Research

Oikos 119: 485–493, 2010
doi: 10.1111/j.1600-0706.2009.17918.x,

Subject Editor: Tim Benton and Thorsten Wiegand. Accepted 1 September 2009

When is connectivity important? A case study of the spatial pattern of sudden oak death

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Although connectivity has been examined from many different angles and in many ecological disciplines, few studies have tested in which systems and under what conditions connectivity is important in determining ecological dynamics. Identifying general rules governing when connectivity is important is crucial not only for basic ecology, but also for our ability to manage natural systems, particularly as increasing fragmentation may change the degree to which connectivity influences ecological dynamics.

In this study, we used statistical regression, least-cost path analysis, and model selection techniques to test the relative importance of potential connectivity in determining the spatial pattern of sudden oak death, a tree disease that is killing millions of oak and tanoak trees along coastal forests of California and Oregon. We hypothesized that potential connectivity, in addition to environmental conditions, is important in determining the spatial distribution of sudden oak death, the importance of connectivity is more apparent when measured using biologically meaningful metrics that account for the effects of landscape structure on disease spread, and the relative importance of environmental variables and connectivity is approximately equal.

Results demonstrate that potential connectivity was important in determining the spatial pattern of sudden oak death, though it was relatively less important than environmental variables. Moreover, connectivity was important only when using biologically meaningful metrics as opposed to simple distance-based metrics that ignore landscape structure. These results demonstrate that connectivity can be important in systems not typically considered in connectivity studies – highlighting the importance of examining connectivity in a variety of different systems – and demonstrate that the manner in which connectivity is measured may govern our ability to detect its importance.

Ecologists have long recognized that connectivity or the degree to which habitats are linked by dispersal can have important implications for spatial patterns of distribution and the dynamics of populations and communities (Taylor et al. 1993, Keitt et al. 1997, Tischendorf and Fahrig 2000, Wiens 2001, Moilanen and Nieminen 2002). Though connectivity was traditionally defined as the degree to which the landscape facilitates or impedes the movement of organisms (Taylor et al. 1993), the term has been used to describe many different ecological properties leading to confusion about what exactly connectivity is and how it should be measured (Moilanen and Nieminen 2002, Calabrese and Fagan 2004, Kindlmann and Burel 2008). To help organize our thinking about connectivity, Calabrese and Fagan (2004) developed a framework for classifying different measures of connectivity. They define three types of connectivity: structural, potential and actual. Structural connectivity refers only to the physical attributes of the landscape without any reference to dispersal (e.g. nearest-neighbor distance, the number of patches in a given area, patch-cohesion). Potential connectivity includes limited information about dispersal ability in addition to information about landscape attributes (e.g. interpatch distance scaled by the frequency distribution of dispersal distances of the organism). Finally, actual connectivity uses observed data on organism movement to provide the most direct and detailed measure of connectivity.

Structural, potential, and actual connectivity are properties used to describe features of the landscape that may influence or represent the degree to which locations are linked by dispersal. Once measured, ecologists can use these properties to ask or answer a variety of different questions. Landscape and conservation ecologists typically focus on measuring connectivity (i.e. structural, potential and actual), identifying the best connectivity measure for different situations, and testing how changes in landscape configuration (i.e. patch removal experiments) and the dispersal of the organism alter connectivity (Cantwell and Forman 1993, Keitt et al. 1997, Urban and Keitt 2001, Moilanen and Nieminen 2002, Minor and Urban 2008). In metapopulation and metacommunity ecology, researchers are generally interested in the mechanisms through which connectivity influences ecological dynamics (Hanski 1994, 1999). These studies are often theoretical, focus on patchy landscapes, and use simple measures of structural or potential connectivity (Moilanen

and Nieminen 2002). Finally, behavioral ecologists are often interested in determining what measures of actual connectivity best predict animal movement or dispersal (Walker and Craighead 1997, Sutcliffe et al. 2003).

With this growing body of research, we know that connectivity can be measured in many different ways (Keitt et al. 1997, Urban and Keitt 2001, Moilanen and Nieminen 2002), that it can influence ecological dynamics (Hanski 1994, 1999, Moilanen and Nieminen 2002) and help describe animal movement (Walker and Craighead 1997, Sutcliffe et al. 2003), and that it can be influenced by many factors (Minor and Urban 2008). However, studies have rarely tested one question that is crucial for developing a complete understanding of connectivity: when is connectivity important in determining dynamics in natural systems and when can it be reasonably ignored? The answer to this question is important not only for increasing our basic scientific understanding of connectivity, but also for our ability to manage and protect ecological systems. As environments become increasingly fragmented, landscape structure and its influence on organism movement are likely to become more important in determining species persistence and ecosystem function. Understanding when connectivity is important is crucial for our ability to respond to these environmental changes.

