at times, been viewed with suspicion by the scientific community due to limited control over the effects of bias and subjectivity of individual opinions (Tversky and Kahneman 1974, Kynn 2008). Often, scientific research aims to reduce uncertainty, whereas the opinions of experts are, by nature, indefinite (Cooke 1991, Burgman 2005). However, well-constructed expert-elicitation techniques aim to reconcile these differences by capturing and quantifying uncertainty rather than avoiding it (Aspinall 2010) and by ground-truthing responses against known quantities, thereby providing a transparent and standardized approach to capture a range of possible outcomes.

We show how combining contemporary expert opinion methods with mechanistic modeling of the interaction between invasive species and human pathways might be incorporated within a broader decision-making framework for invasive species management. Although several studies have used this method to forecast standard population processes, such as the rates of population increase (Murray et al. 2009, Wittmann et al. 2014*a*, 2014*b*, 2014*c*, Kerr et al. 2016), to our knowledge, few have done so for multiple taxonomic groups that would allow for both inter- and intraspecific comparisons (c.f. Zhang et al. 2016). We begin by defining a standardized metric based on common aspects of the invasion process: (1) population growth rate, which influences the probability that species will increase in number and, thus, the potential to be transported by human pathways, and (2) the likelihood of establishment at transported population sizes, defined as the maintenance of a local, reproductive, self-sustaining population (Lockwood et al. 2007), which controls the development of new satellite populations across a landscape and the distribution of new populations to act as sources. We parameterize the model with probability distributions describing demographic factors obtained through an expert-elicitation process, with the aim of considering how generalized patterns of spread are affected by both population growth and establishment probability. By comparing projected rates of spread across a diverse group of aquatic invaders, we provide a standardized index that describes the relationship between taxonomic group and secondary spread, measured in a manner suitable for management intervention (time required for species to saturate available sites). Finally, by identifying species-specific trajectories over time and space, we demonstrate how this process can be used to inform invasive species management in a decision-analytic framework.

Methods

Study system

To demonstrate the utility of our approach, we conducted a model-based assessment of NIS in the Laurentian Great Lakes basin (GLB) including fresh waters of the St. Lawrence River. A total of 60 species across eight taxonomic groups were chosen from the Great Lakes Aquatic Nonindigenous Species Information System (NOAA-GLANSIS; USGS 2016) for assessment, covering algae, bryozoans and hydrozoans, bacteria and viruses, crayfishes, fishes, mollusks, plants, and zooplankton and oligochaetes. A list of species was compiled for those species not already reported as present in all five Great Lakes and the St. Lawrence River (n = 99) to identify those presenting an ongoing threat of spread (Appendix S1). To ensure the survey length remained realistic for expert engagement while maintaining species specificity, groups containing >15 species were randomly subsampled at family level to reduce sample size to 60. Full details of the geographic extent of the study area and species selection criteria can be found in Appendix S2.

Expert-elicitation survey

A variety of methods exist for eliciting expert information (for review see Kuhnert et al. 2010, Martin et al. 2012). We used structured expert judgment (SEJ) to better understand the demographic parameters of invasive species in the GLB. Structured expert judgment is a process that systematically quantifies uncertainty in expert responses as part of a comprehensive survey process by treating expert estimates as scientific data (Cooke 2013). The survey was conducted primarily to obtain species-specific data (species establishment potential and population growth rate). Additional information involving ecological impact and potential mitigation measures was also elicited for a second study. Experts were carefully selected to participate in the SEJ process based on the number of publications and/or years of experience in studying or managing one or more of the taxonomic groups of NIS present in the Great Lakes. The number of taxonomic experts per species group ranged from one (algae, and bryozoans and hydrozoans) to 10 (fishes). Of the 24 respondents, experts mainly held academic or government positions, with an average of 20 yr of relevant research or management experience (Table 1). To capture the full range of expert judgments within each taxonomic group while adhering to SEJ principles, we used a three-point quantitative interval method for obtaining a triangular probability distribution for each response (adapted from Speirs-Bridge et al. 2010). This approach required experts to report minimum, modal, and maximum values for each response, but differs from the four-point method by Speirs-Bridge et al. (2010) fixing the confidence interval to 95%. Such a method thereby captures the full range of expert uncertainty and improves upon a single-point best-guess estimate. Expert responses were incorporated within subsequent stages of the study as triangular probability distributions.

Table 1. List of 24 experts who participated in the study and agreed to recognition.

Name	Affiliation
Shelley Arnott	Department of Biology, Queen's University
Ashley Baldridge Elgin	NOAA Great Lakes Environmental Research Laboratory
Jonathan Bossenbroek	University of Toledo
Lindsay Chadderton	The Nature Conservancy
Randall M. Claramunt	Michigan Department of Natural Resources, Fisheries Division
Mohamed Faisal	College of Veterinary Medicine, Michigan State University
Crysta Gantz	Portland State University, Portland, Oregon (formerly University of Notre Dame)
Don Jackson	University of Toronto
Tim Johnson	Ontario Ministry of Natural Resources and Forestry
Reuben Keller	Loyola University Chicago
Patrick M. Kočovský	United States Geological Survey (USGS)
Brian Lantry	United States Geological Survey (USGS)
Hugh MacIsaac	University of Windsor
Julian Olden	University of Washington
Anthony Ricciardi	Redpath Museum & McGill School of Environment, McGill University
Ed Roseman	United States Geological Survey (USGS)
Lars Rudstam	Cornell University
Jeff Schaeffer	USGS Great Lakes Science Center
Andrew Tucker	The Nature Conservancy
Jake Vander Zanden	University of Wisconsin-Madison
Brian Weidel	USGS Great Lakes Science Center
Gary Whelan	Michigan Department of Natural Resources, Fisheries Division
Anonymous 1	
Anonymous 2	

Note: All responses were held anonymously during analysis.

