Appendix E
Models for Exotic Species Introduction, Establishment, Spread, and Invasion

Models of invasive species introductions, distribution and spread, and establishment are key tools for both understanding the invasive species problem and designing effective prevention and control techniques. Numerous types of models have been developed. In many cases, authors recommend that conservation managers be cognizant of specific factors (e.g., species interactions, climatic factors, spread vectors) in ecosystem management. Some offer clear, ready-to-use models and strategies for conservation managers. *Table E1* below lists examples of models used to predict species invasions.

Although most invasive species spread, distribution, and establishment models are not designed specifically to incorporate climate change variables, several have been developed to explicitly address climate change impacts on species distributions. These include bioclimatic envelope models, discriminant analyses, and logistic regression analyses (*see table below – identified by an asterisk).* Other modeling methods such as ecological niche modeling could be modified to integrate climate variables.

Table E1. Model and description.	Author(s).
Comparative analysis. Authors use descriptive information to identify species with high invasion and impact potential. The three steps include: (1) identifying donor regions and dispersal; (2) selecting potential invaders based on biological traits; and (3) using invasion history. The analysis identifies *Corophium* spp., Mysids, and *Clupeonella caspia* as possible Great Lakes- St. Lawrence River system invaders. Authors recommend focusing on monitoring and applying described guidelines; and developing an accessible electronic database of possible invaders.	(Ricciardi and Rasmussen, 1998)
Comparative analysis. Vermeij recommends an agenda for invasion biology. The author recommends a comparative and systematic approach, comparing factors involved in invasion process (arrival, establishment, and integration), participants, and outcomes at spatial and temporal scales. The author prefers multiple methodological approaches to address invasion biology.	(Vermeij, 1996)
Simple diffusion model. The authors use this type of model to predict zebra mussel spread by (1) comparing current pattern of zebra mussel invasion with estimates of boater movements, and (2) diffusion model data. The model estimates infrequent, long-distance boater movements to predict AIS invasion probability. Managers can use results to predict spread rates and patterns to use in developing management strategies for the Great Lakes. Efforts to curb or stop spread should focus on high frequency long-distance paths such as areas with high boating activity.	(Buchan and Padilla, 2000)
Diffusion. The authors describe and predict dispersal patterns and ecological impacts of five invaders in the Great Lakes. Results show a mix of continuous and discontinuous dispersal. Hypothesized general attributes of invasive species are valuable to predict successful invaders but not for determining impacts. The authors recommend that additional research focus on benthic food webs to understand the primary impact of invaders.	(Vanderploeg et al., 2002)
Diffusion. The authors reconstruct invasion dynamics using museum records, personal collections, and literature at three different scales to determine importance of various means of	(Suarez et al., 2001)

