Article

WORMSPREAD: an individual-based model of invasive earthworm population dynamics

George W. Armstrong[1], **Ahsan Mahmood**[1], **Andie Nugent**[2], **Sonya Dexter**[2], **Emily Hutto**[2], **Timothy S. McCay**[2], **Ahmet Ay**[1,2]

[1]Department of Mathematics, Colgate University, Hamilton, NY 13346, USA

[2]Department of Biology, Colgate University, Hamilton, NY 13346, USA

E-mail: aay@colgate.edu

Received 4 July 2017; *Accepted 12 July 2017*; *Published 1 September 2017*

Abstract

Invasive earthworm species, such as *Lumbricus rubellus*, can cause changes to forest soils, which may result in reduced forest biodiversity. Individual Based Modeling (IBM) offers a way to predict the spread of invasive species and can provide insight for control. We developed an individual-based, spatially explicit, earthworm population dynamics modeling software package (WORMSPREAD). This software accounts for environmental interactions and individual variation that impact population growth and behavior of earthworms. In the model, individual earthworms are affected by temperature and pH, resulting in changes in reproduction, growth, movement and mortality. WORMSPREAD allows ecologists and conservation biologists to test invasion scenarios with simulations that involve variations in landscape structure and demographic parameters that potentially affect abundance and distribution of invasive earthworm species. The user interface is easy to learn and flexible enough to incorporate new data. Results can help determine where to concentrate conservation efforts and control strategies. An example study of the spread of *L. rubellus* in a portion of the Adirondack Park in upstate New York demonstrates computational experiments that can be conducted with WORMSPREAD. WORMSPREAD can be used to predict population growth in real landscapes, with real variation in environmental conditions. However, it will only lead to accurate predictions if the underlying physiological and behavioral traits of the invading species are known. Indeed, our assessment of these traits for *L. rubellus* indicates that more data are needed for this species, and the situation is likely to be more challenging for less well-studied species. Thus we encourage more studies that relate the physiology and behavior of invasive species to variability of environmental conditions in invaded habitats.

Keywords earthworm invasion; individual-based modeling; software; conservation.

Computational Ecology and Software
ISSN 2220-721X
URL: http://www.iaees.org/publications/journals/ces/online-version.asp
RSS: http://www.iaees.org/publications/journals/ces/rss.xml
E-mail: ces@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

Understanding invasion by exotic earthworms in North America has been highlighted as one of the most important conservation topics of the early twenty-first century (Sutherland et al., 2010). Populations of invasive earthworms can alter soil characteristics and biodiversity, compared to areas with fewer or no earthworms (Burtelow et al., 1998; Dempsey et al., 2013; Snyder et al., 2013). Once invasive earthworms are established, eradication may be unfeasible. Therefore, preventing colonization into new areas is the best strategy for protecting local ecosystems and communities from exotic earthworms (Keith and Spring, 2013).

There is strong interest in using models to predict the potential distribution of invasive species (Gallien et al., 2010). Classical differential equation models have been used extensively with ecological problems, typically to demonstrate concepts such as density-dependent population growth or intra- and interspecific competition (Fahse et al., 1998). However, differential equation models are only able to study the average behavior of the system (Hastings, 1997; Uchmanski and Grimm, 1996). Additionally, the population-level parameters that these models depend on can be unavailable (Hooten and Wikle, 2010). These traits of classical models can limit their usefulness for testing hypotheses in ecology.

An Individual Based Model (IBM) is a computational model that uses agents to simulate individual organisms and their histories, as well as their intraspecific and environmental interactions (Deangelis and Mooij, 2005). In contrast to differential equation models, IBMs can easily incorporate heterogeneity of individuals and the environment. Additionally, IBMs can be constructed from individual-level phenomena, such as pH-dependent propagule production, which can be easier to measure than parameters used to characterize population-level traits (Hooten and Wikle, 2010). IBMs have demonstrated usefulness in ecology and wildlife management (Bousquet and Le Page, 2004; Deangelis and Mooij, 2005; McLane et al., 2011). IBMs have been used as tools in the development of conservation strategies for many rare species, including the large blue butterfly (Griebeler and Seitz, 2002), the red-cockaded woodpecker (Letcher et al., 1998), and walleye and yellow perch in zebra mussel-infested waters (Rutherford et al., 1999).

IBMs may be useful tools in the study of invasive, exotic species, but to date that usefulness has largely been untapped. Keith & Spring (2013) developed an IBM to examine the efficacy of control of the invasive red imported fire ant in Australia and use it to make suggestions to increase success of future eradication efforts. IBMs of invasive earthworms have modeled population growth and dynamics from starting densities of adults and propagules, developmental stages, survival probabilities in various environments, and fecundity (Baveco and De Roos, 1996; Pelosi et al., 2008). However, someone who is not experienced with computer modeling and programming may have trouble adjusting these parameters, running the program, and gathering results, which makes these models very species and system specific (West et al., 2011).

We created an IBM based software package, WORMSPREAD, using NetLogo, a common IBM programming language and modeling environment. WORMSPREAD includes a graphical user interface (GUI) that does not assume a high level of programming experience and can be easily tailored to a new terrestrial landscape and soil-dwelling species of interest (e.g., earthworms, millipedes). We demonstrated the functionality of WORMSPREAD by simulating the dynamics of *Lumbricus rubellus,* a European lumbricid earthworm, in a small portion of the Adirondack Park in upstate New York. This species was chosen as a model invasive species due to the availability of life history and environmental-tolerance data. Additionally, *L. rubellus* is currently of interest to soil ecologists due to the earthworms' role in plant loss and decreasing soil quality (Eisenhauer et al., 2007; Sutherland et al., 2010). Individuals representing *L. rubellus* were placed into a simulated environment and progressed through life cycles while moving through the environment and responding to environmental conditions present in the landscape. Whereas the program was originally tested with *L. rubellus*, its flexibility will allow for the modeling of other species. For instance, when the relevant parameters are available, the model could be used to predict population survival and spread of *Amynthas agrestis*, an Asian earthworm species that is actively invading multiple areas of North America (Greiner et al., 2012).

2 Components of WORMSPREAD

In this section the components of WORMSPREAD will be described in detail. The software can be downloaded at https://github.com/aylab/WORMSPREAD and figshare (DOI 10.6084/m9.figshare.5193295.v1)

2.1 The context for invasion

2.1.1 pH

Soil pH was considered because areas of low soil pH can potentially limit the survival and reproduction, and consequently the invasive potential, of earthworms and other soil-dwelling organisms (Bernard et al., 2009; Homan et al., 2016; Peramaki et al., 1992). Most earthworms can survive in a variety of soil pH levels, but will avoid very acidic or basic soils (Ammer and Makeschin, 1994). In addition, propagule production decreases as the earthworms' environment becomes more acidic (Spurgeon et al., 2006). Thus, understanding worms' responses to pH may be particularly important for mapping the invasion of lands with more acidic soils.