General rules for when connectivity is important in determining ecological dynamics can be identified by testing the relative importance of environmental variables (i.e. abiotic and biotic factors) and connectivity across a variety of different systems. The presence or absence of an organism in a given habitat is determined by its ability to survive the abiotic and biotic conditions of the habitat and by its ability to reach the habitat (i.e. dispersal), which itself may depend on landscape structure (e.g. connectivity) and historical events (i.e. time to reach the focal habitat). Evaluating the relative influence of environmental factors, movement, and landscape structure in determining spatial population distribution on relatively small time scales where historical events are less important is therefore a logical way to evaluate 'importance' of connectivity. Comparing results across systems may then highlight system characteristics and situations where we can expect connectivity to be generally important.

Here, we focus on evaluating the relative importance of environmental variables and connectivity in determining the spatial pattern of a plant disease, sudden oak death (SOD). While connectivity has been considered important in determining the spread of animal and human diseases (Ostfeld et al. 2005, Kostova 2009), relatively few studies have considered the importance of connectivity in determining the spatial pattern and spread of plant diseases (Plantegenest et al. 2007) (but see recent body of literature on network theory, Jeger et al. 2007). Because plant pathogens are often transported passively via wind or rain and tend to be sensitive to environmental conditions (Agrios 2005), connectivity has generally been considered less important than environmental conditions in determining spatial pattern of plant diseases. Despite this prevailing paradigm, growing evidence suggests that connectivity may be important in these systems (Holdenrieder et al. 2004, Plantegenest et al. 2007).

The purpose of our study was to test the relative importance of connectivity in determining the spatial distribution of a forest disease, sudden oak death (SOD). We used georeferenced field data on the severity of sudden oak death and environmental conditions, landscape maps derived from satellite imagery, and model selection to test the relative importance of environmental variables and connectivity in determining the spatial pattern of SOD. Because the sudden oak death pathogen, *Phytophthora ramorum*, is microscopic, direct observations of pathogen movement in natural environments are very difficult to obtain. Instead, we focus our investigation on the influence of potential connectivity on the spatial distribution of the disease. We take our investigation a step further to also test whether our ability to detect the relative importance of potential connectivity depends on how it is measured. We compared results obtained with connectivity metrics that either assumed a homogeneous environment or accounted for the effects of landscape structure on pathways of disease spread.

We hypothesized that potential connectivity, in addition to environmental conditions, are important in determining the spatial distribution of sudden oak death (hypothesis 1), the importance of connectivity is more apparent when measured using biologically meaningful metrics that account for the effects of landscape structure on movement and spread (hypothesis 2), and the relative importance of environmental variables and connectivity is approximately equal (hypothesis 3). More specifically, we predicted that: (1) models including environmental variables and measures of connectivity would perform better at explaining spatial pattern of SOD than models with environmental variables alone or connectivity measures alone (supporting hypothesis 1), (2) models incorporating the effects of landscape structure on potential connectivity would perform better than models using simple distance-based measures of connectivity that ignore landscape structure (supporting hypothesis 2), and (3) standardized regression coefficients of environmental variables and connectivity variables would be approximately the same (supporting hypothesis 3).

Methods

Study system

Sudden oak death is a plant disease that has killed millions of oak, *Quercus* sp., and tanoak *Lithocarpus densiflorus* trees in coastal forests of California and Oregon. It is caused by the Oomycete *Phytophthora ramorum*. This pathogen produces infective spores on the leaves of foliar hosts (Davidson et al. 2005) that are transported primarily via wind-driven rain (Ristaino and Gumpertz 2000, Rizzo and Garbelotto 2003, Davidson et al. 2005). The most important foliar host in determining the spread of sudden oak death appears to be California bay laurel *Umbellularia californica*, which is not killed by the pathogen, but produces large numbers of infective spores (Davidson et al. 2005, Rizzo et al. 2005, Meentemeyer et al. 2008a). Long-distance dispersal may occasionally occur in this system (Mascheretti et al. 2008), however, dispersal appears to be primarily localized with spores rarely traveling more than 5 m from an infected patch of host woodland (Davidson et al. 2005, Mascheretti et al. 2008).

