Understanding and predicting population response to anthropogenic disturbance: Current approaches and novel opportunities

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Abstract

Effective conservation of biodiversity depends on the successful management of wildlife populations and their habitats. Successful management, in turn, depends on our ability to understand and accurately forecast how populations and communities respond to human-induced changes in their environments. However, quantifying how these stressors impact population dynamics remains challenging. Another significant hurdle at this interface is determining which quantitative approach(es) are most appropriate given data constraints and the intended purpose. Here, we provide a cross-taxa overview of key methodological approaches (e.g., matrix population models) and model elements (e.g., energetics) that are currently used to model the effects of anthropogenic disturbance on wildlife populations. Specifically, we discuss how these modelling approaches differ in their key assumptions, aspects of their structure and complexity, the questions they are best poised to address, and their data requirements. Our hope is to help overcome some of the methodological biases that might persist across taxonomic specialisations, identify new opportunities to address existing modelling challenges, and improve our understanding of the direct and indirect impacts of anthropogenic disturbance. We guide users through the identification of appropriate model configurations for different management purposes, while also suggesting key priorities for model development and integration.

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Abstract

Effective conservation of biodiversity depends on the successful management of wildlife populations and their habitats. Successful management, in turn, depends on our ability to understand and accurately forecast how populations and communities respond to human-induced changes in their environments. However, quantifying how these stressors impact population dynamics remains challenging. Another significant hurdle at this interface is determining which quantitative approach(es) are most appropriate given data types, constraints, and the intended purpose. Here, we provide a cross-taxa overview of key methodological approaches (*e.g.* , matrix population models) and model elements (*e.g.* , energetics) that are currently used to model the effects of anthropogenic disturbance on wildlife populations. Specifically, we discuss how these modelling approaches differ in their key assumptions, aspects of their structure and complexity, the questions they are best poised to address, and their data requirements. Our intention is to help overcome some of the methodological biases that might persist across taxonomic specialisations, identify new opportunities to address existing modelling challenges, and improve our understanding of the direct and indirect impacts of anthropogenic disturbance. We guide users through the identification of appropriate model configurations for different management purposes, while also suggesting key priorities for model development and integration.

1 Introduction

As the extent and magnitude of human activity continues to expand (IPBES 2019), the urgency to understand how wildlife populations respond to anthropogenic change is accelerating (Larson *et al.* 2016; Venter*et al.* 2016). This information is crucial for effective management and conservation policies (Pimm *et al.* 2014). Ecologists have long tried to understand and predict the impacts of human disturbance on wildlife populations and communities through the use of quantitative modelling approaches (Beissinger & Westphal 1998; Getz & Haight 1989). However, stressors rarely occur in isolation, with animal populations often exposed to multiple direct (e.g., harvesting; Kays *et al.* 2017) and indirect stressors (e.g., habitat fragmentation, Smith *et al.* 2019). Although it is relatively straightforward to determine how individual stressors impact populations, the complex ways that multiple stressors interact make it challenging to predict their combined effect on a population (Paniw*et al.* 2021). As a result, there has been an increasing focus on understanding the population-level effects, such as changes in population dynamics, geographical distribution, and/or population persistence, that can result not only from individual indirect (non-lethal) stressors but from exposure to multiple stressors (e.g., Gosselin *et al.* 2015; Daversa *et al.* 2025; Pirotta*et al.* 2019; Galic *et al.* 2018). Oftentimes, disturbances have indirect effects on populations, such as through changes in food intake, which may lead to changes in energy balance and/or body condition (e.g., Parker *et al.* 2009), or through exposure to pathogens or pollutants, which may result in changes in immune status (Charbonnel *et al.* 2008). These indirect effects can compound, leading to impacts on vital rates (e.g., survival, reproduction) that then shape population dynamics (Fig. 1, Box 1). Explicit consideration of these indirect effects has been formalised for marine mammal risk assessments (NAS 2017). Other efforts have advocated for the inclusion of indirect effects within a standardised mechanistic framework (Johnston *et al.* 2019). However, these are conceptual frameworks and, as such, lack information on specific approaches used to model population-level impacts of disturbance. These frameworks also fall short when considering community dynamics or management actions (but see Urban *et al.* 2022), which can play key roles in predicting population persistence (Fig. 1, Box 1). Interactions among stressors and discrepancies in spatial and temporal scales of impact mean that correlative approaches are often too limited to inform policy or management. Quantitative modelling approaches thus play an important role in understanding and managing ecosystems by clarifying the key mechanisms that might explain the behaviour of ecological systems (Schmolke *et al.* 2010). The main advantage of quantitative approaches to management decision making is their ability to predict the magnitude of effect of alternative scenarios based on underlying processes, which is rarely possible through empirical studies alone (Skogen *et al.* 2024). Many quantitative approaches are available for modelling the impacts of human activity on animal populations, each of which have their own assumptions, caveats, and advantages. The approaches differ in which processes are represented (and how), their spatio-temporal scales, data requirements, and in which questions they are best poised to answer. Inappropriate choices in modelling approach or structure could compromise our ability to make reliable predictions (Gerber 2006), creating greater uncertainty when deciding on management strategies. Despite the vast array of modelling approaches available, several key challenges remain when trying to predict the population-level impacts of human activity on wildlife: 1) how to get the most out of disparate data streams collected at different spatio-temporal scales; 2) how to provide scientifically informed management advice for populations when limited empirical data are available, as is typically the case; 3) how to manage uncertainty when uncertainty is ubiquitous; and 4) knowing which approach(es) to use given the available data and the question at hand. Further challenges arise when considering community dynamics, which is often necessary to accurately predict the implications of human disturbance and potential management strategies on ecological communities (Buckley and Han 2014; Zavaleta *et al.* 2001). While challenges 1-3 have received considerable attention (e.g., Nichols 2021; Simmonds *et al.* 2024; Zipkin *et al.* 2019; Fletcher Jr.*et al.* 2019), guidance on modelling choices for assessing and predicting population-level impacts of human disturbance has received less attention (but see Accolla *et al.* 2021; Hunter-Ayad *et al.* 2020; Thompson *et al.* 2021; Briscoe *et al.* 2019). Here, we provide an overview of key approaches available to model human impacts on animal populations. In doing so, we aim to provide resources for new studies to identify suitable methods and help overcome taxonomic or domain biases in model development. As part of this effort, we highlight important considerations when deciding on a modelling approach and model structure to model the direct and indirect impacts of human disturbance on animal populations. We also use two case-studies on red fox (*Vulpes vulpes*) and European mink (*Mustela lutreola*) to illustrate some of the considerations made during model development and the strategies used to overcome the limitations of different modelling approaches, including model integration and energetic modelling. Further, we extend existing conceptual frameworks for understanding the impacts of human disturbance by incorporating community-level responses to multiple stressors as well as the pathways by which management actions can influence a population (Fig. 1, Box 1). The information presented here can be used to identify appropriate model configurations for different research and management purposes, while also suggesting key priorities for future model development and integration.