Previous studies in aquatic ecology have performed expert-elicitation interviews in person (Rothlisberger et al. 2012, Wittmann et al. 2014*b*, 2014*c*) as recommended in most elicitation guidelines (Martin et al. 2012). While these approaches have advantages (e.g., ensuring consistency, providing direct feedback during surveying, encouraging completion), there is a need for more efficient survey methods to harness expert opinion without compromising the quality of information obtained. This study used a remote surveying method, conducted online through a web-hosted survey platform (SurveyMonkey 2016). Eight versions of the survey were created, one each to elicit demographic information for each species contained within the eight taxonomic groups in the sample (Fig. 1). Regardless of taxon, survey questions followed the same format to obtain two population demographic parameters relating to the establishment potential of an individual species in any of the Great Lakes: (1) propagule size, as the minimum number (density) of individuals, required for a 95% chance of establishment (assuming ideal environmental and demographic conditions), and (2) the rate of population growth, as the minimum length of time, required to reach maximum population density at a release site (see Appendix S2 for survey protocol and instrument). These demographic parameters are referred to as establishment potential and population growth rate, respectively, which were retained for use within an existing mechanistic model of secondary spread (described below; see Drake et al. 2015*a*).

Combining expert judgments

Given their use in estimating unknown parameters, expert-elicitation methods present a challenge in verifying the accuracy and confidence of elicited values. Classical approaches are generally comprised of two components: one to verify

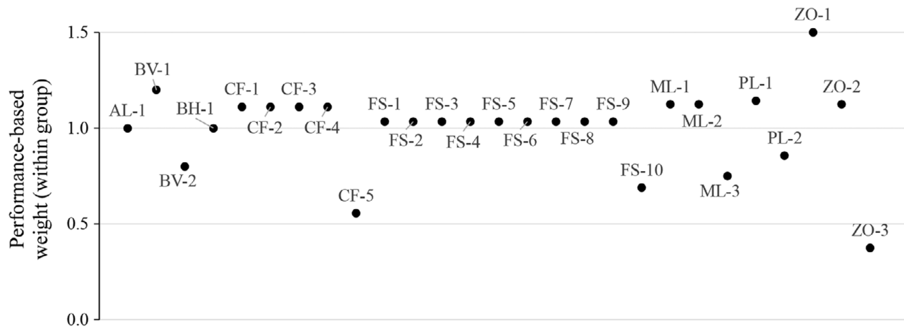

Fig. 1. Individual expert performance-based weights, across all species groups (see *Methods* for calculation). Expert judgments with low variation between them have a value around 1.0, with greater variation between judgments resulting in a score over or under this value. All expert responses were treated anonymously during analysis. AL, algae; BV, bacteria and viruses; BH, bryozoans and hydrozoans; CF, crayfishes; FS, fishes; ML, mollusks; PL, plants; ZO, zooplankton and oligochaetes.

the likelihood that an expert response is close to a true value, a method commonly known as calibration, and one that examines expert confidence in the information provided, through the degree of concentration of their distribution, or informativeness (Cooke 1991, Cooke and Goossens 2000). Together, calibration and information scores can be used to create an individual performance-based weighting system to retroactively adjust expert responses based on these principles (Cooke 1991, Aspinall 2010, Aspinall et al. 2016). Calibration moves beyond simple performance weighting in the statistical complexity of its approach, requiring a minimum number of training questions ("seed variables") in the expert's area of knowledge (McBride et al. 2012, Cooke et al. 2014). However, when conducting a large-scale or rapid elicitation survey, calibration methods may not be appropriate, being overly time-intensive both to the expert and to the elicitors in finding suitable seed variables. For our remote survey method, covering multiple areas of expertise, a large number of seed variables would have been required to follow the classical method of calibrating experts in SEJ (Cooke and Goossens 2000), likely increasing survey time by several hours. Given that the arithmetic mean of all expert judgments is considered the second-best option when calibration is uncertain or not possible (Cooke 1991, Clemen and Winkler 1999, McBride et al. 2012) and that calibration weighting does not always outperform equal (average) weighting (Lin and Cheng 2009, Cooke 2015), we determined that extensive calibration was beyond the scope of this study. We therefore used solely a performance-based weighting approach to examine the similarity of within-group expert performance as a means of determining variation and potential extremes before these parameters were tested in our model. All experts in our study completed the same training question at the beginning of the survey, requiring answers within a similar, but not identical, realm of expertise that would be relevant irrespective of taxonomic specialism and with the true value being known only by the elicitors following later calculation. It is critical that experts cannot improve their scores by seeking additional information (Cooke 1991) and so training question two was subsequently removed from the study due to concerns by the authors over potentially available information. Expert performance on training questions was weighted for closeness to the true value (accuracy) and the width of their uncertainty distribution (informativeness; Cooke 1991) before being ranked against their peers. Individual scores for experts were compiled for accuracy of the modal value (0 = error from true >10 d, 1 = error from true >5 d and <10 d, and 2 = error from true value true value <5 d; see Appendix S3 for methods) and informativeness of the distribution (0 = range did not include true value, 1 = range included true but greater than ±2 standard deviation (SD), and 2 = range included true less than ±2 SD). Accuracy and informativeness scores were summed to produce an individual performance score (m_i) used to rank experts against their peers within their taxonomic groups of expertise. Expert ranks were then converted to an individual within-group performance-based weight (C_i) expressed as follows:

$$C_i = n\left(\frac{m_i}{\sum_{j=1}^{n} m_j}\right) \quad (1)$$

where m_j is an expert's individual within-group performance score, and n is the total number of experts within a species survey group. For inclusion within the model, raw expert parameter estimates were multiplied by individual performance weights before an average was taken to define a single species-specific value in each taxonomic group. This was repeated for the minimum, modal, and maximum values for all species. Model scenarios were run with both raw, unweighted responses and performance-weighted data to assess the sensitivity of species demographic parameters to weighting and to similarly determine the effect of weighting (vs. an unweighted baseline set of responses) on overall model outputs (Appendix S3).

Mechanistic model of secondary spread

Demographic factors derived from the expert-elicitation process were joined with an existing model of secondary spread that had been developed to capture the interactions between introduced NIS and their transport and establishment via domestic ballast-water movements in the GLB (Drake et al. 2015*a*). The model is centered around the species demographic parameters used in the elicitation process and includes the rate of population growth (Drake et al. 2015*a*) and the likelihood of population establishment at a given transported population size (Leung et al. 2004, National Research Council 2011). In the model, the rate of population growth controls the likelihood that a given species will be taken into ballast water, a primary transport mechanism in our study system, where increased growth rate (and resulting increased population density) leads to a higher probability of uptake. Population growth is modeled via a logistic function, given as follows:

$$F(x) = \frac{L}{1 - e^{-k(x-x_0)}} \quad (2)$$

where L is the maximum value of the logistic curve, k is the steepness of the curve, and x_0 is the time in years, whereby 50% of maximum population growth is reached. As we were primarily interested in the value of x_0, both L and k were set to unity to assume a set maximum growth and no Allee effects, respectively. The likelihood of population establishment at a transported population size was modeled following Leung et al. (2004) and National Research Council (2011), and was based on the functional form of a non-Allee establishment relationship, given as follows:

$$p_E = 1 - e^{-\alpha N} \quad (3)$$

where N is the initial population size at introduction, or propagule load, and α is the per-propagule probability of establishment. In our expert survey, we obtained estimates for components of Eqs. 2, 3. Parameter α was elicited as the density of individuals required for a 95% probability of establishment and was subsequently solved for incorporation within the model at different population sizes (Leung et al. 2004, National Research Council 2011). Parameter x_0 was elicited as the time required for a population to reach maximum population size and was subsequently reduced by 50% for inclusion in the model. The likelihood of establishment of a species following an individual ship trip is determined based on the range of transported population densities of known planktonic NIS in the GLB and the survey-derived estimated establishment probabilities (Drake et al. 2015*b*). Because the model incorporates the annual number of ship trips in the GLB, secondary spread can be derived as a rate, such as the number of ports invaded/year or the time required for all five lakes and the St. Lawrence River to contain locally established populations of a species of interest (hereafter referred to as time to saturation). The triangle distributions captured during the SEJ process were used as input parameters for this existing model, providing a structured approach for parameterizing the population attributes known to be relevant in the invasion process. A series of models were run to simulate the minimum, most likely, and maximum demographic scenarios based on all elicited parameter values. When multiple expert responses existed, the mean of the minimum, modal, and maximum values was calculated, thereby allowing model outputs to capture the average range and modal values of expert uncertainty. All model runs were carried out in the R statistical programming language (R Development Core Team 2016).

To provide a generalized relationship between demographic parameters and the expected time to saturation across the recipient landscape (i.e., population development at available localities), we used multiple regression to determine how establishment potential and population growth led to different saturation times across the recipient landscape (establishment potential and population growth rate as predictors, and saturation time or number of ports invaded at 20 yr as response variables).

Results

Variation in expert opinion: capturing uncertainty

Expert judgments varied widely, both within and between taxonomic groups, deviating from the mean by two orders of magnitude on average (Table 2). Variation was consistently large across all three scenarios (minimum, mode, and maximum) but, in all cases, showed no relationship between the number of experts and the amount of variation in the combined responses (e.g., mode: R^2 = <0.001, $F_{1,6}$ = <0.001, P = n.s,). Estimates were less variable within each group when estimating population growth (coefficient of variation [CV] 38–95%) but showed greater variation in establishment parameters (CV 79–202%). Triangular distributions were particularly useful in visualizing both variation and consensus between experts. For example, when estimating establishment potential of the Red Swamp Crayfish, *Procambarus clarkii*, four out of five experts consistently demonstrated confidence in their estimates (small min–max variation), with a fifth expert providing a wider estimate of between 25 and 1200 individuals/m^3 required for establishment success (Fig. 2A). Even in groups with a large number of experts, such as fishes (n = 10), we found more than half of all experts were in close agreement of most likely (modal) values (e.g., Tench, *Tinca tinca,* Fig. 2B). This trend was generally true across all taxonomic groups; therefore, emphasis was placed on subsequent comparison of modal values when considering variation between species groups.