Study area

Data describing environmental conditions, disease severity, and landscape structure were collected in 2005 from a previously established network of 86 plots on Sonoma Mountain in Sonoma County, CA (Fig. 1a). Sudden oak death was first identified on Sonoma Mountain in 2000 and annual monitoring has demonstrated that the disease is now widely distributed throughout the region (Cushman and Meentemeyer 2008, Meentemeyer et al. 2008b). Eighty-six field plots (225 m^2, 15 × 15 m) were randomly established within host woodlands, stratified by woodland patch size and distance to forest-grassland boundary. In each plot, environmental conditions and disease severity were measured as described in Condeso and Meentemeyer (2007). A map of host (i.e. woodland) and non-host (e.g. grassland, agricultural land, residential developments) land cover classes of the area was previously derived from ADAR multispectral aircraft imagery (Condeso and Meentemeyer 2007) (Fig. 1a).

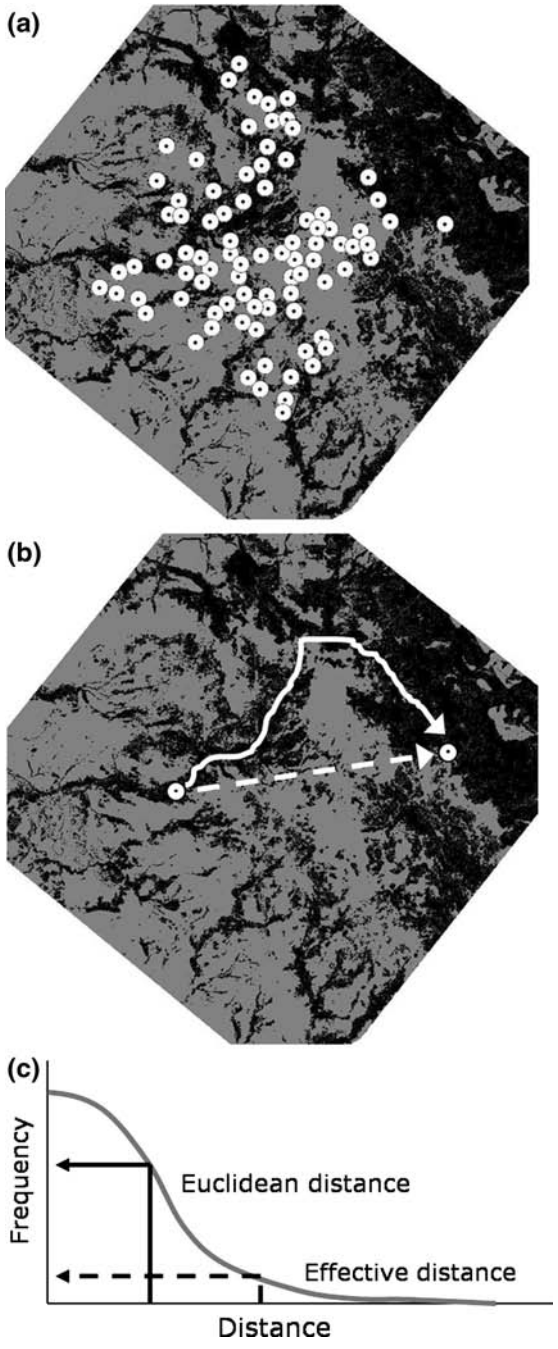

Figure 1. (a) two-class raster map of study area on Sonoma Mountain, CA illustrating host (black) and non-host (gray) land cover and plot locations (white circles). (b) example of a Euclidean path (dashed line) and an effective path (solid line) between two plot locations (effective path could be shorter than Euclidean path in some situations, see text). (c) frequency of propagules traveling a given distance from a source and illustration of how different estimates of the number of propagules or the force of infection between locations can be obtained when using Euclidean or effective distances.