2 Approaches to modelling the effects of disturbance on wildlife populations

We provide an overview of the key approaches for understanding and predicting the impacts of disturbance on individuals, populations, and communities. We use a broad definition of human disturbance, wherein we include natural processes (e.g., climate variation, disease, wildfire) that can be exacerbated by human activity. We have categorised the quantitative approaches into four sections based on the general level at which disturbance is usually modelled for each of the modelling approaches. These have been broadly broken down into responses at the individual, population, community, or geographical range scales. We recognise from the outset that some modelling traditions include or link components from multiple scales and that some approaches represent broad categories of model families while others are specific to a single model or method. We also discuss some of the benefits, challenges, and data requirements for specific approaches using case studies. We provide reference to more in-depth reviews in the Supplementary Material.

2.1 Individually-focused dynamics

Below, we describe the most widely used approaches to model the effects of human-related stressors at the individual or group level. These approaches typically allow individuals (or groups of individuals) to vary within a population in terms of a variety of traits related to behaviour, genetics, or energetics. Accounting for such variation may be more representative of real populations than those that assume all individuals are identical (Denny 2017), which can improve predictions of population dynamics (Gerber 2006).

2.1.1 Individual-based models

Individual-based models (IBMs or agent-based models) are a broad class of simulation models that depict relevant processes at the individual or group level (the agent). Population-level properties (e.g., population growth rate) emerge from the behaviour of, and interactions among, discrete agents through time. This key property makes IBMs particularly useful when intraspecific trait variation, local interactions, adaptive behaviour or heterogeneous environments are assumed to influence population level responses to disturbance (Chevy *et al.* 2025; DeAngelis & Grimm 2014), as well as for small populations (Caughley 1994). Disturbance is typically implemented by comparing different simulation scenarios with varying disturbance levels. IBMs are frequently used to assess the population impacts of disturbance, either as a stand-alone method or in conjunction with other approaches described throughout this section. Such applications include investigating the effects of climate change and habitat connectivity (Andersen *et al.* 2022) and toxicant exposure (Hall *et al.* 2018) on population dynamics.

2.1.2 Cell-lattice models

While not technically individually-focused, cell-lattice models analyse spatially-explicit demographic processes through an array of discrete grid cells, that enable fine-scale dynamics to be modelled. Discrete cells can be characterized by variation in important landscape attributes, such as habitat type, food availability, or predation risk, that influence demographic rates. Dispersal between adjacent cells is used to depict simple patterns of redistribution by a fraction of the subpopulations arising from neighbouring cells. Cell-lattice models are a computationally simple way to evaluate the influence of habitat arrangement, mobility, and behavioural decision-making on rates of resource gain and mortality risk among subpopulations occurring in different cells at a given point in time (Tonini *et al.* 2014). Similar to IBMs, disturbance effects are typically inferred based on comparisons of model outputs among simulation scenarios. Because of their inherent spatial nature, cell-lattice models are particularly relevant for applications involving movement barriers (e.g., road infrastructure; Holdo *et al.* 2011), the effects of invasive species (Tonini *et al.* 2014), and disease spread (Jeltsch*et al.* 1997).

2.1.3 Stochastic dynamic programming

Stochastic dynamic programming is an optimization method frequently used to identify optimal decisions and behaviours of individual animals (Houston *et al.* 1988; Mangel & Clark 1988). As a way to implement state-dependent life-history theory, it is based on the underlying assumption that individuals act to maximize some future expected reward (e.g., Darwinian fitness), which varies depending upon one or more state variables. Energy reserves are often used as physiological state variables, hence there is typically an energetic component when addressing disturbance impacts. Discrete locations characterized by environmental features (e.g., resource availability) can also be included, allowing for spatiotemporally-explicit models. Once identified, optimal decisions for each combination of state variables across the time horizon (e.g., the lifespan of an individual) can be used in an IBM framework to characterize emergent population properties in the presence (and absence) of disturbance scenarios. In the context of disturbance, stochastic dynamic programming has primarily been used to identify optimal movement, habitat, and reproductive decisions to quantify the potential effects of variation in prey resources (e.g., due to climate change; Reimer *et al.* 2019) and acoustic disturbance (McHuron *et al.* 2021; Pirotta *et al.* 2019).

2.1.4 Dynamic energy budget models

Dynamic energy budget (DEB) theory (Kooijman 2010) provides a mechanistic basis to model the acquisition and allocation of energy by organisms across their lifespan. DEB thus allows for the study of density-dependent feedback effects between a population and its environment, and resulting patterns of life-history evolution (de Roos & Persson 2013). This approach is based on the concept that rates of basic physiological processes are proportional to surface area or body volume, which differs from other energetic approaches like the Metabolic Theory of Ecology (van der Meer 2006). The generalised nature of the framework allows for easy adaptation to a range of disturbance types and taxonomic groups. Because DEB models are specified at the individual level, we need other tools to extrapolate to the population level. As such, DEB theory has been integrated into IBMs (DEB-IBMs), matrix models (Klanjscek *et al.* 2006), integral projection models (Smallegange*et al.* 2017; Thunell *et al.* 2023), and physiologically structured population models (Metz & Diekmann 1986; de Roos 1997). In particular, DEB-IBMs allow for explicit consideration of individual variation, local interactions and/or adaptation (Martin *et al.* 2012). DEB-IBMs have been applied to investigate the impact of toxicant exposure and disease (Silva *et al.* 2020), acoustic disturbance (Soudijn *et al.* 2020) and habitat loss due to climate change (Johnson *et al.* 2024) through explicit changes in an individual's physiology resulting from these disturbances.

2.2 Population dynamics

Modelling human impacts at the population level has a long history (Boyce 1992; Lande 1993). These approaches directly link human disturbances to population viability by quantifying how shifts in key demographic processes (Morris & Doak 2002), such as survival and reproduction, influence population growth and structure (Caswell 2000). As a result, these approaches have been widely applied to project long-term population viability under various disturbance scenarios (Engelen *et al.* 2025; Morris & Doak 2002) and to assess the evolutionary consequences of human activities (Palstra and Ruzzante 2008; Hendry *et al.* 2008). More recently, frameworks have been developed to integrate biological mechanisms underpinning responses to anthropogenic threats, highlighting the role of mechanisms in conservation planning (Urban *et al.* 2016).

2.2.1 Matrix population models

Matrix population models are structured population models that describe the dynamics of a given population in discrete time and stages (e.g., developmental stage) (Caswell 2001). By providing a direct link between age and/or stage-structured vital rates and population dynamics in a relatively simplistic framework, matrix population models are an accessible tool to project population trends under alternate environmental conditions (Fieberg & Ellner 2001). Matrix population models have been applied extensively to explore population response, for example under land-use change (Tucker *et al.* 2021), climate change (Penman *et al.* 2015) and hunting (Simon & Fortin 2019), with the effects of disturbance typically included via changes in vital rates. Matrix models are also often integrated with other modelling approaches, such as DEB models (Billoir *et al.* 2007), to examine population-level consequences of vital rate changes on population dynamics.