The pH-dependent survival provided by the user is represented by $\sigma'_{(pH)}$. This function, like others described here, can be updated with new data and for other species. The details of making these changes are provided in the WORMSPREAD User Manual. The user provides a probability of pH-dependent survival that is potentially measured over a period of multiple days, so we account for the decrease in survival probability over time due to extended exposure. The time-adjusted pH-dependent survival, $\sigma_{(pH)}(t_c)$, is shown below:

$$\sigma_{(pH)}(t_c) = e^{-h * t_c}$$

where t_c is the number of days spent on a patch with the same pH, and

$$h = -\frac{\ln \sigma'_{(pH)}}{d}$$

where d is the number of days over which the original experiment to obtain data was performed.

2.1.2 Temperature

All soil-dwelling organisms, including earthworms, are temperature-sensitive, although the soil in which they live can act as a buffer against harsh environmental conditions (Zheng et al., 1993) and the animals typically can survive within a wide temperature range. For example, *Lumbricus* species can survive for up to a week in soil temperatures as low as -1°C and for several days in temperatures as high as 25 °C (Daniel, 1992; Meshcheryakova and Bulakhova, 2014). Extreme temperatures may negatively affect movement, feeding activity, and growth (Duiker and Stehouwer, 2008). Users of WORMSPREAD supply soil temperatures of their region for each day to be simulated. These may be based on historical data or projections from climate models. The survival function is based on interpolation among available empirical data and is represented by the parameter, $\sigma_{(T)}$, which is the temperature-dependent survival of earthworms when the temperature is T (°C). Users may change the survival data as necessary by following instructions provided in the WORMSPREAD User Manual.

2.1.3 Landscape

The landscape within which agents move in WORMSPREAD is based on actual variability in soil environmental factors that may be relevant to soil-dwelling animals. Geographic Information System (GIS) integration enables WORMSPREAD to make population projections in a simulated real-world environment. The developers recommend study areas between 200 and 300 km^2 for the default resolution of WORMSPREAD, given the loss of landscape information associated with larger areas and the lack of detail needed for predictions on a smaller scale. Users can upload GIS shapefiles, a standard geospatial vector data format.Within the United States, it is possible to find geo-referenced soil data on Web Soil Survey website (http://websoilsruvey.sc.egov.usda.gov/), butdata availability varies by county. For utilization outside of the

U.S., data are available for other global regions from sources such as the European Soil Data Center (http://esdac.jrc.ec.europa.eu/) and Australian Soil Resource Information System (http://www.asris.csiro.au/).

The model is temperature and pH-dependent, as described above, and the data we have used to form our models are available to the user in the supplemental materials. Users can also upload additional GIS filesif they also provide a properly formatted key linking environmental values to location. Instructions to upload additional data are available in the WORMSPREAD User Manual. Future work could incorporate other available soil attributes, such as moisture, that could be relevant to earthworm movement or behavior. Currently, there are not enough data to establish a dependence on other parameters, such as detailed burrowing behaviors, interspecific competition, or intraspecific competition. If more information about the earthworms were to become available, only knowledge of NetLogo and minimal coding experience would be required to add support for new features.

2.2 Demography of the invader

2.2.1 Mortality

We assumed that non-optimal environmental conditions of pH and temperature could cause earthworms to have lower survival than optimal conditions, and that the chance of mortality was additive with the underlying chances of dying due to senescence. Temperature- and pH-dependent mortality rates were each calculated daily using survival probabilities based on empirical evidence as follows:

$$\mu_{(pH)}(t_c) = 1 - \sigma_{(pH)}(t_c)$$
$$\mu_{(T)} = 1 - \sigma_{(T)}$$

In addition to the mortality due to non-optimal soil conditions, we assumed thatindividuals senesce and die at a rate based on a survivorship curve. For *L. rubellus*, we used a Type III survivorship curve(Baveco and De Roos, 1996). The age-dependent mortality curve for *L. rubellus* was obtained from Baveco and De Roos (1996), represented by $\mu_{(a)}$ where a is the age of the earthworm in days.

The overall mortality probability, $M,$ is then calculated as a function of the age-, pH-, and temperature-dependent mortality probabilities.In our simulations, we used the mortality function:

$$M = \mu_{(a)} + \mu_{(pH)}(t_c) + \mu_{(T)}$$

where the mortality function is calculated for each worm at each time interval. Specific interactions between the mortality factors could be incorporated if needed by modifying a single line of the WORMSPREAD source code. By adjusting sliders in the GUI while setting up simulations, the user may change the earthworms' tolerance to pH (τ_{pH}) and temperature (τ_T). Doing so will translate the survival probability functions to the left or right according to the tolerance shift—a positive shift will translate the curve to the right, a negative shift will translate the curve to the left. Incorporating these tolerances results in a modified version of the mortality function:

$$M = \mu_{(a)} + \mu_{(pH + \tau_{pH})}(t_c) + \mu_{(T + \tau_T)}$$

An increase in τ_{pH} is analogous to a decrease in the environmental pH and an increase in τ_T is analogous to a decrease in temperature within the region.

2.2.2 Production of propagules

Time that it takes an individual to reach sexual maturity is considered to be a Gaussian variable (Edwards, 2004). So in the program, maturation ratewas sampled from a Gaussian distribution with parameters based on empirical data, for each individual. The agents are each randomly assigned to one of four reproduction temperature ranges in order to handle the uncertainty of the actual temperature range within which organisms produce propagules (eggs in cocoons in the case of earthworms).Whenever the global temperature falls within the individual's temperature range, a counter is incremented by the user-provided, weekly rate of propagule production. When the counter reaches the reproduction threshold, a propagule is produced and the counter resets. Each organism also has a pH-dependent propagule-production rate provided by the user. We assumed that temperature and pH affect reproduction rates independently.We use a conservative estimate of their combined effects by taking the minimum of the two rates at any given time as the propagule-production rate. Again, interactions between the production factors could be incorporated in our code if needed.