Modeling approach

To test the hypothesis that potential connectivity and environmental conditions are important in determining the spatial distribution of sudden oak death (hypothesis 1), we modeled the spatial pattern of sudden oak death severity and compared the performance of models using environmental predictors alone, connectivity predictors alone, and both environmental and connectivity predictors. To test the hypothesis that the importance of potential connectivity is more apparent when measured using biologically meaningful metrics that account for the effects of landscape structure on movement (hypothesis 2), we compared models where connectivity was measured using simple Euclidean distance between locations (e.g. Fig. 1b) – which ignores landscape structure – to models where connectivity was measured using effective distances – which are Euclidean distances modified to account for how landscape structure can influence dispersal or spread (e.g. Fig. 1b) (Adriaensen et al. 2003). Effective distance is a concept that tries to capture the fact that the Euclidean distance between two locations is not always the best representation of the actual ability of an organism or disease to move between the locations. If two habitats are equidistant from a central one, and one of the two habitats is much easier to get to because of, for example, a corridor, then its connectivity is higher. In this case, we say that the effective distance to the habitat connected with a corridor is shorter than the effective distance to the other. Metrics using Euclidean distances can give higher or lower estimates of the number of propagules exchanged between locations than metrics using effective distances depending on landscape structure (Fig. 1b–c).

The full model including both environmental and connectivity variables was:

$$Y_i = \beta_0 + \sum_{j=1}^{8} \beta_j X_j + \beta_9 \lambda_i \quad (1)$$

where Y_i is the average number of symptomatic leaves per stem, X_j are the abiotic and biotic predictor variables described below, and λ_i is potential connectivity. Connectivity (λ_i) was modeled using a negative exponential dispersal kernel:

$$\lambda_i = \sum_{k=1}^{n} [SL_k \times \exp(\frac{-d_{ik}}{a})] \quad (2)$$

where SL_k is the total number of symptomatic leaves in plot k, d_{ik} is the distance between plot i and plot k calculated either as Euclidean distance or effective distance. The parameter a is used to modify the form of the dispersal kernel with low values of a indicating very limited long-distance dispersal (i.e. narrow-tailed distribution) and high values of a indicating a relatively high probability of long-distance dispersal (i.e. fat-tailed distribution) (Fig. 2a) (Havel et al. 2002). A negative exponential dispersal kernel was used because previous studies have demonstrated that this may adequately describe dispersal for many rain-splash dispersed plant pathogens (McCartney and Fitt 1985, Fitt et al. 1989). The dispersal kernel was multiplied by disease severity (SL_k) to account for potential differences in the number of infective propagules coming from each location (Fig. 2b). Thus, λ_i represents connectivity and the force of infection between locations. For consistency, we refer to λ_i as the connectivity term.

Disease severity

Disease severity was quantified in all 86 plots in 2005 by visually assessing foliar blight symptoms on bay laurel trees, the key infectious hosts of the sudden oak death pathogen, *P. ramorum* and the best indicator of pathogen inoculum load (Condeso and Meentemeyer 2007). A team of six researchers counted the number of symptomatic leaves on each bay laurel stem greater than 2 cm diameter at breast height (DBH) for 90 s between 28 March and 29 April 2005. Prior to sampling, a pilot study demonstrated no significant differences in the number of symptomatic leaves counted by different observers (Condeso and Meentemeyer 2007). We then calculated the average number of symptomatic leaves per stem, per plot for use in the models described below.

Environmental variables

Previous studies have identified several abiotic and biotic variables that could be important in determining the dynamics and spread of sudden oak death: canopy cover class (1–4), total precipitation (cm), average number of daily hours at optimal relative humidity for growth of *P. ramorum* (> 95%), average number of daily hours at optimal growth temperature for *P. ramorum* (10–25°C), potential solar irradiation (PSI), topographic moisture index (TMI), total host diameter at breast height (DBH) (~1.4 m), and total bay laurel DBH (Kelly and Meentemeyer 2002, Meentemeyer et al. 2004, 2008a, 2008b, Davidson et al. 2005). We used all of these variables in our models. Data on understory temperature and relative humidity were obtained from microclimate data loggers installed in 32 of the 86 plots studied here (Condeso and Meentemeyer 2007). Loggers recorded temperature and relative humidity every hour between 1 December 2004 and 21 June 2005, the period of peak pathogen production. From this we calculated the average number of daily hours between 1 December 2004 and 21 June 2005 that were at the optimal relative humidity for the growth of *P. ramorum* (> 95% humidity), and the average number of daily hours at the optimal growth temperature for *P. ramorum* (10–25 C) (Condeso and Meentemeyer 2007).