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dispersal. Human-mediated jump-dispersal plays an important role in invasion dynamics and may affect invasion rates. Authors recommend using stratified diffusion models when species use more than one dispersal process. Control measures should focus on new foci or preventing new foci. Identifying the range of long-distance, jump-dispersal will help future modeling efforts. Reconstructing spatial scales of invasion dynamics may make strategies for management and eradication more effective.	
Reaction-diffusion model. The author describes population behavior at the population level. The model assumes "random movement, continuous positive population growth, a homogenous environment, and no taxis or interspecific interactions." This model is used to highlight differences in invasions between marine and terrestrial species. It provides insights on invasions at a broader scale (not individual scale). Results show that using data on one invasion may not be a good predictor of other conspecific invasions.	(Grosholz, 1996)
Reaction-diffusion model. The author tests whether Skellam's model for areal spread describes *Mimosa pigra* invasion and finds that it does not. Skellam's model is continuous, deterministic, and assumes (1) population increasing exponentially; (2) diffusing outward randomly; and (3) normally distributed distribution. The author finds that climatic conditions such as rainfall and flooding increase rate of spread.	(Lonsdale, 1993)
Dispersion model. Authors use a two-level dispersion model (fragments spread at (1) short distances and (2) long distances) for *Caulerpa taxifolia*.. Research needs identified include studying biomass as a function of depth and time, surface variability, competition, settlement, local currents, accurate knowledge, functional analysis of the ecosystems, ability to analyze large sites.	(Hill et al., 1998)
Integrodifference matrix population (IMP) models. Integrodifference equation (IDE) are used to predict spread rate of invasive species populations. The models are useful for combining demographic models with spatial dispersal models and can be used by conservation managers for issues that involve spatial processes in order to stop an invasive species spread or to evaluate relative risk. When projecting rate of spread, one should also conduct perturbation analyses in order to determine management strategies based on what changes the rate of spread.	(Neubert and Parker, 2004)
Stochastic mathematical models are useful when numbers are small to model invasions, spread, and persistence. For species arrival, the shape of dispersal and distribution are important. For establishment, high reproductive rate is important. For persistence, carrying capacity is important. Mollison recommends using stochastic models over deterministic and diffusion models for modeling control zones to prevent spread of invasive species.	(Mollison, 1986)
Discriminant analysis.* The author uses multiple discriminant analysis to determine correlation between species distribution and climatic variables to predict plant species invasions. The model identifies areas in Australia, Africa, and the Americas as areas that may harbor South Florida invasive species. The author concludes that climatic-matching can be an important part of a multi-level management strategy and recommends that future research focus on determining whether species live in similar habitats as the host region to which they are invasive.	(Curnutt, 2000)
Discriminant analysis. Authors use 10 life-history characteristics and a jackknifed classification procedure to predict pine (*Pinus* subgenus) invasions, which can be used as an initial sign of potential invasiveness. Results indicate three traits predict invasive species: short juvenile period, short interval between large seed crops, and small seed mass. The best predictor for herbaceous plants is their latitudinal range. Authors recommend this model as general screening tool for detection of invasive, woody seed plants.	(Rejmanek and Richardson, 1996)
Discriminant function and principal component analyses.* Mandrak compares ecological characteristics of possible invading species to recently invading species to determine potential invaders' response to climate change. Analyses show that 27 of the 58 possible invaders are considered to be potential invaders of the lower and upper Great Lakes. Eight potential invaders are thermally restricted to the Lower Great Lakes, however, under climate change, their spread could be relatively swift. Management implications include changing the practice of maintaining cool and cold water fisheries.	(Mandrak, 1989)