2.2.2 Integral projection models

Similar to matrix population models, integral population models track population dynamics in discrete time, but along a continuous stage classification (e.g., size) to describe how an individual's state influences its vital rates. Integral population models are constructed from regression models that predict vital rates from state variables, and can incorporate factors such as density dependence (Metcalf *et al.* 2008), environmental drivers (Merow *et al.* 2014), and stochastic dynamics (Ellner & Rees 2006). By integrating vital rates with environmental covariates, integral population models provide semi-mechanistic insight into ecological patterns including population dynamics, species distributions or life-history strategies (Merow*et al.* 2014). Integral population models have been applied directly to explore the eco-evolutionary dynamics of populations under a range of human pressures, including size-selective hunting (Wallace*et al.* 2013). Integral population models have also been integrated with DEB theory to provide additional mechanistic insights into ecological patterns under disturbance (Smallegange *et al.* 2017; Thunell *et al.* 2023). This approach allows for the investigation of ecological and evolutionary patterns from an energy budget perspective, such as sensitivity to shifts in environmental variability (Smallegange *et al.* 2020; Rademaker *et al.* 2024) or the eco-evolutionary consequences of climate change for populations (Thunell *et al.* 2023).

2.2.3 Physiologically structured population models

Physiologically structured population models can describe a population's demography using DEB theory, but differ by treating time as continuous rather than discrete (Metz & Diekmann 1986; de Roos 1997). This approach has been applied to investigate the population-level impacts of food limitation (e.g., Hin *et al.* 2019) and environmental stress (Silva *et al.* 2020). Finally, a computational approach (de Roos 2021) exists that merges discrete and continuous DEB population modelling approaches that can be used for life histories with continuous development through time (de Roos *et al.* 2008). For example, this approach has been applied to show how habitat deterioration impacts life history evolution in metamorphosing species (ten Brink *et al.* 2020).

2.2.4 State-space models

State-space modelling is a highly flexible hierarchical framework used to estimate parameters while explicitly separating the underlying ecological process (the true, unobserved state) from the observation process (measurements). This distinction allows for the independent estimation of uncertainties arising from biological stochasticity and sampling-related measurement errors, therefore reducing bias in parameter estimates compared to models that account for only a single source of uncertainty (Auger-Methe *et al.* 2021). Ecological applications of state-space models include estimating demographic rates, assessing population abundance, and projecting population growth and viability (Buckland *et al.* 2004), using a range of datatypes (e.g., capture-recapture, abundance data). State-space models are highly adaptable, allowing structuring by age (Bret *et al.* 2017), life stage (McCaffery *et al.* 2012), or spatial location (Rogers*et al.* 2017). State-space models can also capture temporal trends and density-dependence effects (Lebreton & Gimenez 2013). In addition to studying the effects of a variety of disturbances, such as climate change and habitat destruction (e.g., Westcott *et al.* 2018; McCaffery *et al.* 2012), they can also model host-parasite dynamics (Karban & De Valpine 2010) and be combined with population models such as integrated population models (White *et al.* 2016).

2.2.5 Integrated population models

Integrated population models (IPMs) combine population count data and demographic data within a single statistical model to infer population dynamics. These models are frequently implemented using Bayesian methods with a state-space model formulation to deal with uncertainties in parameter estimates. Typically, the core of an IPM is a matrix model (or integral projection model; Plard *et al.* 2019) that is formulated in discrete time to describe changes in age- or stage-structured population sizes. IPMs can help reduce uncertainty in parameter estimates, estimate confounded or hidden parameters, and disentangle sources of uncertainty when forecasting population trajectories (Schaub & Abadi 2011). Disturbance applications of IPMs include climate change (Gamelon *et al.* 2023), land use changes (Zhao *et al.* 2019), invasive species (Oppel *et al.* 2022), and electrocution on power poles or collision with wind turbines (Millsap *et al.* 2022). Some work has also focused on extending these models to multiple species, incorporating interactions such as competition (Peron & Koons 2012) and predation (Queroue *et al.* 2021).

2.2.6 Machine learning models

Machine learning algorithms are computational approaches that learn patterns from large and complex datasets capturing non-linearities and complex interactions between variables to generate accurate predictive models without explicit programming (Pichler & Hartig 2023). In the context of disturbance, machine learning models are most commonly used in correlative SDMs, but they have also been used to predict population dynamics under various pressures (e.g., climate change; Amstrup *et al.* 2008), and to understand the impact of disturbance on animal behaviour (Berger *et al.* 2020; Fardell *et al.* 2021; Tedonzong *et al.* 2020).

2.2.7 Partial differential equations

Partial differential equations are a class of mathematical equations used to describe systems where variables change continuously over both time and space. A partial differential equation expresses relationships between the rates of change of these variables with respect to time, spatial dimensions, or both. A typical partial differential equation in ecology might describe how the rate of change in animal population density at a specific location depends on factors like the movement of individuals (diffusion), behavioural interactions, and local birth and death rates (Moorcroft & Lewis 2006; Otto & Day 2011). There have been several applications of partial differential equations to study the consequences of human disturbance on populations, including climate change (Chhaytle *et al.* 2023; Goel *et al.* 2020), invasive species (Laplanche *et al.* 2018) and pest control (Banks *et al.* 2020).

2.3 Range dynamics

This section reviews some of the methods used to understand and predict the effects of human disturbance on the range dynamics of wildlife populations. From a disturbance ecology perspective, range dynamics can tell us where populations may be at greater risk of exposure to stressors, highlight potential areas of refuge, and identify key habitat requirements for a population to persist. This information can be used to prioritise, for example, areas for protection or management.

2.3.1 Species distribution models

Correlative species distribution models (a.k.a. ecological niche models or habitat suitability models; hereafter, SDMs) identify statistical relationships between species occurrence or abundance to spatio-temporal patterns of environmental variation to explain or predict species distributions (Elith & Leathwick 2009). Habitat suitability is typically predicted from static physical features (e.g., land use type, topography) and/or dynamic environmental variables (e.g., temperature, precipitation). Data can be fitted using a range of approaches, including generalized linear and additive models, boosted regression trees, and machine learning algorithms (Guisan *et al.* 2017). Disturbance can be incorporated as an additional predictor variable (e.g., urbanization; Russo *et al.* 2023) or effects can be inferred based on spatial or temporal shifts in habitat suitability (e.g., climate change; Russo *et al.* 2023). They are also frequently integrated as a spatial layer for other modelling approaches, such as connectivity models (e.g., Rezaei *et al.* 2022) and IBMs (e.g., Andersen *et al.* 2022; Jordt *et al.* 2016), providing boundaries for movement or dispersal.

2.3.2 Process-explicit range models

Process-explicit range models extend correlative SDMs to explicitly model the underlying processes that drive population dynamics, such as physiology, dispersal, demography, and evolution (Briscoe *et al.* 2019). There are a broad range of modelling approaches that can be categorised as process-explicit range models, including occupancy or abundance dynamics models, coupled SDM-population models, demographic distribution models, eco-physiological models, and IBMs (Briscoe*et al.* 2019). Applications of process-explicit range models are limited but they have increased in recent years (Kelleher *et al.* 2024; Uribe-Rivera *et al.* 2023), particularly as they are often assumed to provide more accurate range prediction when extrapolating to novel conditions (Evans *et al.* 2015, but see Uribe-Rivera *et al.* 2023). For example, demographic-based process-explicit range models have been used to assess the effect of wind farms (Bastos *et al.* 2016), movement barriers (Pratzer*et al.* 2023), and climate change (Mathewson *et al.* 2017; Santika *et al.* 2014).