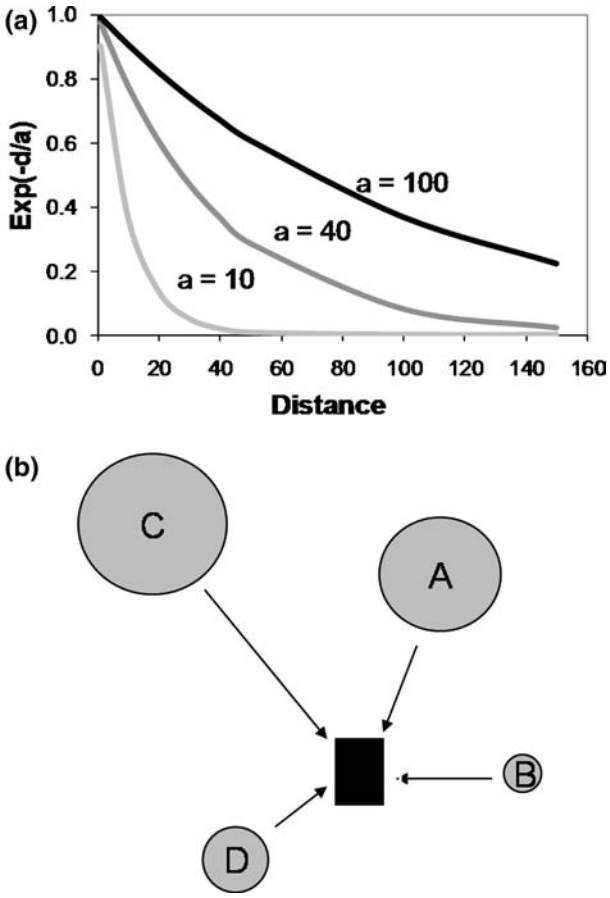

Figure 2. (a) hypothetical example of the load of individuals (exp (–d/a)) versus distance for different values of a in the dispersal kernel (Eqn. 2). High values of a indicate low dispersal limitation, low values of a indicate highly localized dispersal. (b) illustration of force of infection based on disease severity in surrounding plots (gray circles). Plots A and B are the same distance from the focal plot (black square), but A has much higher disease severity and, thus, a higher force of infection. Plot C is much farther away than plot D, but because it has a much higher disease severity, the force of infection may be higher for plot C.

Using data from Condeso and Meentemeyer (2007), the amount of precipitation at each plot location was spatially interpolated from a network of 16 rain gauges distributed across the Sonoma Mountain region using co-kriging, a geostatistical method that incorporates the effects of ancillary variables in addition to spatial dependence (Goovaerts 2000) in ArcGIS 9.1. PSI (i.e. the cosine of illumination angle on slope) (Dubayah 1994) was calculated as the average for the wet season (November to April 2005) at noon and TMI (i.e. the natural log of the ratio between upslope drainage area and the slope gradient, with high values indicating moister sites) was calculated according to Moore et al. (1991). PSI and TMI were derived from a USGS 10 m digital elevation model. Canopy cover was estimated by visually assessing the percent canopy cover in each plot and ranking each plot into one of four classes: < 25%, 25–50%, > 50 and ≤ 75%, and > 75% cover (Condeso and Meentemeyer 2007). The diameter at breast height (DBH) (~1.4 m) of every host stem > 2 cm DBH was measured in each plot. From this we calculated the total DBH of bay laurel (thought to be the most

important foliar host) and total DBH of all foliar hosts in each plot.

Connectivity

To test the hypothesis that the importance of connectivity is more apparent when measured using biologically meaningful metrics (hypothesis 2), we compared models where connectivity was calculated using Euclidean distances in the connectivity term ($-d_{ik}$ in Eq. 2) to models using effective distances in the connectivity term ($-d_{ik}$ in Eq. 2). Euclidean distances were calculated from the X and Y coordinates of plot locations in ArcGIS 9.1. We used least-cost path analysis in a GIS environment to derive effective distances between plot locations based on our land cover map (Adriaensen et al. 2003). This analysis finds the pathway of least resistance between locations, called the least-cost path, based on friction values assigned to each landcover type and the specific distribution of those types (Adriaensen et al. 2003). We first created 86 Boolean 'source' maps, each containing a single plot and created a friction surface from our map of host and non-host land cover types with friction values of the two land cover types set according to described scenarios (below). The isotropic growth algorithm in IDRISI 15 (The Andes Edition, Clark Labs/Clark Univ. 2006, Worcester, MA), was used to create a cost distance surface for each plot or source map. A given cell in the cost distance surface contains a value corresponding to the accumulated cost for the least-cost pathway between the source and that cell (in grid cell equivalents [GCE]). The size of each grid cell in our friction map was 1×1 m. Thus, if each cell in the friction surface is given a friction value of 1 (i.e. the environment is essentially homogeneous) then the least-cost pathways between plots are the Euclidean paths and the accumulated 'cost' in the output cost surfaces are the true Euclidean distances in meters between the source plot and all cells in the map. If friction values differ between land cover types, then the cost surface represents the effective distances between the source and all non-source cells. To obtain the length of the least-cost path (i.e. effective distance) between a source plot and all other plots, we extracted the cost values from the cells in the cost surface map where each plot was located. This was repeated for each source map (i.e. for each plot). In the IDRISI algorithm, the cost distance surface is generated through a sequential process where the distances are accumulated in radial bands from the friction surface (Eastman 1989). The cost of movement is equal in all directions and, since it is based on eight-neighbor-cell algorithm, it allows for movement along diagonals. Diagonal movement produces a total cost of 1.41 times the friction value assigned to each cell (Eastman 2006).