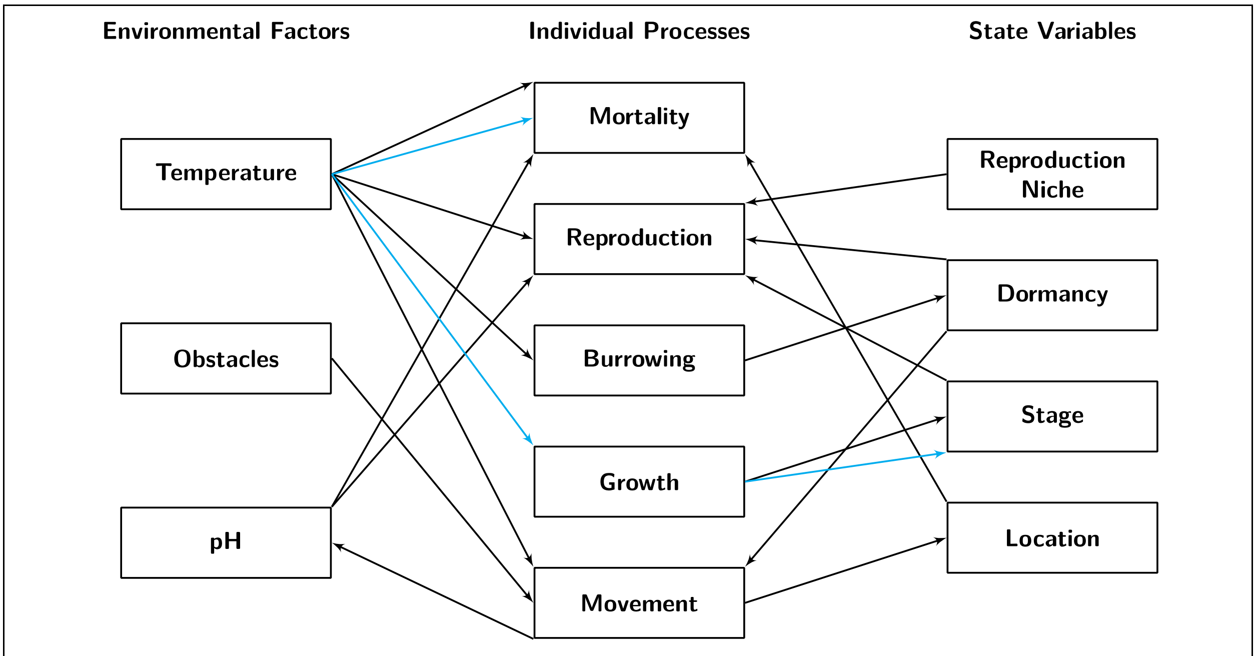

Fig. 1 Summary of the relationships between demographic determinants. Arrows indicate dependencies; black arrows are adult-specific and cyan arrows are propagule-specific.

2.2.3 Hatching of propagules

Temperature accumulation (or degree-days) can be used as an accurate measure of the length of time required for a propagule to develop to hatching or germination(Ameden et al., 2009; Butt, 1991; Greiner et al., 2011).We use Ameden et al.'s (2009) method of calculating degree-days as the sum of the mean daily temperature. The length of time required to hatch or germinate is consequently dependent upon the daily temperature.We assumed that the number of degree-days needed to hatch propaguleshas a strong genetic component, so organisms in our model inherit this trait from their parent.Butt (1991) observed a relationship between earthworm cocoon hatchability and temperature; therefore, we assumed that propagule survival is temperature-dependent and that any propagule surviving until its required number of degree-days will hatch. The two relevant parameters are the degree-day threshold, which is based on available data (Butt, 1991), and temperature-dependent propagulesurvival, which is supplied by the user.

2.2.4 Barriers to movement

Local conditions influence how organisms move. When an organism is in soil, we assumed that it had a uniform average speed of s meters per day, which the user can control. Organisms in our model are unable to move through rock outcroppings and other areas with no soil. Many soil-dwelling organisms can survive extended periods of time in water (e.g., *L. rubellus*, Roots [1956]). Therefore organisms in the model maintain the same mortality rates in water. However, we assumed that soil organisms were averse to entering water, and consequently have a low probability (0.0001%) of moving forward at a single time step if there is a large water feature, such as a lake, directly in their path. Interaction of individuals with small water features such as streams and drainage ditches are ignored by WORMSPREAD due to the intended scale and resolution of the software.

Gundale et al. (2005), indicated that roads are an important mechanism for facilitating the spread of invasive earthworms and Tyser and Worley (1992), have shown that the presence of roads can increase the speed of invasion of non-native invasive species of plants. We have thus implemented the facilitation of invasion by soil organisms along roads by assuming that organisms will travel faster when they are in the immediate vicinity (contained within the same patch in the NetLogo world) of a roadway. The magnitude of the distance from a road an organism is required to be within in order for its speed to increase is dependent upon how much land a single patch in NetLogo represents in the user's selected area of interest.

2.2.5 Burrowing

To avoid mortality during periods of intolerably cold temperatures (i.e., winter) individuals may burrow deeper into the soil and remain dormant until the temperature reaches an acceptable range. An individual organism in our model will burrow if the cumulative survival probability due to temperature is less than $\sigma_L$over t_b days, where the user could specify t_b and the threshold σ_L. We assume that during dormancy, organisms cannot move or reproduce, and that the surface temperature does not affect mortality during dormancy.

2.2.6 Additional variables

The current implementation of WORMSPREAD incorporates the most important factors for invasion by earthworms as example soil-dwelling organisms (Fig. 1). However, the software is modular and flexible enough to incorporate other factors, such as moisture, as more data are available.

2.3 Features of the user experience

2.3.1 User-Friendliness

NetLogo features have allowed us to create a user-friendly interface for ecologists to set up and run simulations. Users save and manipulate the files with a GUI. The GUI allows users to manipulate existing environments, import from GIS vector data, or create their own environment with the controls provided (Fig. 2). Users can choose to input their own functions for pH-dependent survival, pH-dependent propagule production, and temperature-dependent survival. This adds flexibility to the software, so it can continue to be useful as more data become available.

2.3.2 Output

WORMSPREAD has the ability to record data within regions designated by the user. Currently, by default, the program will record organism abundance, organism density, τ_{pH}, and $\tau_T$within specified regions of interest. These measurements are recorded for each week of the last year of the simulation and users may summarize those data as they wish (e.g., average over the entire year, maximum over the year). The program also outputs maps that display the earthworm population represented as colors (heat maps) for every five years of the simulation.