2.4 Community and ecosystem dynamics

While ecological models often focus on a single species, unintended management outcomes can result when species are viewed in isolation (Buckley and Han 2014). Models that explicitly consider the interactions and feedback among species can help better inform population-level responses to disturbance and management. Community and ecosystem models vary substantially in their complexity, from simple food webs (e.g., Varriale and Gomes 1998) to complex end-to-end ecosystem models (e.g., Fulton 2010). Here, we focus on metacommunity and food web models as these approaches are more frequently applied to disturbance studies, though their application is still relatively rare.

2.4.1 Metacommunity models

Metacommunity models represent the multiscale dynamics of species inhabiting discrete habitat patches, where populations face measurable extinction risk, can recolonize after local extinction, and experience asynchronous local population dynamics. Patterns in local extinctions versus regional survival are central to these models and are driven by processes such as environmental filtering, biotic interactions, dispersal, and drift (Chase *et al.* 2020; Lerch *et al.* 2023). As these models are united by underlying theory rather than a standard method, there exists a wide variety of modelling approaches that may represent time and space differently (Ovaskainen and Hanski 2001; Bond *et al.* 2023; Souto-Veiga *et al* . 2024). Dynamics may be represented using IBMs (e.g., Radchuk *et al.* 2013) and matrix population models (e.g., Takashina 2016), among others (e.g., Brandell *et al.* 2021; Zhang *et al.* 2021). Metacommunity models are still rarely used to study disturbances (but see Dugger*et al.* 2011); however, the theory is analogous to metapopulation models that have been used to address how changes in landscape structure influence colonization and extinction dynamics (Bond *et al.* 2023) and the impacts of broader environmental changes (e.g., extreme weather) across metapopulations (Radchuk *et al.* 2013).

2.4.2 Food web models

Food web models aim to represent the demographic impact and rates of transfer of material or energy between different elements of the community matrix as a result of trophic interactions such as predation, parasitism, or mutualism (e.g., Baudrot *et al.* 2020). These models encompass a wide variety of computational approaches, ranging from partial differential equations (e.g., Lusardi *et al.* 2024) to individual-based or cell-lattice models (e.g., Fryxell *et al.* 2020). Community structure, behavioural details (e.g., decision-making, mobility, and cognition), sources of heterogeneity affecting interaction rates, and landscape configuration are often key components influencing model outcomes. The response to disturbance in food web models, such as that caused by invasive species or habitat loss (e.g., Roemer *et al.* 2002), is often determined through impacts on community structure or changes in the functional relationships between community components.

2.4.3 Structural equation models

Structural equation models aim to capture the complex interactions that are inherent in communities and ecosystems. By integrating multiple processes, structural equation models can help disentangle the relative influences of many processes on community or ecosystem dynamics. As in food web models, structural equation models allow researchers to assess both direct and indirect effects of disturbance on trophic interactions, such as the cascading impacts of habitat loss or invasive species (e.g., Curveira-Santos *et al.* 2024; Schwensow *et al.* 2022). Their ability to account for multiple causal pathways makes them a valuable tool for predicting community-level responses to disturbance (Schweiger*et al.* 2016). However, relationships are assumed linear which may not always be appropriate in real world systems.

3 Case-studies

To illustrate how quantitative approaches can be selected for a given application, we highlight two case-studies: 1) the ever-abundant red fox and 2) the critically endangered European mink. The red fox is a well-studied species that has been modelled extensively to address a range of management purposes. The European mink, on the other hand, is a data limited species of high conservation concern, with only one modelling application. Through this endeavour, we hope to illustrate some of the decisions that are made in the model development process, how others have overcome the limitations of different approaches, and how mechanistic pathways can be used to help address data scarcity challenges.

3.1 Case-study 1: Red fox

Disturbances of wildlife populations are often unintentional, occurring as a by-product of other human activities. In some cases, however, they may result from targeted management actions that may occur in isolation or conjunction with other disturbances. One example species is the red fox, a small carnivore that has a wide distribution across the northern hemisphere (Box 2). Foxes are often perceived as a nuisance species, are potential vectors of zoonotic disease, but also play important ecological roles (e.g., prey regulation). As a relatively well-studied species of high management interest, a range of modelling approaches have been used to address disturbances in red fox populations. Here, we provide a brief overview of some of these models, focusing on two disturbances where multiple methods have been used to address similar questions, namely rabies and harvesting/culling.

3.1.1 Rabies/Disease

Rabies, a zoonotic disease, is often viewed as a natural feature in the environment. However, its dynamics, along with those of other diseases, can be shaped by human influences, including spill-over from domestic species, shifts in wildlife densities driven by urbanization, and changes in behaviour or ranges associated with climate or land use change. Rabies has been extensively studied in red foxes, which serve as critical hosts and vectors for specific strains of the disease. Although now eradicated in many regions, rabies remains a valuable case study due to the diverse modelling efforts it has inspired, offering opportunities to compare alternative approaches that may be applied to other diseases of interest. Here, we compare two methods for modelling rabies dynamics: 1) an IBM with a cell-lattice framework (Tischendorf *et al.* 1998) and 2) a combined Bayesian state-space and metapopulation model (Baker *et al.* 2020). Tischendorf *et al* . (1998) employed spatially-explicit grid cells to simulate localised interactions, transmission heterogeneity, and clustering effects in highly immunized fox populations, offering insights into fine-scale processes and enabling targeted interventions. In contrast, Baker *et al.* (2020) used three decades of rabies case data to assess regional spatial coupling, density-dependent dynamics, and localized transmission to capture broader trends and demographic influences of rabies on fox populations. These methods provide complementary insights into rabies dynamics by focusing on different scales and mechanisms of disease spread. Both models incorporated seasonality and dispersal, essential for capturing temporal variations in long-distance transmission and changes in the number of susceptible individuals. However, their use of empirical data differed. Tischendorf *et al* . (1998) relied on literature-derived movement patterns, while Baker *et al* . (2020) used Bayesian approaches to estimate dispersal rates from observed rabies cases. Tischendorf *et al.* (1998) also used theoretical landscapes, while Baker *et al.* (2020) represented regions as five German states between which dispersal could occur. Notably, only Baker*et al.* (2020) explicitly integrated density dependence (represented as declines in survival and reproduction as metapopulations approach carrying capacity) and demographic processes, critical for realistic modelling of contact rates, with parameters informed by studies on urban foxes. In Tischendorf *et al.* (1998), these processes were somewhat implicitly represented through the number of occupied cells, mortality rates due to infection, and dispersal rates of subadult foxes. The use of integrated models in both cases demonstrates the benefits of integration for addressing disease dynamics, while managing the trade-offs inherent with modelling complex systems. For example, both approaches captured spatial elements of rabies dynamics and tracked disease progression over time, demonstrating that different approaches can achieve similar goals. Both approaches also emphasised the importance of spatio-temporal processes in understanding rabies dynamics. Both studies found that incorporating dispersal-mediated transmission across habitat regions was important to reproduce key empirical patterns. Despite these strengths, both models faced challenges with missing data, such as population size and fine scale distribution of foxes and vaccination campaigns. Ultimately, each approach underscored the necessity of accounting for local interactions and spatial heterogeneity to model the complex fox-rabies system, strengthening the conclusions despite data limitations.