Because we had no apriori information to quantify differences in the tendency of the sudden oak death pathogen to move or spread through host and non-host land cover classes, we repeated the entire procedure for several friction scenarios. We assumed that the friction of host land cover would always be equal to or less than the friction of non-host land cover because previous studies have suggested that dispersal from a forest area into open habitats is limited (Davidson et al. 2005), and that disease severity is highest in areas surrounded by contiguous forests (Condeso and Meentemeyer 2007). We assigned host vegetation a friction value of 1, and then varied the friction value of non-host land cover from 1 (equal movement through two landcover types) to 200 (no movement through non-host landcover): 1, 5, 10, 20, 40, 60, 80, 100, 150 and 200. Friction values for the border cells outside of our study area were set to 0 so that movement pathways could not pass through them (i.e. a reflecting barrier). We also calculated least-cost distances between plots using non-zero values for border cells, however, because our plots were relatively far from the boundary of our land cover classification map, results obtained with reflecting barriers were identical to those obtained with an absorbing boundary layer.

Fixation of shape parameter

The optimal value of the parameter a in the connectivity term (Eq. 2) for each connectivity scenario (d_{ik} = Euclidean distances, and effective distances from nine least-cost scenarios) was obtained by regressing the average number of symptomatic leaves (Y_i) versus the connectivity term (λ_i) (Eq. 2) and identifying the value of a that maximized the fit of this simplified linear model. This allowed us to use all 81 plots to obtain a better estimate of a than if we simultaneously varied a and all possible combinations of predictor variables (where only 32 plots with microclimate data could be used). We tested models with a equal to 1, 20, and then increasing by 20 up to 500 and then increasing by 100 up to 1000 for each connectivity scenario (i.e. Euclidean and all least-cost distances), and then iteratively narrowed it down until the integer value of a that maximized model fit for each cost scenario was identified. The average number of symptomatic leaves per stem was ln(x+1)-transformed to meet assumptions of normality

Model selection

We used several model selection procedures to identify the combination of environmental and connectivity variables that best explained variation in our observed measure of disease severity and to test our predictions that: (1) models including environmental variables and measures of potential connectivity perform better than models with environmental variables alone or connectivity measures alone (supporting hypothesis 1), and (2) models incorporating the effects of landscape structure on connectivity would perform better than models using simple distance-based measures of connectivity that ignore landscape structure (supporting hypothesis 2). Of the 86 plots in the study area, five did not contain any bay laurel trees. Because the response variable for our models was based on the number of infected bay leaves, these plots were removed from the analysis. The average number of symptomatic leaves per stem was ln(x+1)-transformed, and the DBH of bay laurel and of all foliar hosts were square-root transformed to meet assumptions of normality. We determined the combination of predictor variables that best fit the data using all possible regressions with selection based on R^2, adjusted R^2, and Mallow's cp, forward selection with P-to-enter and/or P-to-remove equal to 0.05 and 0.10, backward selection with P-to-enter and/or P-to-remove equal to 0.05 and 0.10, and stepwise regression

with P-to-enter and P-to-remove equal to 0.05 and 0.10. All nine selection methods were performed in SAS 9.1 (SAS Inst.). We selected the top two models that model selection procedures consistently identified when connectivity was calculated with Euclidean distances, and the top four models that were consistently identified when connectivity was calculated with effective distances. Two of these top models did not contain the connectivity term. We compared AIC and BIC scores for all of the top models and identified the model with the highest explanatory power based on these scores. For the best model, we tested for normality of residuals and examined residual plots (i.e. residuals vs predicted values and vs each independent variable) to test model assumptions.