3 Example Study

We conducted an example studybased on a portion of the Adirondack Park in upstate New York (Adirondacks), where monitoring the spread of *L. rubellus* is relevant to conservation of native biodiversity. We selected the Adirondacks because its generally acidic soils and cold winters may offer abiotic resistance to invasion by certain species of earthworms (Bernard et al., 2009; Homan et al., 2016; Sullivan et al., 2006). Simulations in this type of environment may help conservation biologists determine whether conditions might deter earthworm invasion and what sorts of changes may reduce abiotic resistance to invasion. A 259 km^2 area encompassing Raquette Lake and the surrounding forest was selected (Fig. 3). This area is representative of the

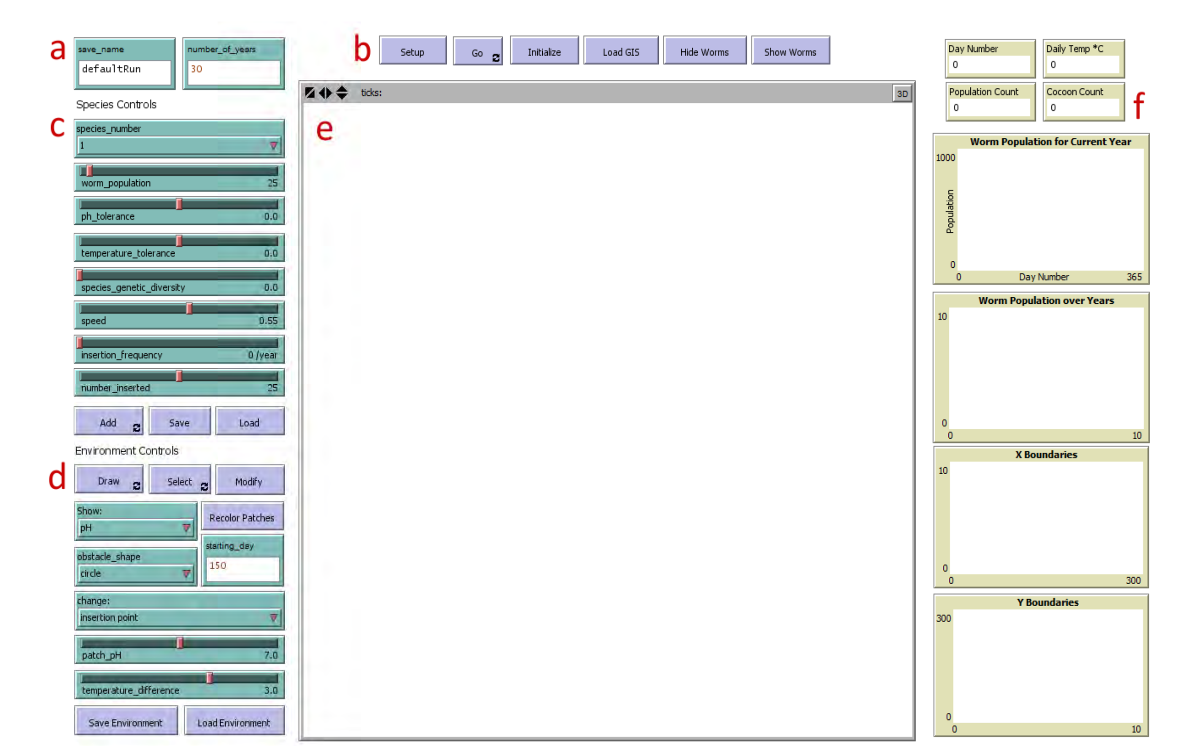

Fig. 2 WORMSPREAD GUI. a) Simulation parameters b) Simulation controls c) Species controls d) Environment controls e) NetLogo world. f) Plots and monitors.

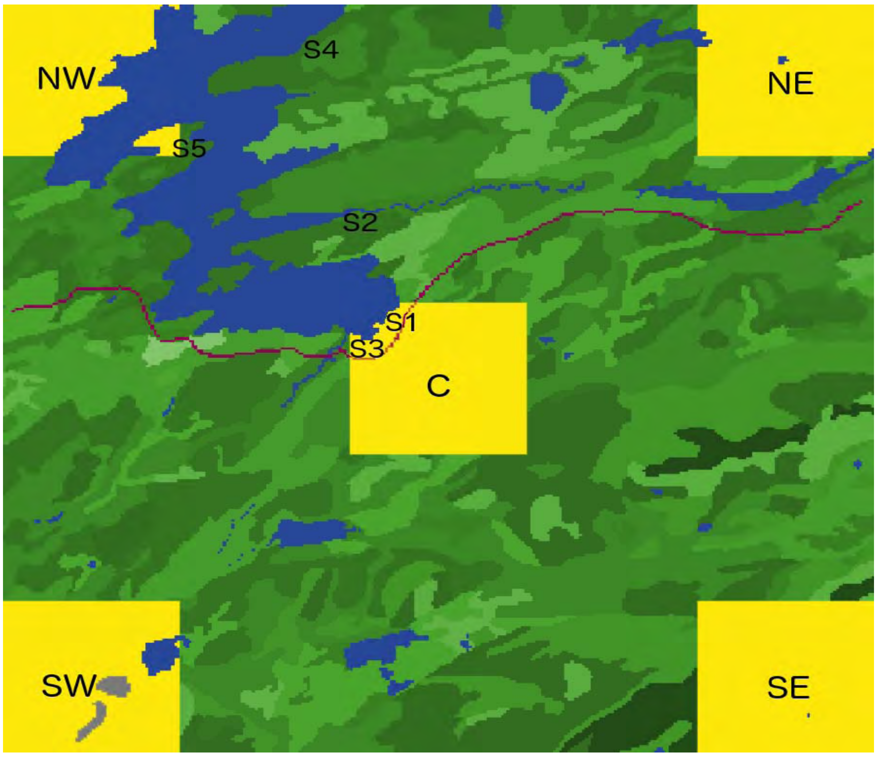

Fig. 3 Map of 259 km^2 region. Locations of regions NW, NE, SW, SE, C and random introduction points, S1-S5. Yellow indicates the extent of the areas that were monitored, grey represents rock outcroppings, blue shows where there are large bodies of water, and magenta denotes roadways. pH ranges from 4.0 (dark green) to 5.7 (light green) in the study area. Worm density was calculated in each region for each variation in environmental parameters. Points S1-S5 were chosen due to their locations near popular fishing sites (Adirondack.net, n.d.), areas believed to be possible introduction points for *L. rubellus*. In Fig. 3 – Fig. 6, S1 was used as the primary introduction point. In Fig. 7, the primary introduction point was varied between S1-S5.

variety of land-use types in the Adirondacks that may have variable susceptibility to earthworm invasion and includes aquatic habitats, residential developments, and undeveloped forest. We simulated the effects of environmental variables within this landscape on earthworm survival, reproduction, and movement.