3.1.2 Culling

Foxes are subject to lethal predator control through harvesting, fertility control, and poisoning due to their perceived negative impacts on wildlife, livestock, and human health, with the aim to limit depredation impacts and/or reduce disease spread (Hoffmann & Sillero-Zubiri 2021). However, the impact of culling on fox population dynamics remains unclear due to a lack of evidence of potential compensatory mechanisms (Lieury *et al.* 2015). Beyond foxes, understanding the effectiveness of predator control remains a key issue in conservation management. Here we discuss two approaches used to evaluate the impact of culling on fox population dynamics: 1) a spatially-explicit IBM (Hradsky *et al.* 2019) and 2) a Bayesian state-space IPM (Nater *et al.* 2024). These two approaches had different management purposes and thus required different data and considered different processes. Hradsky *et al.* (2019) focused on the impact of poisoning to evaluate population responses to diverse baiting designs at scales relevant to management, while Nater *et al* . (2024) assessed the impact of harvesting on vital rates, population structure, and rate of population change in an expanding fox population. To evaluate and plan effective fox baiting programs, Hradsky *et al.* (2019) used customisable habitat-cells to specify habitat patches and indicate the location and type of bait stations. The model used a relatively fine temporal scale that allowed for fox sociality and territoriality to be incorporated. At each time step, foxes could disperse and, depending on their sex and social status, join a fox-family and reproduce. In contrast, Nater *et al.* (2024) used a non-spatial, female only model to understand the drivers of fox population dynamics. The model was built on an annual time step, during which the population changes in response to natural mortality, harvesting, immigration, and reproduction. The impact of seasonal and inter-annual changes in food availability on local demography and immigration rates were also investigated. To investigate the effects of culling in their respective contexts, the authors utilised different data and evaluated their models in different ways. Hradsky *et al.* (2019) parameterised their IBM using site-specific data from the literature, including population density and dispersal distances. Their model was applied to four case-studies and model outputs were validated against individual- and population-level empirical estimates. Nater *et al.* (2024), on the other hand, used a range of disparate data streams to estimate age-specific demographic rates (number, age, and reproductive status of harvested foxes), reproductive rates (placental scar data and opportunistic pup counts from hunters and camera traps), immigration rates (genetic data). Data on food availability (rodent abundances and reindeer carcasses) at different spatial and temporal scales were also used to infer natural mortality and immigration. The IPM was then evaluated by comparing model predictions with genetic data on emigration. Overall, both approaches provided complementary insights on the impact of culling on fox populations. Hradsky *et al.* (2019) showed that fox density is more sensitive to the frequency of baiting than the spatial density of baits, due to the recruitment of individuals from neighbouring patches. In contrast, Nater *et al.* (2024) identified the key drivers of year-to-year population change, highlighting the interactive role of food availability, showing that harvesting is more efficient when it coincides with low rodent abundance. Both studies highlighted the importance of better understanding density-dependent and compensatory fecundity and immigration, which appear to be key drivers of fox population dynamics. Potential immigration-mediated compensation for intentional mortality has rarely been investigated due to the lack of data on dispersal. In this regard, the IPM developed by Nater*et al.* (2024) shows a very promising use of genetic data for estimating migration rates.

3.2 Case-study 2: European mink

Many species are subject to data limitation challenges, making it difficult to assess conservation status and to identify the associated drivers of population decline. Regardless, management decisions are needed, often at timescales that are much shorter (years) than it takes to amass the data to conduct robust analyses on population dynamics (decades). Rare species present a particular challenge because their scarcity makes data inherently difficult to collect, while also being at high risk of extinction (Davidson *et al.* 2009). The European mink, a mustelid that has been extirpated across much of its historic range, is one example of this dilemma. Remaining local populations are critically endangered and active intervention to prevent extinction and promote recovery is ongoing (Box 3). For understanding disturbance impacts and informing management decisions for European mink, correlative SDMs are an obvious first choice as presence data exist and remote sensing and climate modelling make it possible to include dynamic and disturbance-relevant predictor variables. SDMs have been developed to predict habitat suitability for European mink (and American mink, *Neovison vison* , an invasive competitor) in Spain under historical conditions and various socioeconomic and emissions pathways (Goicolea *et al.* 2023). Spatial maps produced from SDMs can help identify areas for protection, restoration, and captive release, and illustrate changes in habitat suitability and interspecific overlap under climate change. The latter relies on assumptions that correlative relationships remain unchanged in time, accurately represent species requirements, and hold when extrapolated outside the range of input data. However, in many instances, these assumptions are likely to be violated. Many of the potential causes of the decline in the European mink could have strong impacts on energy balance (Fig. 3, Box 3). Energetic modelling approaches are well suited to data limited species because many energetic processes scale allometrically or are evolutionarily conserved (McGrosky and Pontzer 2023; Kooijman and Augustine 2022), allowing models to be parameterized in the absence of species-specific data. In addition, while energetic measurements from data-limited populations may be difficult to obtain, data collected from proxy species or animals managed in human care may be more readily available. For example, metabolism and reproductive energetics have been measured in American mink and other terrestrial mustelids (e.g., Iversen 1972; Wamberg and Tauson 1998; Chappell *et al.* 2013), while data relevant to energetic models have been collected from European mink in captive breeding programs (Kiik *et al.* 2017). These data can thus inform the energetic requirements and challenges of the European mink. There are a range of energetic modelling frameworks that can be used including traditional bioenergetics models and DEB models. One key advantage of DEB framework is that it is grounded in the first principles of fundamental biological and physical laws. It assumes that all organisms (regardless of their taxonomy) follow the same basic principles of energy acquisition, allocation, and expenditure. DEB therefore allows for the transfer of information across species by leveraging standardized allometric relationships and shared biological principles, allowing for predictions even in species for data are lacking (Lika *et al.* 2011). This assumption also facilitates the application of existing models to new species, as could be the case with American and European mink (Desforges *et al.* 2017). By capturing the underlying processes of energy flow, DEB models can make useful predictions about organism responses to environmental changes such as resource availability, temperature, and stress (e.g., Molnar *et al* . 2010; Harwood *et al.* 2020), providing an explanatory framework linking physiology and ecology. For the European mink, DEB models could be used to investigate the effects of habitat loss and fragmentation including reduced prey availability, interspecific competition, altered activity budgets due to habitat fragmentation, and antagonistic interactions with American mink (Fig. 2). Other disturbances indirectly related to energetics could be incorporated, such as pollution or reduced mating opportunities, to understand synergistic impacts. Such models could help identify thresholds at which resource scarcity begins to negatively affect individual survival, assess the long-term impacts of disturbances, and quantify the impacts of stressor removal (e.g., eradication of American mink). By combining DEB with individual-based movement models and habitat suitability maps (from SDMs), spatially-explicit DEB models could be used to evaluate the potential outcomes of management decisions. For example, this approach, coupled with targeted surveys, would allow for the identification of suitable areas to release captive-bred individuals based on resource availability. It could also inform habitat restoration efforts by highlighting areas where interventions would likely have the greatest impact on the species' recovery.