Relative importance of model variables

To test the hypothesis that the relative importance of environmental variables and connectivity is approximately equal (hypothesis 3), we calculated the standardized regression coefficients for the top models identified above. We first tested for homoskedasticity by plotting residuals versus predicted values. None of the models violated this assumption. We then calculated the standardized standard deviation of each variable and used this to calculate the standardized regression coefficient (according to Bring 1994). The standardized standard deviation for each variable was calculated as:

$$S_i^* = \frac{Si}{\sqrt{VIF_i}} \times \sqrt{\frac{n-1}{n-k}} \quad (3)$$

where S_i^* is the standardized standard deviation for variable i, S_i is the standard deviation of variable i, VIF_i is the variance inflation factor for variable i, n is the sample size, and k is the total number of independent variables in the model.

The standardized regression coefficient was then calculated as:

$$B_i^* = \check{B}_i S_i^* \quad (4)$$

where $\hat{B}_i$ is the estimated regression coefficient using unstandardized variables.

Results

Results demonstrated that models including environmental variables and measures of connectivity performed better than models with environmental variables alone or connectivity measures alone (supporting hypothesis 1), and that models incorporating the effects of landscape structure on connectivity performed better than models using simple distance-based measures of connectivity that ignore landscape structure (supporting hypothesis 2). When the connectivity term was calculated using Euclidean distances (Eq. 2), model selection procedures identified two top models, neither of which contained the connectivity term: models A (relative humidity, canopy cover, PSI; R^2 = 0.48, AIC = –12.91, BIC = –9.25) and B (relative humidity, canopy cover, PSI; R^2 = 0.51, AIC = –12.75, BIC = –8.01). When connectivity was calculated using effective or least-cost distances (Eq. 2), model selection procedures identified 4 top models that contained the connectivity term. These four models generally performed better than models A and B (e.g. for non-host land cover friction value = 40, model 1: relative humidity, canopy cover, PSI, connectivity, R^2 = 0.56, AIC = –15.77, BIC = –12.25; model 2: relative humidity, canopy cover, PSI, temperature, connectivity, R^2 = 0.58, AIC = –15.52, BIC = –10.95; model 3: relative humidity, canopy cover, PSI, host DBH, connectivity, R^2 = 0.58, AIC = –14.91, BIC = –10.50; model 4: relative humidity, canopy cover, PSI, temperature, host DBH, connectivity, R^2 = 0.61, AIC = –14.76, BIC = –9.00) (Fig. 3). However, when friction values for non-host land cover were < 10, then models A and B (that did not include the connectivity term) performed similar to or better than models 1–4 (that included the connectivity term) (Fig. 3). For the connectivity terms in these models, the value of parameter a that maximized the proportion of variability in the average number of symptomatic leaves that was explained by the connectivity term increased as the cost given to non-host land cover increased from 5 to 60, but then decreased at costs > 60 (Fig. 4). The value of a was ~85 for all non-host land cover costs > 100 (Fig. 4b). When the connectivity term was calculated with Euclidean distances, the optimal value of a was 276.

When the connectivity term was calculated using Euclidean distances, only one model selection procedure (selection based on adjusted R^2) identified a model that included the connectivity term (disease severity ~ f (canopy cover, relative humidity, PSI, TMI, and connectivity); R^2 = 0.55, AIC = –11.10, BIC = –3.95). Because this model was ranked third based on adjusted R^2 and was not selected with any other model selection procedure, it was not identified as a top model. Overall, it performed worse than models with connectivity calculated using effective distances (hypothesis 2) and worse than the top models with no connectivity term (i.e. model A and B).

Based on both AIC and BIC, model 1, which included the connectivity term calculated with effective distances and non-host land cover friction approximately equal to 40, performed best (Fig. 3). Residuals of this model were normally distributed and residual plots did not indicate that regression assumptions were violated. Other measures of model fit for the top models from model selection (adjusted R^2, and MSE) are listed in Table A1 in Supplementary material Appendix 1.