Sensitivity of model outputs to calibration weighting

Within their specialist taxonomic group, experts showed similar performance-based scores when compared with peers (SD < 2; Fig. 1). Zooplankton experts showed the greatest within-group variation in individual performance scores (SD = 1.52) and, despite having the highest number of experts, the fishes group demonstrated least variation (SD = 0.32). Compared with an unweighted average, performance-based weighting had a small effect on modal values of model outputs (Table 3), indicating that results were not overly sensitive to weighting. The mean difference in number of ports showed an average 1% increase and saturation time (establishment of one or more local populations in all five of the Great Lakes) throughout the GLB an average decrease of 6%. Within-group taxonomic variation was generally minimal, with half of all groups showing no change in response to weighting for numbers of ports invaded over time.

Table 2. Variation within expert judgments when estimating species' establishment potential (number of individuals), for minimum, most likely, and maximum scenarios.

(Scenario estimate)	Minimum		Most likely (mode)		Maximum	
Species group (# spp.) [# experts]	Mean	CV (%)	Mean	CV (%)	Mean	CV (%)
Algae (12) [1]	22.92	57	117.92	164	238.33	162
Bacteria and Viruses (5) [2]	34.10	183	311.00	191	855.00	175
Bryozoans and Hydrozoans (3) [1]	1.00	0	10.00	0	100.00	0
Crayfishes (2) [5]	8.90	70	56.50	75	292.50	140
Fishes (10) [10]	33.49	136	116.62	138	421.23	246
Mollusks (8) [2]	11.54	168	105.42	182	1420.00	184
Plants (8) [2]	23.19	160	129.06	141	390.00	103
Zooplankton and Oligochaetes (12) [3]	13.72	171	238.36	158	2772.64	136

Notes: Mean is the average across all species within a species group and between experts where more than one expert exists. Coefficient of variation (CV) allows comparison between groups, given different mean values.

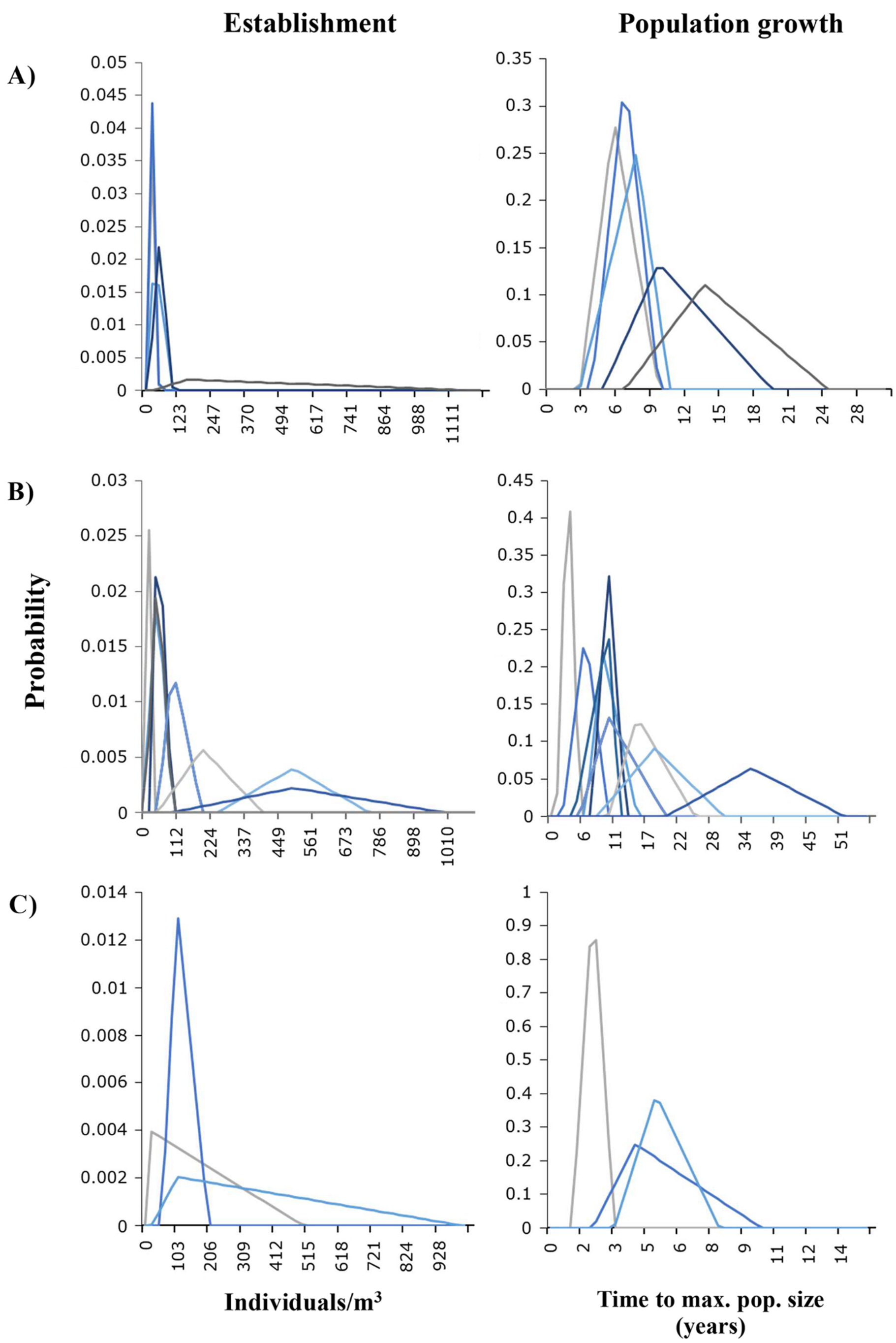

Fig. 2. Triangle probability distributions showing variation in raw expert estimates of establishment potential (survey Q1. "minimum number of individuals for establishment success," left) and rate of population growth (survey Q2. "time to maximum population size," right). Individual triangles represent the minimum, mode, and maximum distribution of estimates per expert, related to a probability value. Estimates are for the following species: (A) Red Swamp Crayfish, *Procambarus clarkii,* showing a generally high level of expert agreement. (B) Tench, *Tinca tinca,* showing more uncertainty across experts. (C) Bloody Red Shrimp, *Hemimysis anomala,* showing more agreement for establishment, but less for population growth.