The parameters that we used to create models for temperature and pH tolerance profiles are available inthe supplementary material. Data collected for the congeneric *Lumbricus terrestris* were used for these parameters when *L. rubellus* data did not exist (Baveco and De Roos, 1996). With the exception of the simulations that vary the location of initial introduction, in each simulation the individuals were inserted at a single introduction point near the geometric center of our landscape (Fig. 3). Earthworm density was then recorded after 30 simulated years in five, 16.2km^2 regions, which included the four corners and the center of the area of interest (Fig. 3). One-way ANOVA with blocking was used to determine differences in earthworm density under varying environmental and physiological conditions. In our analysis we used logarithmic (base 10) transformation of the density of earthworms. Location was used as a blocking factor.

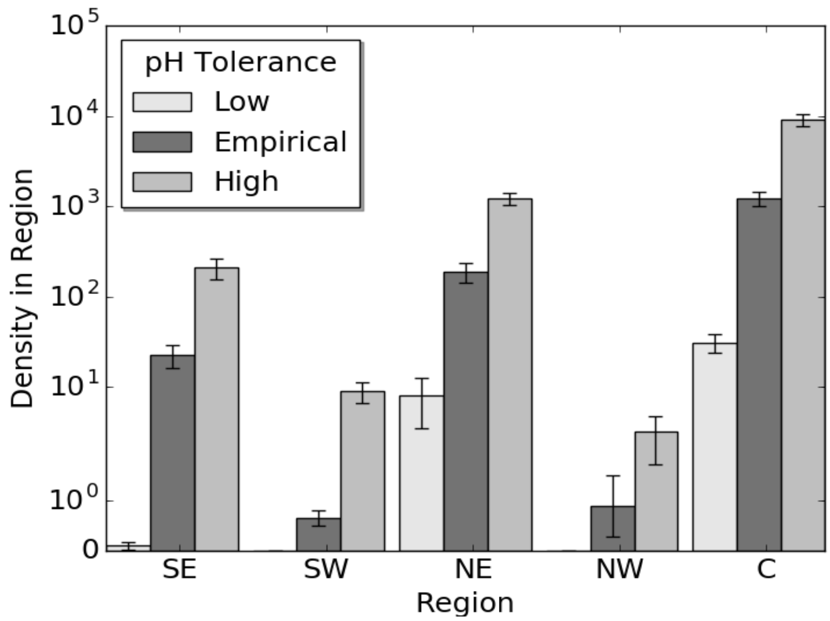

Fig. 4 Density of earthworm populations (individuals / square-kilometer) in regions (see Fig. 2) after varying pH tolerances (τ_{pH}) after ten 30-year simulations.τ_{pH} is the deviation from our empirical estimated pH tolerance profile. An increase in τ_{pH} increases the pH profile such that tolerance at a specific pH is shifted to the tolerance of the pH that is τ_{pH} pH units more than the original pH. Each earthworm's survival depends on a curve that fits pH- and temperature-dependent survival values supplied by user. The mortality curve for these simulations was extracted from Butt (1991). τ_T is constant and equal to 0.2 in this figure. S1 was used as the primary introduction point. Earthworms with $\tau_{pH} = -0.1, 0.0$, and 0.1 represent the low, empirical, and high groups, respectively. In all regions, density is significantly affected by τ_{pH}(p < 0.01). As τ_{pH} increases, density levels increase. In regions SW and NW, no earthworms of $\tau_{pH} = -0.1$ became successfully established.

Since pH is correlated with earthworm survival (Peramaki et al., 1992), the first series of simulations varied τ_{pH} and examined the ability of simulated agents to invade the landscape. Changing the pH tolerance of earthworms or acidity of the soil in a region could result in drastically different invasion scenarios (Fig. 4). This type of experiment allows users to investigate the importance of changing pH for a region (e.g., by liming), or the adaptation of organisms to more acidic environments. Our simulations suggest that pH tolerance has a significant effect on earthworm spread in this region ($p < 0.01$, $F = 110.305$, $df = 2$).

Earthworms with $\tau_{pH} = 0.1$, meaning that the tolerance of the earthworms was increased by 0.1 pH, exhibited a larger spread across the area of interest, represented by higher densities in the five regions, than the group with the empirical pH tolerance. Earthworms with $\tau_{pH} = -0.1$ exhibited a smaller spatial spread across the area of interest (Fig. 4). These results suggest that acidic conditions may indeed restrict invasion by *L. rubellus* in the Adirondacks.

We also simulated the potential spread of earthworms with varying temperature tolerance(τ_T). Adjusting τ_T allows users to observe the impact of changing global temperatures or temperature niche adaptation. Our analysis shows that temperature tolerance has a significant effect on earthworm spread ($p < 0.01$, $F = 71.504$, df = 4). In allregions, earthworms with $\tau_T = 0$, were able to spread to the monitored regions more effectively than individuals with $\tau_T < 0$ *or* $\tau_T > 0$ (Fig. 5). This is most likely a result of an increased temperature-dependent mortality rate due to high temperatures when$\tau_T > 0$, and an increased temperature-dependent mortality rate due to cold temperatures when $\tau_T < 0$.

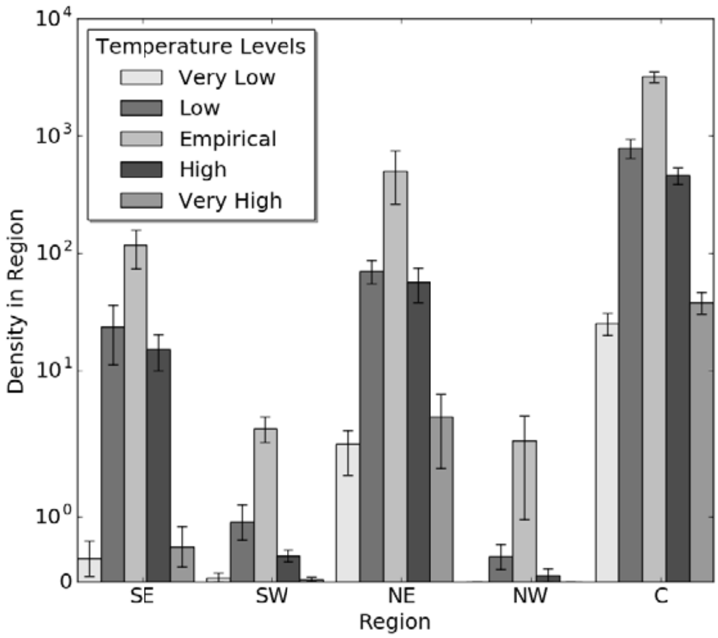

Fig. 5 Density of earthworm populations (individuals / km^2) in the regions after varying temperature tolerance (τ_T) after ten 30-year simulations. τ_T is the deviation from our empirical estimated temperature tolerance profile. An increase in τ_T increases the temperature profile such that the optimal temperature is shifted by τ_T. Density is scaled logarithmically. Like pH tolerance, temperature tolerance is specified by the user-determined relationship between temperature and mortality ($\mu_{(T+\tau_T)}$). Individuals with $\tau_T = -0.5, -0.3, 0.0, 0.3,$and 0.5 represent the very low, low, empirical, high and very high groups, respectively. S1 was used as the primary introduction site. Density is significantly affected by τ_T($p < 0.01$). In all regions, the earthworms with the empirical temperature tolerance profile have a higher population density than the individuals whose τ_T has been altered