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Ecological niche modeling. This approach assumes (1) species distribution is limited by its ecological niche; and (2) a species can only disperse to an area with similar ecological characteristics. Results indicate that the ecological niche constrains the distribution potential of a species. The author notes that invasive species predictions can be integrated with global change predictions.	(Peterson, 2003)
Ecological niche modeling/ Genetic algorithm for rule-set production (GARP). These models relate ecological traits of areas where a species is located to points sampled randomly from the rest of the test area to determine decision rules that best describe those traits associated with the species' presence. Authors conclude that the ecological characteristics of a species' native range predict potential invasive geographical range with high accuracy.	(Peterson et al., 2003)
Ecological niche model/ GARP. Underwood et al. developed a model using GARP to predict non-native species' environmental niches in Yosemite Valley, considering elevation, slope and vegetation structure. Results demonstrate the predictive potential of GARP for identifying potential invasion sites. Authors conclude that similar models can be developed for other national parks, and that such models may increase efficiency and decrease cost to managers.	(Underwood et al., 2004)
Ecological niche model/ GARP. The authors describe ecological niche modeling as a "proactive tool" for risk assessments. It could be used for all species not native to an area and to create avoidance strategies based on what activities could result in invasions. There is need to enlist support of those with biodiversity data that can be used in the model, explore new models and approaches to invasion biology, and enhance technology.	(Peterson and Vieglais, 2001)
Bioclimate envelope model.* Authors review bioclimate envelope models, discuss limitations, and propose the model can be useful as a first approximation to understand climate impact on biodiversity. The authors state that it is not possible to accurately predict biogeographical responses to climate change, but that bioclimate models may be the best available guide for making policy decisions. Authors recommend a hierarchical modeling framework with climate as a dominant factor on a large, continental scale and biotic factors dominant at micro-scales.	(Pearson and Dawson, 2003)
GIS. The authors use multiple regression analysis with (1) bathymetry, (2) sediment type, and (3) Side Scan Sonar (SSS) data to predict percent cover by zebra mussels. The model indicates that zebra mussels spread across soft substrates and transform soft substrates to hard substrates. Mussels on soft substrate may serve as a "positive feedback" for more mussels. This approach can be used to predict spread of mussel onto soft-substrates in other lakes.	(Haltuch and Berkman, 2000)
GIS. Authors developed a catchment management system using GIS. Five processes modeled separately include: (1) fire occurrence, (2) spread and establishment of alien plants, (3) growth between fire cycles, (4) rainfall to run off ratio, and (5) effects of biomass on stream flow. The model shows how much water could be lost per year if alien plant invasions are allowed to continue uncontrolled. The model shows that, over a 100-year period, alien cover increases from 2.4% to 62.4%. Authors recommend removing invasive plant species to ensure water availability.	(Le Maitre et al., 1996)
GIS. Mapped *Phragmites* coverage over 9 different years using aerial photos in Great Lakes region. Conducted spatial analysis of total area covered each year. Abundance changes were analyzed using geometric or logarithmic growth equations. GIS maps show distribution was dynamic from 1945 to 1999 and increased exponentially from 1995 to 1999.	(Wilcox et al., 2003)
Regression analysis. Ricciardi uses impact history of invasive species to determine result of introduction into new area and determine impact on multiple invaded sites to create a statistical model of impact. Correlating models of invader abundance and physical environmental traits to models of invader impact to abundance may allow predictions as to habitats vulnerable to high impacts.	(Ricciardi, 2003)
Logistic regression analysis.* Collingham et al. use statistical models of presence / absence of three weed species at coarse and fine scales. Authors evaluate ability of model at one scale to predict distribution at larger scale. Results show some correspondence between environmental factors at different spatial scales. Authors recommend modeling species at more than one scale. This is important for managers, because weed control happens at a fine scale, but understanding processes on a larger scale is important for long-term management.	(Collingham et al., 2000)