Table 3. Sensitivity of model outputs to combined (average) expert performance weighting.

	No. of ports invaded (20 yr) (% change)	Time to establishment in all lakes (yr) (% change)
Algae	0	−1
Bacteria and Viruses	0	7
Bryozoans and Hydrozoans	0	3
Crayfishes	1	5
Fishes	0	1
Mollusks	1	−3
Plants	−1	5
Zooplankton and Oligochaetes	−4	27

Notes: Modal values are compared and reported as percentage change in one of two model outputs: (1) the number of ports invaded at the end of a 20-yr model simulation and (2) the time taken for a species to become established in all five Great Lakes (saturation time, years). Negative values indicate a faster rate of invasion.

However, the expert group with the greatest within-group variation (zooplankton) also showed the most pronounced effect of performance-based weighting, with an increase in number of ports by 4% and saturation time by 27%. As experts were relatively consistent within their taxonomic group, the assumptions of leaving responses in their raw form—that all judgments hold equal weight—remain valid as weighting techniques imposed relatively small differences on the resulting spread forecasts.

Spread scenarios for NIS in the Great Lakes

Based on modal average forecasts and the unweighted method, all species groups demonstrated the ability to fully saturate—that is to become established in all five Great Lakes and potentially also the St. Lawrence River—well within the 20-yr time frame simulated in the model (Fig. 3). Based on most likely estimates, bacteria and viruses demonstrated the most rapid rate of human-mediated spread (<5 yr for saturation across the landscape), while fishes took considerably longer to establish (>7 yr) owing to generally reduced establishment potential and lower population growth rates. Both the establishment and population growth parameters were shown to be highly influential in predicting saturation time, defined as the time taken to establish at all possible ports, ($F_{2,57}$ = 452, P < 0.0001, R^2 = 0.941) and number of ports invaded ($F_{2.51,57}$ = 225.4, P < 0.0001, R^2 = 0.888),

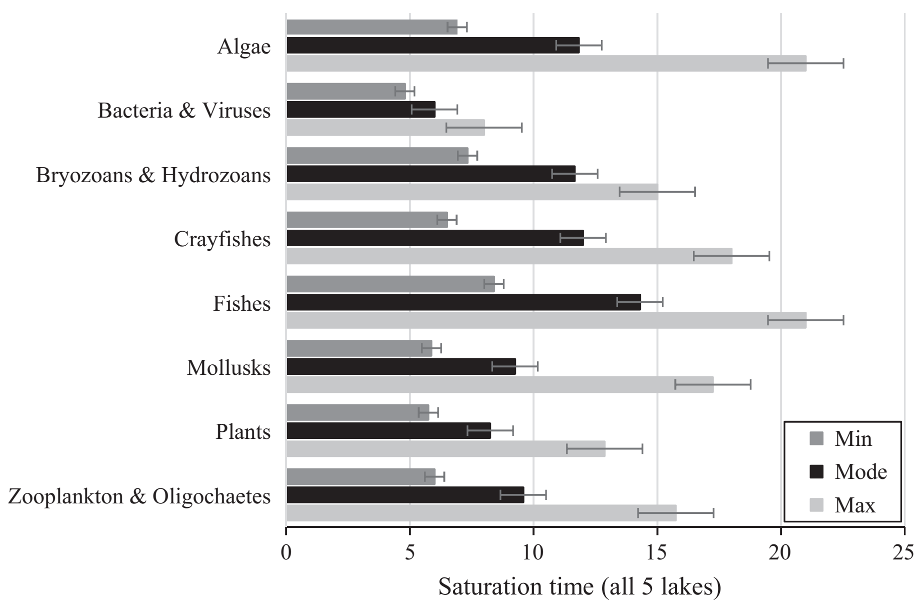

Fig. 3. Model outputs of saturation times in the Great Lakes (defined as the number of years to establish in all five lakes), based on combined average expert estimates. Minimum (fastest), modal (most likely), and maximum (slowest) spread scenarios presented by combined species in each survey group.

confirming that demographic factors matched the mechanisms underlying the spread model. Overall, the rate of spread exhibited by all taxonomic groups was accelerating within the first five years of introduction (Fig. 4), which is both a feature of the logistic function used to model population growth and the specific logistic growth parameters identified by experts. A notable exception to this general finding is the Freshwater Jelly, *Craspedacusta sowerbyi*, for which establishment potential was estimated to be high (α = 0.34), but population growth is slow (x_0 = 12.5 yr), resulting in a greater than 20-yr timeframe for saturation based on most likely values (Fig. 4iii). Two groups (algae, and bacteria and viruses) demonstrated little within-group variation in their invasion timeline (Fig. 4i), whereas over half of all groups had saturation times and number of ports at 20 yr that were highly species-specific. In particular, expert estimates for mollusks (Fig. 4vi) and for zooplankton and oligochaetes (Fig. 4viii) resulted in the widest variation in spread rates at the species level with a saturation time ranging 6–15 yr.