We examined the effect of roads on earthworm survival and dispersal. Using GIS data, current state and US highways were incorporated into the IBM. Earthworm dispersal was compared in two scenarios, one with current roads and one with possible future roads. Future road locations were selected to connect popular tourist and residential areas with the highways within the area of interest. This type of experiment is useful in evaluating the ecological impact of intended road construction. We increased the overall kilometers of road from 18.2 km in the original simulation to38.6 km with additional roads. Heat maps of the results after a 30-year simulation indicated that with the addition of new roads, earthworms spread to locations they did not spread to with the current highways.Population density increased in the areas close to roads, as well as some areas that are farther away (Fig. 6). The spread to areas farther from the road is likely due to the new roads facilitating the spread of *L. rubellus* to areas of higher suitability.

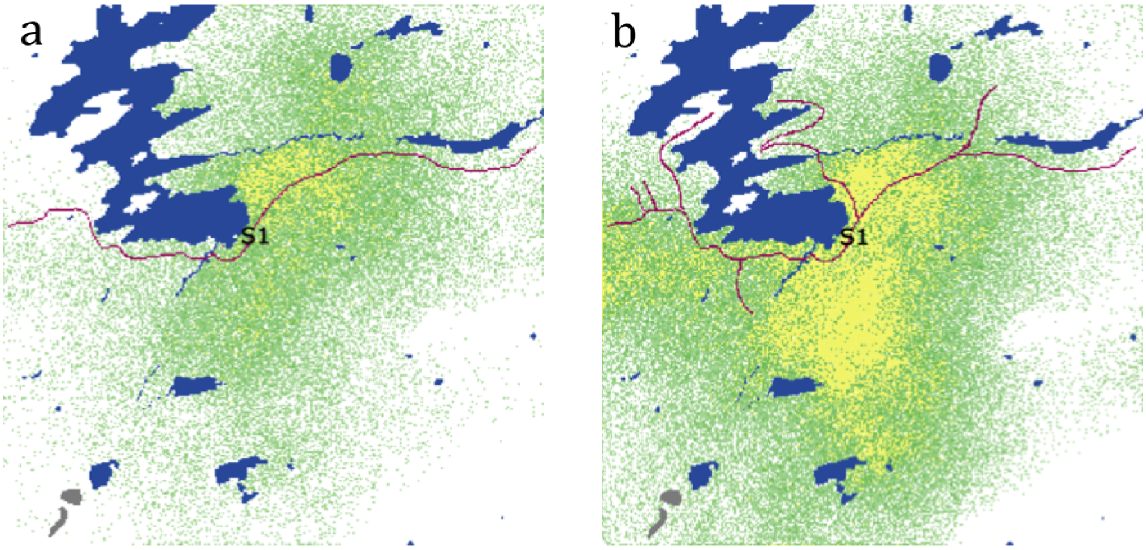

Fig. 6 Maps that display the earthworm population at the conclusion of a simulation, represented as colors with current roads (a) and with potential future roads (b). S1 was used as the primary site of introduction. The color green indicates a low earthworm density (between 0 and 5 individuals/m^2) while yellow indicates a higher density (as high as 50 individuals/m^2). Individuals exhibit a similar spread in both scenarios; however, increasing the number of roads appears to increase worm density in most regions of the map. In (a) the population density was lower in the areas that they did manage to spread to. (b) shows higher densities of individuals in new locations.

We also varied the frequency of introductions of earthworms. Earthworms are often introduced to new regions by human activity, such as soil or plant transportation and bait abandonment after fishing (Edwards, 2004; Tiunov et al., 2006). The results of such an experiment can be used to evaluate the efficacy of regulation and education efforts about the introduction of invasive earthworm species. Our study initially introduced 25 *L. rubellus* individuals around Raquette Lake at sites S1-S5, which were determined to be popular fishing sites in the area (Adirondack.net, n.d.). In this part of our study, we introduced earthworms 0, 5, or 10 additional times during the summer months. The location of the introduction is chosen randomly between sites S1-S5 at the time of each introduction. This is intended to simulate the spread of earthworms due to fishing. In all monitored areas, earthworm population density was affected by frequency of random insertions ($p < 0.01$, $F = 29.193$, $df = 2$). The density increased when the frequency of random insertionswas increased, thus providing evidence for the potential influence of propagule pressurein earthworm invasion (Fig. 7).

Finally, density of earthworms was examined after primary introductions at certain pre-selected locations (Fig. 8). Experiments like this one can help determine what locations are most likely to result in an invasion if earthworms are introduced. This allows conservation practitioners to make an informed decision about what areas their efforts should be most concerned about in terms of preventing introduction. Twenty-five individuals were introduced at a single point (S1-S5) and the simulationswere run without further introductions. The earthworm density was then measured after thirty years in each of the five designated regions. Varying the introduction site in our example had a significant effect on earthworm density ($p < 0.01$, $F = 10.508$, $df = 4$). Since the location of introduction was important, a more in-depth study might include a more comprehensive examination of potential initial introduction sites.