3.3 Summary of case-studies

These case-studies have exemplified the diversity and complementarity of modelling approaches for predicting the population consequences of human disturbance. Our fox case study demonstrated that IBMs are particularly well suited for assessing human impacts on species with extensive ecological knowledge available thus enabling detailed simulations of individual behaviour and interactions. Our European mink study highlighted the potential for energetics modelling to overcome data limitation issues that are common for species of conservation concern. Although particularly suited to data limited species, energetics approaches are also useful for other species exposed to indirect stressors (Johnson *et al.* 2024). Despite the breadth of existing research, a notable gap exists in the red fox literature regarding the integration of energetics with disturbance modelling. Given the growing body of empirical research on red fox energetics, there is an exciting opportunity to link disturbances to population dynamics through changes in individual energetics and vital rates. Doing so could quantify the energetic costs of disturbances (e.g., by measuring the energetic demands imposed by habitat fragmentation or reduced prey availability) or predict long-term population consequences by linking individual energy budgets to reproduction and survival rates.

4 Discussion

An impressive variety of quantitative modelling approaches are being used to understand and predict wildlife responses to human disturbance – and even to address the same conservation or management problems, as exemplified by our red fox case-study. Understandably, it may be daunting for someone who is not familiar with modelling, or who is only familiar with a specific family of models, to decide on which modelling approach(es) to use. We hope that this manuscript can provide guidance and broaden horizons for those wishing to model the impacts of human disturbance on wildlife. Broadening our perspective of what constitutes disturbance can open ecologists up to other research areas and approaches. For example, some ecologists may not consider disease to be a human-mediated disturbance, since it is a part of the evolutionary history of most organisms, but it is also affected by human-mediated environmental change. Approaches used to model disease impacts, and their associated considerations, may thus provide insights into the modelling of other disturbances that may act via similar mechanisms. A broader perspective can also expose ecologists to some of the ways that modelling approaches can be integrated to overcome the limitations of the different singular approaches. It is interesting how different processes are being pulled into models to address different disturbances. This was illustrated well for red foxes, where dispersal and immigration were explicitly incorporated when assessing the impacts of regulatory management, since these processes appear to drive the difficulties in regulating red fox abundance. Similarly, spatial dynamics, movement, and dispersal were key processes included for predicting disease transmission, because movement of infected individuals drives disease spread. Yet there remains an opportunity to incorporate other processes that impact population responses to human disturbance, including eco-evolutionary feedbacks and sociological processes. Since evolutionary changes following disturbance may enable populations to adapt to disturbances, such as increasing temperatures, eco-evolutionary feedbacks play a crucial role in the long-term responses of populations to disturbance (Loeuille 2019). Social dynamics can also play a key role in population dynamics and although they are sometimes considered for social wildlife (e.g., Brandell *et al.* 2021; Grente *et al.* 2024), the human element is often neglected. Not only are human disturbances inherently driven by human behaviour, but so are the perceptions of management actions (Bro-Jorgensen *et al.* 2019). Such interdisciplinary approaches are already well developed (e.g., Dobson *et al.* 2019) but greater uptake in disturbance ecology modelling could improve conservation and regulatory management outcomes. We were pleased to see increasing use of energetic modelling applications across a range of quantitative approaches. Since energetics act in a summative way and many non-lethal disturbances have impacts on energy acquisition or use, energetic models can help us better understand the impacts of multiple stressors on wildlife populations. Subsequently, the inclusion of energetic mechanisms represents an important avenue to scale individual-level responses to population-level impacts. By integrating models, energetics can be incorporated into most of the quantitative approaches available for modelling population responses to human disturbance. Perhaps most importantly, energetic models may offer the only viable way both scientists and decision-makers can anticipate the impact of demographic responses to complex patterns of global climate change that will surely continue for the foreseeable future. If we do not accommodate changes in behaviour, space use, and demography that will accompany the relentless change in climatic drivers, even the best of models will only have value for understanding the past rather than predicting the future. While DEB theory is not new (Kooijman 2000), it appears to be having a resurgence to address the growing concerns of human-mediated threats to wildlife. Given the common challenge of data availability, the DEB approach may be more attainable than traditional energetic approaches that require detailed energetic data that may not be readily available. This is one of the reasons why we explored this avenue in our European mink case-study. However, traditional energetics approaches can also utilise data from proxy species and allometric relationships, and may be more intuitive to some ecologists. The intricate tie between individual behaviour and energetics makes these a powerful combination for assessing population responses to disturbance. Despite the developments and integrations of quantitative modelling approaches, models can only ever be a simplified representation of natural systems. All quantitative approaches rely on assumptions, imperfect data, and simplifications of the processes they aim to represent. Consequently, there is a great deal of uncertainty associated with input parameters and data, model structure (Refsgaard *et al.* 2006), and resulting model predictions (Rounsevell *et al.* 2021). Several approaches have been developed to minimise or quantify the level of data or model uncertainty. For example, sensitivity analysis aims to determine the influence of uncertain parameters in model outputs, which can highlight priority areas for data collection or model development (Cariboni *et al.* 2007). Alternatively, ensemble modelling aims to reduce model uncertainty by combining predictions from multiple models. This approach has become more common for species distribution modelling (Hao *et al.* 2020) but has received criticisms due to the ‘smoothing out’ of model outputs. Challenging models with different assumptions against each other (i.e., robustness analysis (Levins 1966) or model intercomparison) is another approach to quantifying uncertainty in model outputs, as well as investigating the influence of different model structures. With this approach, there is no averaging of model outputs, but the resulting model predictions may be vastly different. Quantifying uncertainty brings about its own challenges. When providing predictions to managers, it is important to highlight the degree of uncertainty in model predictions, yet uncertainty can make it more difficult for managers to make decisions. This makes knowledge transfer crucial, as stakeholders are able to conceptualise uncertainty in model outputs and make informed decisions when clearly communicated (Mahevas & Sigrid 2024). Nonetheless, the acceptance of modelling tools as a decision support tool depends on whether different stakeholders agree with the representation of the system and their understanding of its components. For this purpose, participatory modelling is a widely used approach (Voinov & Bousquet 2010) that aims to increase and share knowledge of a system and its dynamics under different conditions and to anticipate the impact of management actions to support decision-making. However, the involvement of stakeholders is no guarantee for the appropriation of model results, especially if their participation is limited.

5 Conclusion

The diverse methodological toolkit available highlights the adaptability of modelling approaches to address specific stressor types and questions for wildlife conservation and management. Here, we have provided an overview of the key modelling options available for predicting population responses to human disturbance, indicating how different models can be combined to leverage the strengths of alternative approaches. We also highlighted the important role that energetics plays in predicting the impacts of indirect stressors on population dynamics, and suggest other areas of development in modelling the complexities of indirect or multiple stressors, such as eco-evolutionary and sociological mechanisms. We hope new studies will consider alternative approaches or integrations and identify the processes that should be incorporated for assessing the specific disturbances impacting a given study system. Throughout we have illustrated the value of integrating different modelling approaches to address population consequences of disturbance, demonstrating that science is stronger with multi-disciplinary collaboration. In much the same way, collaboration between stakeholders, managers, decision-makers, and ecologists enables efficient uptake and implementation of management recommendations.