Discussion

In many ways, this study reiterates the challenge of making informed management decisions to control invasive species given the wide range

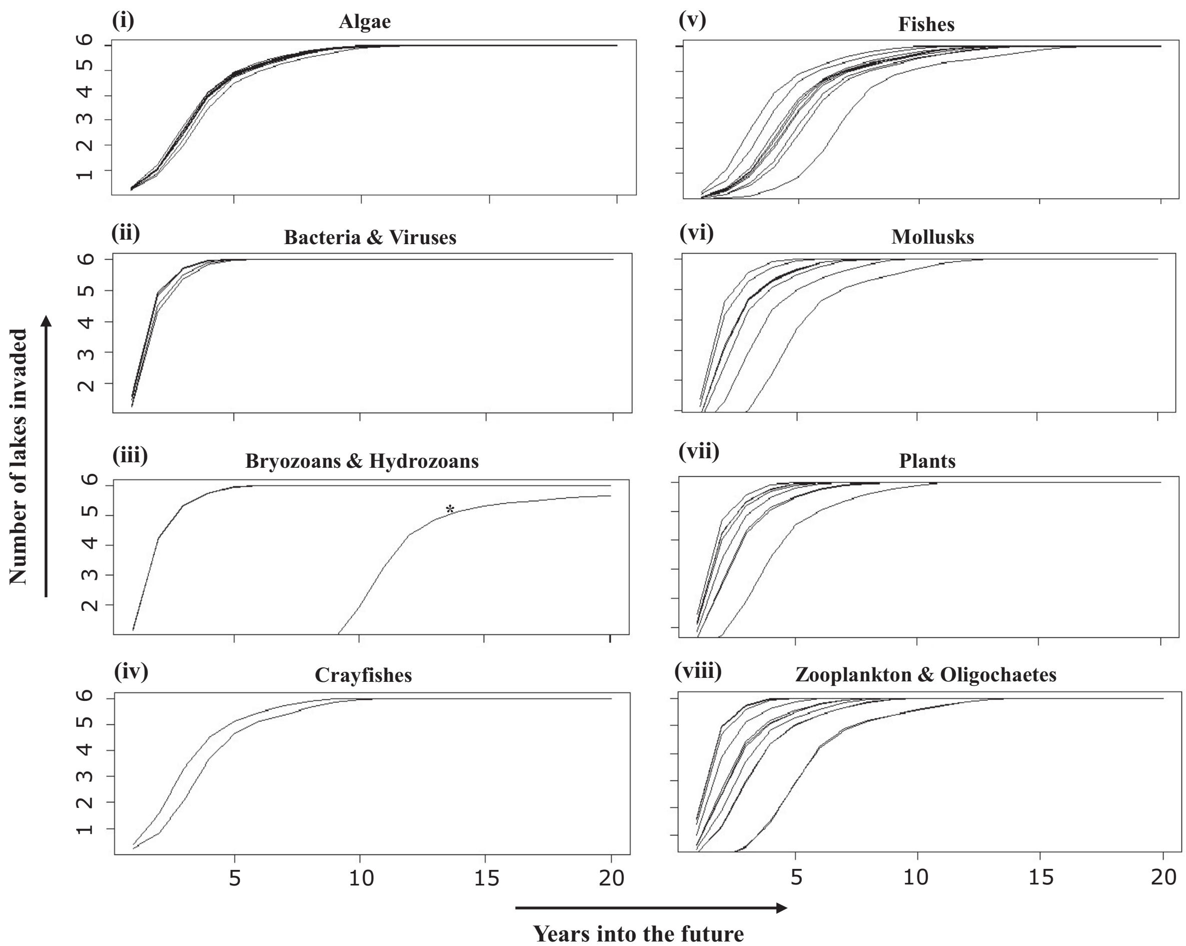

Fig. 4. Model outputs for saturation times (establishment of populations in all five Great Lakes and St. Lawrence River) for all taxonomic groups surveyed. Each line represents a single species within each group and is based on expert averages for modal scenario estimates. *Freshwater Jelly, *Craspedacusta sowerbyi*, referenced in text.

of spread dynamics exhibited at the species level. However, the true utility of the joint-elicitation modeling approach lies in the ability to capture more than one form of uncertainty. This method takes two processes that are understood mechanistically (species establishment and population growth, including the interactions of these biological processes with human pathways) and captures the variability of both expert opinion and model outputs. This overall variation arises due to a combination of two forms of uncertainty in this framework—a lack of current knowledge (epistemic uncertainty) and because we cannot predict such values precisely (stochastic variation). The distinction between types of uncertainty is important, as it allows the interpretation of model outputs from two perspectives: directing where further research may be useful to reduce epistemic uncertainty and assisting with the determination of relative risk for management applications. Using triangular probability distributions, we have demonstrated a simple approach for capturing the variation within expert estimates and elicited values. The approach allows for computing a range of species spread dynamics that may be of direct benefit for rapid decision making. For example, in considering the multiple expert responses obtained for *P. clarkii*, the most likely spread timeline can be determined based on the average modal outcome and management response structured according to this scenario while recognizing the trade-offs involved if the minimum or maximum scenarios were to occur. (Fig. 2A). This technique has clear advantages over other best-guess methods, where SEJ has generated a series of hypotheses formed as best- and worst-case alternatives that may be evaluated in advance in a management decision-making context or in real time as actual spread progresses. This usefully allows these outcomes to be considered in the face of ecological and socioeconomic trade-offs, while flexibly allowing the incorporation of new expert estimates as knowledge about a species or system increases. Most species assessed here were forecast to spread on the scale of decades, rather than centuries. Understanding the range of spread dynamics presented may allow managers to further refine and justify an appropriate response in a species-specific scenario, for example, weighing the potential ecological, social, and economic value of delaying spread by a certain number of years, given that saturation may be possible in just one or two decades. On a larger scale, this understanding may provide concrete information to managers about how much time is available to enact spread prevention measures before a species establishes in multiple lake basins. Finally, by enabling integration of different risk scenarios, such methods may also account more fully for risk tolerance as part of the decision-making process, such as the ability to justify management intervention when spread scenarios differ.