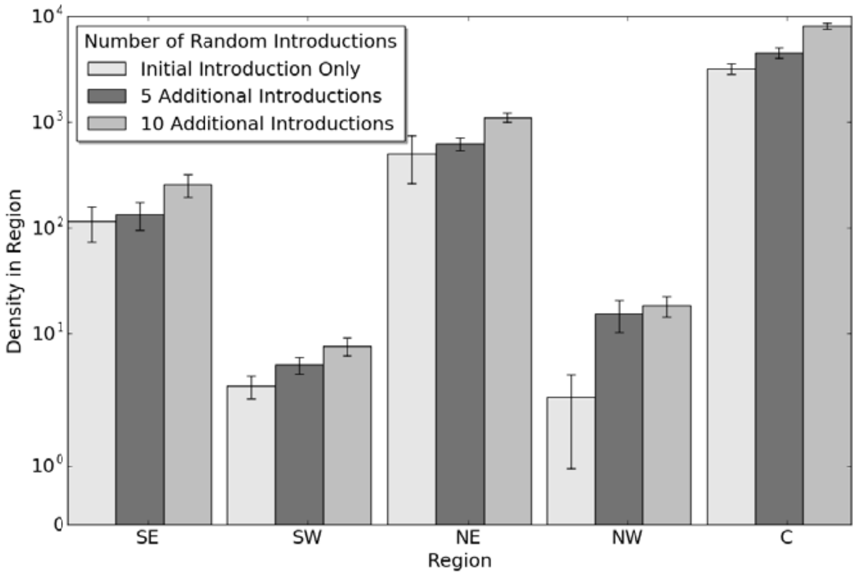

Fig. 7 Effect of random introductions in five regions of interest after ten 30-year simulations. Introduction points S1-S5 were chosen at popular fishing sites near Raquette Lake. Additional introductions only occurred during the summer months, when fishing is most likely, and each introduction consisted of 25 individuals. Trials that did not include additional introductions served as the control. Other trials included 5 or 10 introductions per year to determine if anthropogenic introductions of *L. rubellus* assist in the spread of the species. The number of introductions makes a statistically significant difference in long-term worm population density is dependent upon the starting location ($p < 0.01$).

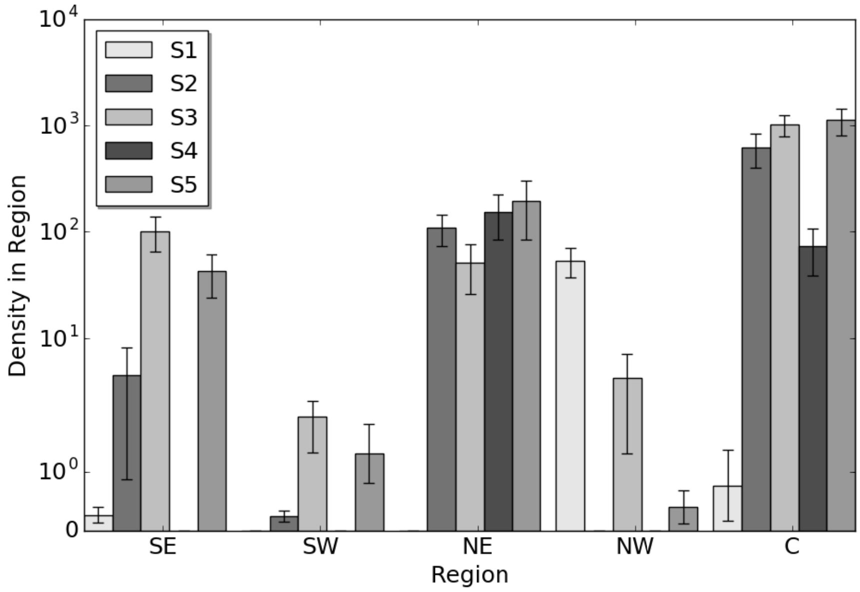

Fig. 8 Density of earthworms (individuals/ km^2) in regions of interest after single introduction from various starting locations. Twenty-five individuals were introduced at a single site (S1-S5), and no further earthworms were introduced. The worm density was then measured after 30 years in each of the five designated regions. Density is significantly affected by the initial introduction location ($p < 0.01$). This result suggests that it is important to monitor specific sites more carefully. Specifically, it may be more detrimental to have an introduction at S3 versus S2 or S5, thus more resources should be spent on preventing an introduction at S3.

4 Conclusion

WORMSPREAD is a user-friendly tool that allows the user to take basic environmental conditions and organism tolerances and create population simulations. The IBM we present here could help researchers understand how factors such as pH, temperature and urban development interact with each other within an ecosystem to influence invasion by soil-dwelling species. The information received from this program could help ecologists and conservation biologists create informed strategies to manage invasive populations(Patten, 2013).

Our example implementationwas limited by the lack of data available regarding behavior, physiology, and demography of *L. rubellus*. In particular, we found that data were sparse or non-existent for burrowing behaviors and rate of movement. This paucity of information will be more limiting for species that are less well-studied than *L. rubellus*. Our understanding of invasion dynamics in real landscapes is dependent on our understanding of how factors such as pH, temperature, soil moisture, and soil composition affect the movement speed, mortality, and fecundity of invaders. With more data, *WORMSPREAD* could become even more useful in predicting earthworm distribution over vast areas. The software could then be easily adapted to incorporate new or more specific parameters, which would increase the accuracy of predictions. We therefore encourage studies that relate demographic processes to environmental conditions for invasive species.

Acknowledgements

This work was supported by Colgate University Picker Interdisciplinary Science Institute and NASC Division Funds. We would like to thank Amanda Liberman for critically reading our manuscript and Damhnait McHugh for her valuable comments.

References

Adirondack.net. (n.d.). Fishing Raquette Lake in the Adirondacks. Retrieved from http://www.adirondack.net/business/raquette-lake-12505/#tab-about

Ameden HA, Boxall PC, Cash SB, Vickers DA. 2009. An agent-based model of border enforcement for invasive species management. Canadian Journal of Agricultural Economics, 57(4): 481-496

Ammer VS, Makeschin F. 1994. Effects of simulated acid precipitation and liming on earthworm fauna (*Lumbricidae Oligochaeta*) and humus type in a mature Norway Spruce. Forstwissenschaftliches Centralblatt, 113: 70-85

Baveco JM, De Roos AM. 1996. Assessing the impact of pesticides on lumbricid populations: An individual based modelling approach. Journal of Applied Ecology, 33(6): 1451-1468.

Bernard MJ, Neatrour MA, McCay TS. 2009. Influence of soil buffering capacity on earthworm growth, survival, and community composition in the Western Adirondacks and Central New York. Northeastern Naturalist, 16(2): 269-284

Bousquet F, Le Page C. 2004. Multi-agent simulations and ecosystem management: a review. Ecological Modelling, 176(3-4): 313-332

Burtelow AE, Bohlen PJ, Groffman PM. 1998. Influence of exotic earthworm invasion on soil organic matter, microbial biomass and denitrification potential in forest soils of the northeastern United States. Applied Soil Ecology, 9(1): 197-202

Butt KR. 1991. The Effects of temperature on the intensive production of *Lumbricus terrestris L.* (*Oligochaeta: Lumbricidae*). Pedobiologia, 35: 257-264

Daniel O. 1992. Population dynamics of *Lumbricus terrestris L.* (*Oligochaeta:Lumbricidae*) in a meadow. Soil Biology & Biochemistry, 24(12): 1425-1431