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Text boxes

Box 1: From individuals to communities - pathways for human impacts on wildlife

The impacts of human disturbance, and many other stressors, occur not only via directly altering the vital rates (e.g., survival, fecundity) of a population but also indirectly via changes in the behaviour and/or physiology of individuals (NAS 2017). When sustained, stressors can lead to chronic impacts that erode the health and immune status of individuals. Stressors may also have an acute impact on vital rates, such as mortality resulting from an injury. These individual level responses can then be scaled up to the population-level by considering multiple individuals, and ideally their interactions, within a population. Representing multiple interacting stressors requires the explicit consideration of multiple mechanistic pathways through which these stressors are acting. For example, the European mink (see 3.2) is exposed to a range of stressors including the direct effects of road mortality, which relates to individual movement patterns and habitat connectivity, and indirect effects of wetland loss and competition with American mink, resulting in behavioural and energetic impacts on the population.

Community and ecosystem dynamics are important when identifying appropriate conservation or management strategies, since a lack of consideration can lead to adverse management outcomes (e.g., Buckley and Han 2014; Zavaleta *et al.* 2001) . Despite this, these dynamics are rarely accounted for in disturbance models, particularly mechanistic models, likely due to the increasing complexity when considering multiple populations or species. Nonetheless, the increasing impact of human activities on ecological systems and their continued degradation (IPBES 2022) emphasises the need for human disturbance modelling to incorporate community dynamics. There are many approaches that can be used to account for community dynamics (Geary *et al.* 2020), which can be integrated with other quantitative approaches to leverage off the benefits of each approach. For example, individual-based models can be combined to create community models (e.g. Radchuk *et al.* 2013) or can be integrated within matrix community models (Lytle & Tonkin 2023), depending on the specific data available. Community models also lend themselves well to energetics approaches (Szangolies *et al.* 2024), permitting mechanistic evaluation of community dynamics.

The mechanistic pathways of impact are not only relevant for studying the impacts of stressors on wildlife, they can also be used to measure the effectiveness and appropriateness of management actions. By considering how management actions are intended to impact the target population, such as through improved resource availability, ecological models can help identify if management strategies will have their intended outcome or if alternative strategies may be more worthwhile. This may be particularly beneficial when considering community dynamics, where unintended consequences are more likely to occur.

Box 2: Ecology of the red fox

Distribution and conservation status: The red fox has the largest geographical range of all members of the order Carnivora. It is widespread throughout the northern hemisphere, from the Arctic Circle to southern North America, Europe, North Africa, the Asian steppes, India and Japan. Introduced populations also persist in Australia where they have caused significant damage to native ecosystems. The species is listed as Least Concern (LC) on the IUCN Red List (Hoffmann & Sillero-Zubiri 2021).

Ecology: Red foxes can be found in habitats as diverse as tundra, deserts, mountains (up to 4,500 m), forests, and urban areas. Foxes are opportunistic omnivores and scavengers with highly plastic diets that vary according to the availability of food resources. Their diet may consist of mammals (voles, rabbits, young hares, or lambs), ground-nesting birds, poultry, invertebrates, fruit, and food waste, to varying degrees. Females become sexually mature around 10 months old and generally give birth to a litter of 4-6 young per year. Red fox densities vary widely, from as low as 0.02 ind/km2 in rural areas (Meia 1994), up to 30 ind/km2 in urban areas where there is an oversupply of food (Harris & Rayner 1986). It can be solitary at low densities but also forms social groups (Macdonald 1981).

Main threats and management actions: Threats to this species from humans include habitat degradation, loss and fragmentation in certain areas, exploitation, and persecution (Hoffmann & Sillero-Zubiri 2021). Hunting and trapping are widespread in most areas, with large kill bags. Hunting is mostly seen as sport, while trapping and regulatory shooting aim to reduce population size and depredation, but there is increasing debate about whether fox control is achieving its goals. While no longer considered a concern, red fox have historically been impacted by vulpine rabies epidemics.

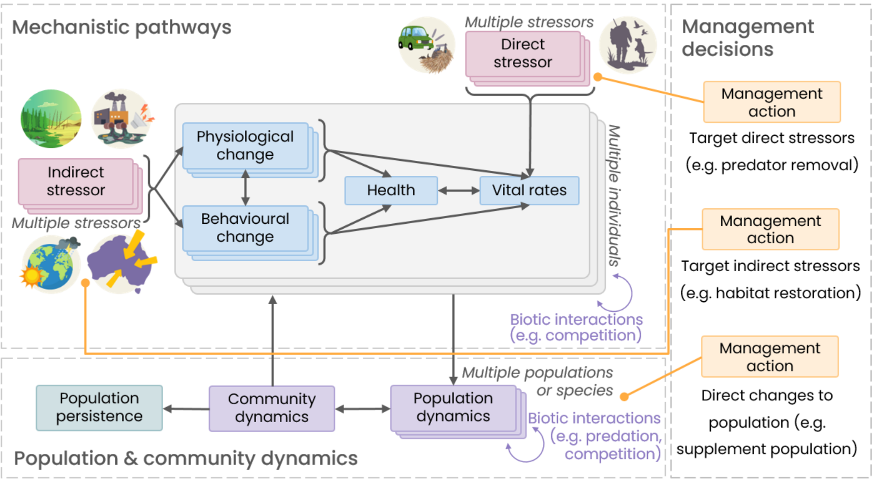
Box 3: Ecology of the European mink

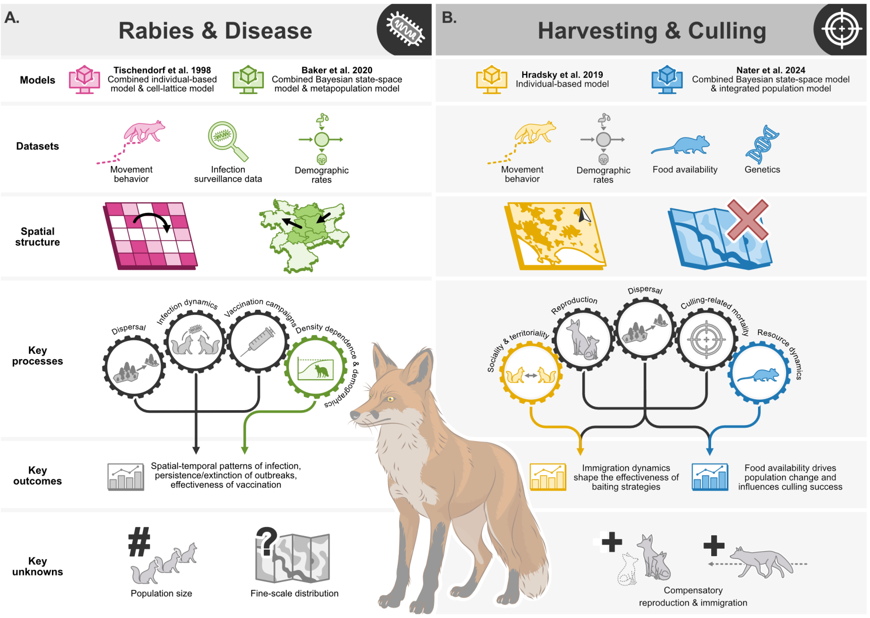
Distribution and conservation status: The European mink is the most endangered mammal in Europe and was classified as Critically Endangered (CR) on the IUCN Red List in 2016 (Maran *et al.* 2016). Over the last 150 years, the species has declined by more than 90% and has been extirpated or severely depleted across most of its former range. The current range of the endemic wild population consists of a few isolated fragments in northern Spain and western France, the Danube delta in Romania, Ukraine and Russia (Maran *et al.* 2016).