There are, of course, caveats to this approach. Following a thorough review of studies testing the accuracy of expert judgments, Burgman (2005) concluded that expert opinions tend to show consistent bias and are habitually overconfident (Burgman 2005). This, as with any form of model parameterization, means particular care must be taken to avoid opinion biasing model outputs (Kuhnert 2011). Following a structured method helps to ensure careful design of the survey process to better control against bias early on—incorporating steps such as testing the clarity of questions and choosing to elicit values in units familiar to the expert (Table 4). Such considerations are likely to make for more successful incorporation of expert judgments within a model framework. In addition, there are several methods for mitigating the effects of, or correcting for, confidence and other forms of bias, of which testing expert performance is often identified (Cooke and Goossens 2000, Cooke et al. 2014). The performance-based weightings tested here suggest it may not always be necessary to weight experts when joining their estimates with modeling processes, particularly where multiple elicitations are run alongside one another making judgments between groups noncomparable; however, additional research into the minimum number of training questions required would be valuable (Aspinall 2010, Cooke et al. 2014). The results of our sensitivity analysis to performance-based weighting suggest that, in cases where experts are performing equally within-group, outputs may demonstrate negligible effects (Table 3). In even the most disparate and heavily weighted group, zooplankton and oligochaetes, the total number of ports invaded at the end of a 20-yr

Table 4. Framework for joining expert opinion and modeling methods.

Process	Description	Literature
1. Defining research question	Consideration of the type of model available to answer the defined research question, and whether the parameters required could feasibly be estimated using expert opinion. 1. Expertise available: Do specialists exist in that taxonomic or subject area? 2. Potential of knowledge transfer: Can the parameters required be reasonably estimated? 3. Time and resources available for study: Based on expert geographic location and researcher availability, can the study be conducted in person or is a remote elicitation process necessary?	**General guidelines** Burgman (2005) Low Choy et al. (2009) Martin et al. (2012) Drescher et al. (2013)
2. Survey design	Experts are chosen and a survey created with specific questions relating to the parameters required for the model. 1. Appropriate format chosen: for example, face-to-face, e-mail, and online 2. Questions do not "lead" but guide expert: bias avoided in elicitation questions as well as responses 3. Calibration/training questions designed	**Identifying and avoiding biases** Tversky and Kahneman (1974) Kynn (2008)
3. Expert elicitation	Run elicitation (data collection). A decision should also be made as to how multiple expert judgments will be combined (if applicable). 1. Based on parameters required, decide if will use direct or indirect elicitation. That is, is it possible for experts to estimate values in units that are familiar, or will additional data manipulation be required? 2. Determine number of experts to be consulted, and obtain confirmation of willingness to participate. 3. Process for combining multiple expert judgments/incorporation of calibration or performance-based weighting decided (if applicable), or equally weighted averaging	**Elicitation software** James et al. (2010) Fisher et al. (2011) **Calibration and combination of expert judgments** Cooke (1991) Burgman et al. (2011) Cooke (2015)
4. Model encoding and analysis	Joining expert outputs with modeling techniques to answer the research question. 1. Synthesis expert data: clean and ensure in correct format for encoding within model. 2. Model simulations run sensitivity analysis conducted to consider both the variation and sensitivity of expert estimates within the model. 3. Analysis of outputs testing research hypothesis: statistical analysis to determine significance of outputs and acceptance or rejection of research statement	**Models** *(Bayesian)* Low Choy et al. (2009) Kuhnert et al. (2010) *(Species richness/distributions)* Murray et al. (2009) Fisher et al. (2011) Wittmann et al. (2014*a*) *(Food web)* Wittmann et al. (2014*b*) Zhang et al. (2016)

simulation varied by an average of just 4%. In groups with a single expert or low within-group variation (e.g., fishes, $n = 10$, SD = 0.32), weighted data varied from unweighted data by zero or 1%. This suggests that incorporating expert opinion within a modeling framework may, in some cases, form a more robust means of prediction than opinion alone, where the mechanisms behind parameter estimates and, therefore, confidence in model structure are well understood. It is important to note that such analyses are a critical component of model formulation and, in cases where parameter sensitivity is high, the necessity of expert accuracy and weighting would be of greater importance in ensuring the validity of model outputs.