Deangelis DL, Mooij WM. 2005. Individual-based modeling of ecological and cvolutionary Processes. Annual Review of Ecology, Evolution, and Systematics, 36: 147-168

Dempsey MA, Fisk MC, Yavitt JB, Fahey TJ, Balser TC. 2013. Exotic earthworms alter soil microbial community composition and function. Soil Biology and Biochemistry, 67: 263-270

Duiker S, Stehouwer R. 2008. Earthworms. Penn State College of Agricultural Sciences. Retrieved from http://extension.psu.edu/plants/crops/soil-management/soil-quality/earthworms/extension_publication_file

Edwards CA. 2004. Earthworm Ecology (2nd ed.). CRC Press, Boca Raton, FL, USA

Eisenhauer N, Partsch S, Parkinson D, Scheu S. 2007. Invasion of a deciduous forest by earthworms: Changes in soil chemistry, microflora, microarthropods and vegetation. Invasion of a Deciduous Forest by Earthworms: Changes in Soil Chemistry, Microflora, Microarthropods and Vegetation. Soil Biology & Biochemistry, 39: 1099-1110

Fahse L, Wissel C, Grimm V. 1998. Reconciling classical and individual‐based approaches in theoretical population ecology: a protocol for extracting population parameters from individual‐based models. The American Naturalist, 152(6): 838-852

Gallien L, Münkemüller T, Albert CH, Boulangeat I, Thuiller W. 2010. Predicting potential distributions of invasive species: Where to go from here? Diversity and Distributions, 16(3): 331-342

Greiner HG, Kashian DR, Tiegs SD. 2012. Impacts of invasive Asian (*Amynthas hilgendorfi*) and European (*Lumbricus rubellus*) earthworms in a North American temperate deciduous forest. Biological Invasions, 14(10): 2017–2027

Greiner HG, Stonehouse AMT, Tiegs SD. 2011. Cold tolerance among composting earthworm species to evaluate invasion potential. The American Midland Naturalist, 166(2): 349-357

Griebeler EM, Seitz A. 2002. An individual based model for the conservation of the endangered Large Blue Butterfly, Maculinea arion (*Lepidoptera: Lycaenidae*). Ecological Modelling, 156(1): 43-60

Gundale MJ, Jolly WM, Deluca TH. 2005. Susceptibility of a northern hardwood forest to exotic earthworm invasion. Conservation Biology, 19(4): 1075-1083

Hastings A. 1997. Population Biology: Concepts and Models. Springer Science and Business Media, New York, USA

Homan C, Beier C, McCay T, Lawrence G. 2016. Application of lime (CaCO3) to promote forest recovery from severe acidification increases potential for earthworm invasion. Forest Ecology and Management, 368: 39-44

Hooten MB, Wikle CK. 2010. Statistical agent-based models for discrete spatio-temporal systems. Journal of the American Statistical Association, 105(489): 236-248

Keith JM, Spring D. 2013. Agent-based Bayesian approach to monitoring the progress of invasive species eradication programs. Proceedings of the National Academy of Sciences of the United States of America, 110: 13428-13433

Letcher BH, Priddy JA, Walters JR, Crowder LB. 1998. An individual-based, spatially-explicit simulation model of the population dynamics of the endangered red-cockaded woodpecker, *Picoides borealis*. Biological Conservation, 86(1): 1-14

McLane AJ, Semeniuk C, McDermid GJ, Marceau DJ. 2011. The role of agent-based models in wildlife ecology and management. Ecological Modelling, 222(8): 1544-1556

Meshcheryakova EN, Bulakhova NA. 2014. Cold resistance of three species of earthworms (*Oligohaeta, Lumbricidae*) in Western Siberia. International Journal of Environmental Studies, 71(5): 749-754

Patten BC. 2013. Systems Analysis and Simulation In Ecology (3rd ed). Elsevier, USA

Pelosi C, Bertrand M, Makowski D, Roger-Estrade J. 2008. WORMDYN: A model of *Lumbricus terrestris* population dynamics in agricultural fields. Ecological Modelling, 218(3-4): 219-234

Peramaki P, Itamies J, Karttunen V, Lajunen LHJ, Pulliainen E. 1992. Influence of pH on the accumulation of cadmium and lead in earthworms (*Aporrectodea coliginosa*) under controlled conditions. Annalis Zoologici Fennici, 29(1): 1005-1111

Roots BI. 1956. The water relations of earthworms. Journal of Experimental Biology, 33(1): 29-44

Rutherford ES, Rose KA, Mills EL, Forney JL, Mayer CM, Rudstam LG. 1999. Individual-based model simulations of a zebra mussel (*Dreissena polymorpha*) induced energy shunt on walleye (*Stizostedion vitreum*) and yellow perch (*Perca flavescens*) populations in Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences, 56(11): 2148-2160

Snyder BA, Callaham MA, Lowe CN, Hendrix PF. 2013. Earthworm invasion in North America: Food resource competition affects native millipede survival and invasive earthworm reproduction. Soil Biology and Biochemistry, 57: 212-216

Spurgeon DJ, Lofts S, Hankard PK, Toal M, McLellan D, Fishwick S, Svendsen C. 2006. Effect of pH on metal speciation and resulting metal uptake and toxicity for earthworms. Environmental Toxicology and Chemistry, 25(3): 788

Sullivan TJ, Fernandez IJ, Herlihy AT, Driscoll CT, McDonnell TC, Nowicki NA, et al. 2006. Acid-base characteristics of soils in the Adirondack Mountains, New York. Soil Science Society of America Journal, 70(1): 141

Sutherland WJ, Bardsley S, Bennun L, Clout M, Cote IM, Depledge MH, et al. 2010. Horizon scan of global conservation issues for 2011. Trends in Ecology and Evolution, 26(1): 10-16

Tiunov AV, Hale CM, Holdsworth AR, Vsevolodova-Perel TS. 2006. Invasion patterns of Lumbricidae into the previously earthworm-free areas of northeastern Europe and the Western Great Lakes Region of North America. Biological Invasions, 8(6): 1223-1234

Tyser RW, Worley CA. 1992. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). Conservation Biology, 6(2): 253-262

Uchmanski J, Grimm V. 1996. Individual-based modelling in ecology: what makes the difference? Trends in Ecology and Evolution, 11(10): 437-441

West AD, Stillman RA, Drewitt A, Frost NJ, Mander M, Miles C, et al. 2011. WaderMORPH - a user-friendly individual-based model to advise shorebird policy and management. Methods in Ecology and Evolution, 2(1): 95-98

Zheng D, Hunt ER, Running SW. 1993. A daily soil temperature model based on air temperature and precipitation for continental applications. Climate Research, 2: 183-191