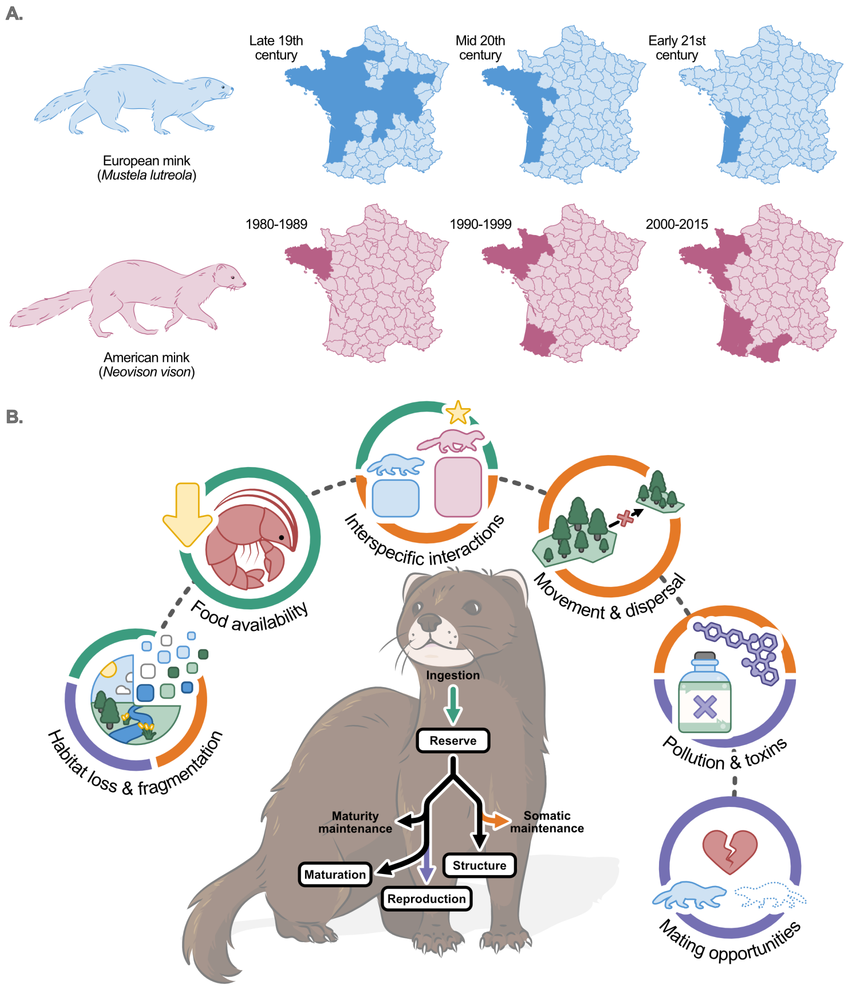
Ecology: European mink are small semi-aquatic mustelid carnivores (males: 0.5-1.5 kg, females: 0.3-0.7 kg). They inhabit densely vegetated banks of rivers, streams, and lakes with stagnant or slow-flowing water across a variety of landscapes (forests, agricultural, hedgerows, marshes, polders, etc.), using underground burrows or dense vegetation for resting and reproduction. Diets primarily consist of amphibians, crustaceans (crayfish), fish, small mammals (rats and voles), birds and, to a lesser extent, insects and eggs (Palazon *et al.* 2004; Libois 2001). Predators include the red fox, dogs, and raptors (Maran *et al.* 2017; Podra 2021). Females reach sexual maturity at 11 months and give birth to a litter of 2-7 young per year. Longevity in the wild has been reported to be up to five years (Manas *et al.* 2016).

Main causes of decline and management actions: The main hypothesised threats contributing to the current decline are (1) habitat loss and fragmentation of wetlands, (2) road mortality, (3) harvesting and (4) the impact of the invasive American mink through interference competition. The species is protected by law in Europe. In an effort to recover European mink populations, captive breeding and reintroduction programs have been implemented in Spain (Gomez 2018; Maran *et al.* 2017; Podra 2021), Estonia (Maran *et al.* 2017), and France (DREAL*et al.* 2021).

Data availability: Across the three extant populations, available data include presence data, home range size estimates, diet information in the presence and absence of invasive competitors, habitat requirements, trait data, behavioural responses to humans, and post-release survival estimates for captive bred individuals.


Mechanistic pathways
Multiple stressors
Direct stressor
Indirect stressor
Multiple stressors
Physiological change
Behavioural change
Health
Vital rates
Multiple individuals
Biotic interactions (e.g. competition)
Multiple populations or species
Population persistence
Community dynamics
Population dynamics
Biotic interactions (e.g. predation, competition)
Population & community dynamics
Management decisions
Management action
Target direct stressors (e.g. predator removal)
Management action
Target indirect stressors (e.g. habitat restoration)
Management action
Direct changes to population (e.g. supplement population)


A.
Rabies & Disease
B.
Harvesting & Culling
Models
Tischendorf et al. 1998
Combined individual-based model & cell-lattice model
Baker et al. 2020
Combined Bayesian state-space model & metapopulation model
Hradsky et al. 2019
Individual-based model
Nater et al. 2024
Combined Bayesian state-space model & integrated population model
Datasets
Movement behavior
Infection surveillance data
Demographic rates
Movement behavior
Demographic rates
Food availability
Genetics
Spatial structure
Key processes
Dispersal
Infection dynamics
Vaccination campaigns
Density dependence & demographics
Sociality & territoriality
Reproduction
Dispersal
Culling-related mortality
Resource dynamics
Key outcomes
Spatial-temporal patterns of infection, persistence/extinction of outbreaks, effectiveness of vaccination
Immigration dynamics shape the effectiveness of baiting strategies
Food availability drives population change and influences culling success
Key unknowns
Population size
Fine-scale distribution
Compensatory reproduction & immigration


A.
Late 19th century
Mid 20th century
Early 21st century
European mink
(*Mustela lutreola*)
1980-1989
1990-1999
2000-2015
American mink
(*Neovison vison*)
B.
Interspecific interactions
Food availability
Movement & dispersal
Habitat loss & fragmentation
Pollution & toxins
Mating opportunities
Ingestion
Reserve
Maturity maintenance
Somatic maintenance
Maturation
Structure
Reproduction