One of the greatest challenges in managing invasive species is determining suitable actions in the absence of biological data. By treating all species consistently, we created a uniform and standardized approach to predicting the potential spread of species, based on a common currency (demographic parameters underlying establishment and population growth). Spread is an important part of the probability of introduction component of ecological risk assessment (Mandrak and Cudmore 2015). In conjunction with magnitude of impacts, not only does spread contribute to calculating overall risk (Mandrak and Cudmore 2015) but also may provide a timeframe on which the risk may be realized, as does our model. Not all species are likely to exhibit the same rates of secondary spread, even within a taxonomic group, suggesting that the key advantage of the joint-elicitation modeling method is the ability to reduce uncertainty in the trajectory of secondary spread. Simberloff (2003) described the perils of failing to act early in the eradication window and was strongly in support of applying the precautionary principle to contain new invasions. The arguments against rapid action are that not all species will successfully establish, nor will they all have ecological impacts (Williamson and Fitter 1996). In practical terms, this means that undertaking control prior to widespread population expansion may be difficult to justify to managers and stakeholders in the absence of expectations that spread may be rapid and widespread. Joining existing mechanistic models with expert opinion, therefore, contributes significantly to defining how much data are required to make eradication and control decisions, by providing an alternative means to forecast spread trajectories and invasion dynamics, leading to informed decisions in a relatively short period of time. Similarly, studies combining joint methods allow researchers to obtain broad estimates of species invasion potential, exploring the relationship between standard variables that allow comparison across taxonomic groups in a unified way.

The ability to identify broad relationships between species-specific demographic parameters and rates of spread has profound implications for understanding how invasive species interact with human pathways. Our findings have shown that the rate of spread is driven by key demographic parameters and their interaction with human-mediated mechanisms of movement. On average, species with low detection probabilities, such as bacteria and viruses, demonstrated the potential to spread rapidly and extensively within the GLB, thereby presenting significant threats to recipient ecosystems. Fishes demonstrated similar saturation times based on their most likely trajectories of spread, whereas plants and zooplankton exhibited far wider and

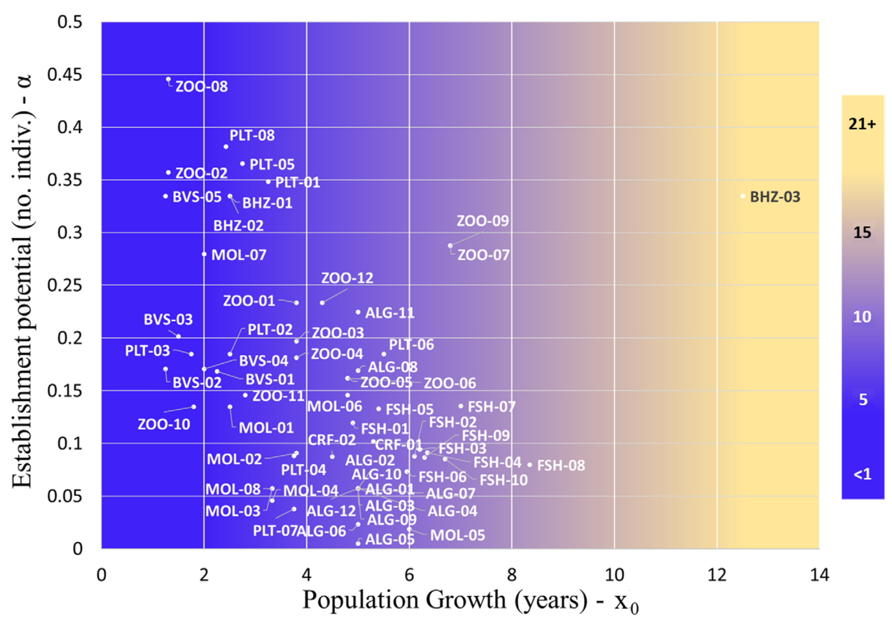

Fig. 5. Species-specific combinations of demographic parameters against saturation time throughout the Great Lakes and St. Lawrence River Basin, based on modal expert estimates (unweighted average with multiple experts). Species codes can be found in Appendix S1. x_0 represents time to 50% of maximum population size, whereas α is the natural logarithm of the per-propagule probability of establishment, based on the formulation in Leung et al. (2004).

less predictable spread rates within their respective groups (Fig. 5). These patterns point to a generalized index of spread that could account for both spread and potential impact of a species based on taxonomic group. One key benefit of this approach is that it moves a step closer to providing a broad framework for rapid decision making by using taxonomic group as a decision-making variable.

We have shown that joining expert-elicitation methods with mechanistic models can be used to predict species dynamics in the absence of published or experimental data, thereby providing valuable estimates of ecological phenomena in the absence of empirical information. The main limitations lie in interpretation—expert judgment is not intended to replace empirical data, but to enable decisions to be made despite ongoing uncertainty. Obtaining multiple estimates from experts for the same parameter allows modelers to make more informed choices when parameterizing their models and using a process such as SEJ provides a much-needed standardization for what is otherwise an unregulated process. It might be expected that as expert elicitation becomes more widely accepted in ecology, the quality of expert information should increase in both informativeness and accuracy in line with expert familiarity and proficiency in responding to structured-survey methods (Cooke 1991). This joint approach may be beneficial beyond invasion ecology, such as estimating vital parameters for population viability analyses in endangered species management or estimating expected recovery times of newly restored habitats or protected areas based on existing scientific knowledge.

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Data Accessibility

R scripts used in this study are available on GitHub https://github.com/EmilyChenery/chenery-drake-mandrak. Expert estimates for all species surveyed can be accessed from the Figshare digital repository https://doi.org/10.6084/m9.figshare.11301722

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3011/full