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For example, analyses show that climatic variables affect species' ranges; thus, range may be affected by future environmental change.	
Multiple logistic regression analysis. Goodwin et al. conducted analysis with (1) biological attributes and (2) biological attributes and geographical range. Geographic range of a species is a successful predictor of invasiveness, while the biological attributes tested are not. However, geographic range is likely correlated with biological traits (model showed a significant positive relationship between geographic range and flowering period). Results demonstrate that predicting invasions on a species by species level will not adequately deal with the accidental introduction of species.	(Goodwin et al., 1999)
Regression and Akaike's Information Criteria (AIC). Authors use logistic regression to determine relationship between successful establishment and biological variables; multiple regression to evaluate relationship of a measure of spread and the average abundance of an invasive species with biological variables; and AIC as an unbiased estimate of the regression model fit. Results show that different characteristics favor different stages of invasion (e.g., establishment, spread). Authors find that human preference affects invasion and recommend stopping the transport and release of non-native fish to prevent invasions.	(Marchetti et al., 2004)
Spatially explicit, individual-based simulation (SEIBS). Authors use factorial design and simple linear regression- factors ((1) adult fecundity, (2) dispersal ability, (3) time to reproductive maturity, (4) temporal frequency of post-fire recruitment opportunities, and (5) fire survival by adults) to quantify interactions between factors on spread rate. All but fire survival can significantly affect *Pinus* spread rates. Efforts need to focus on obtaining empirical data for the four relevant factors. It is important for models to incorporate spatial scale of ecological processes.	(Higgins et al., 1996)
Taxonomic model. Lockwood uses taxonomy to predict success of avian invaders. Results indicate that some taxa are more likely to successfully establish themselves than others and that human action (e.g., importing certain species) obscures trait-based taxonomic patterns in successful establishment.	(Lockwood, 1999)
Quantitative taxonomic model. Kolar and Lodge review publications that use quantitative methods to assess characteristics of introductions and of species that invade to document taxa-specific trends. Results indicate that propagule pressure is positively related to establishment success; and region of origin is significantly associated with establishment success. Authors recommend that predictive models be broadened to include earlier stages of invasion.	(Kolar and Lodge, 2001)
Quantitative taxonomic models. Kolar and Lodge use discriminant analysis and categorical and regression tree analyses to predict invasive species and their impacts. Results show that using quantitative models and taxon, ecosystem, and invasion stage specific data can be used for risk assessments and for guiding policy, education, and management efforts to prevent future invasions.	(Kolar and Lodge, 2002)
Probability. Huston uses dynamic equilibrium model of species diversity to address (1) the probability of an invader's successful establishment and (2) the probability the invader will become dominant in the invaded ecosystem. Productivity, disturbance, and environmental factors can be used to predict invasions. Areas with minimal productivity are easily invaded. Productive, undisturbed and very unproductive areas are seldom invaded. The easiest areas to invade, establish, and impact are disturbed, productive areas.	(Huston, 2004)
Demographic model. Authors create a probabilistic risk assessment framework to evaluate the possibility of solid wood packing material (SWPM) pest establishment. The approach addresses (1) pest life history traits, (2) suitable host availability and environmental factors that affect establishment, (3) population dynamics, and (4) implications of uncertainty on estimates of risk and risk reduction. Results indicate that small increases in effectiveness of treatment of SWPM can have significant impact on reducing risk of pest establishment.	(Bartell and Nair, 2003)
"Tens" model. One in 10 imported species appears in the wild; one in 10 introduced species becomes established, and one in 10 established species becomes a pest. Three sets of factors are important for the tens rule and deviations from it: (1) propagule pressure; (2) factors allowing species to survive; and (3) factors determining local abundance.	(Williamson and Fitter, 1996)
Screening system. Daehler and Carino tested three systems ((1) North American- decision	(Daehler and

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tree, (2) South African-"linear series of five modules," and (3) Australian-49 questions with score based on responses) for their ability to screen for invasive species in Hawaii. The North American and Australian screening systems had the best results for predicting invasive species in Hawaii and both need only minor changes to be used in new areas.	Carino, 2000)
Multiple competing models. Authors test the association of invasive bullfrogs with non-native fish, finding that non-native fish facilitate survival of bullfrog tadpoles. Adams et al. recommend regarding fish as a "keystone invader" in ponds or lakes that were fishless.	(Adams et al., 2003)
Neutral landscape models based on percolation theory is used to determine how landscape structures impact invasive species dispersal. With finds that poor dispersers may spread more readily when the disturbance area is large or concentrated in space. Good dispersers may spread better with small and localized disturbance. With recommends developing land management actions to control invasive species based on whether dispersal or demography affects spread more.	(With, 2004)
Economic model. Perrings creates a model of biological invasions based on fixed parameters (invasion rate, restoration rate) and a variable control rate. The model demonstrates that the higher the control rate, the lower the proportion of space occupied by the invasive species. In cases where the system is not controllable or observable, Perrings recommends control choices that reflect the precautionary approach.	(Perrings 2002)
Rejmanek provides a **review of approaches:** (1) stochastic; (2) empirical taxon-specific; (3) biological characterization; (4) habitat compatibility; and (5) experimental. Rejmanek examines various approaches to address (a) prevention / exclusion of invasive species; (b) early detection and rapid response; and (c) control / containment / eradication. The author considers models and research approaches, considering management needs.	(Rejmanek, 2000)

*** Model considers climate variables and/or climate change factors.**