Results also demonstrated that environmental variables were relatively more important in determining spatial pattern of sudden oak death than connectivity, which does not support our original hypothesis that their relative importance would be approximately the same (hypothesis 3). Overall, canopy cover and relative humidity had the largest impact on disease severity (Table 1). Potential solar irradiation and connectivity had a slightly lower impact on disease severity, while host DBH and temperature had a substantially lower relative impact on disease severity. Potential solar irradiation was negatively related to disease severity possibly because high values of potential solar irradiation may represent relatively hot and dry locations, which are unsuitable for the survival of *Phytophthora ramorum*

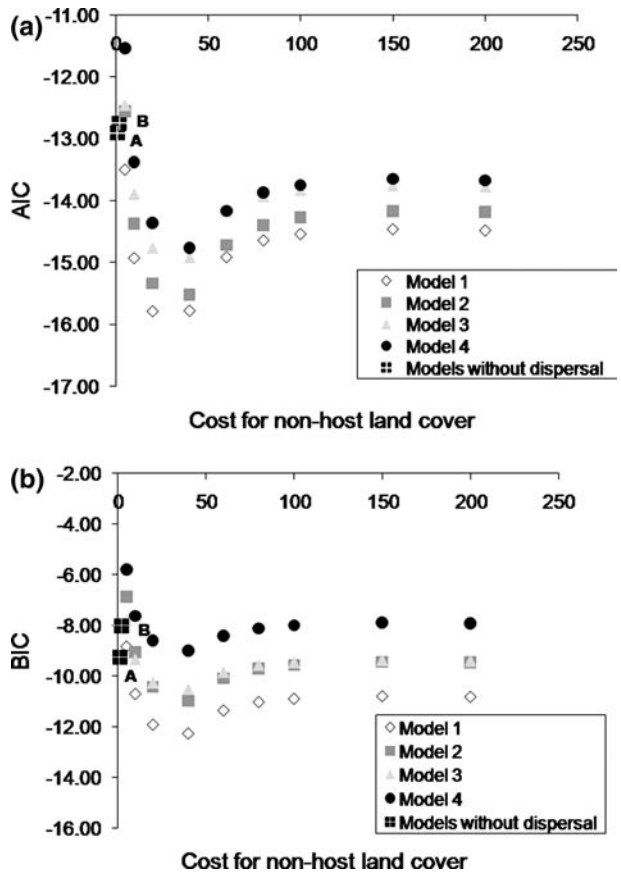

Figure 3. (a) AIC scores for top models and each friction scenario, (b) BIC scores for top models and each friction scenario. Details of each model are described in Table 1 and the text. Model A and B (labeled on graph) did not include the connectivity term as an important variable.

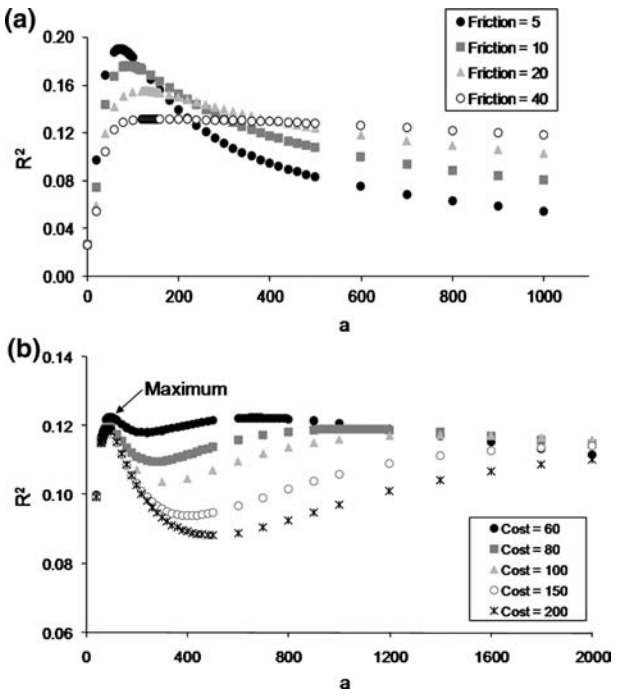

Figure 4. Value of a that maximized R^2 for linear regression between disease severity and connectivity (Eq. 2) and for each least-cost distance scenario. (a) results for scenarios with non-host land cover friction values less than 60, (b) results for scenarios with non-host land cover friction values greater than 40. The maximum value of a for each model in graph (b) was between 83 and 95. Friction for host land cover in all models = 1.

(Davidson et al. 2005). Host DBH was also negatively related to disease severity. Higher total host DBH may correspond to higher tree richness/diversity and a lower abundance of bay laurel. Because bay laurel is thought to be the most important producer of infective spores in many locations, a lower abundance of this species could generate lower disease severity. Consistent with previous studies, all other variables were positively related to disease severity (Condeso and Meentemeyer 2007). Standardized regression coefficients are listed in Table A2 (Supplementary material Appendix 1).

Discussion

Though connectivity has been examined from many different angles and in many ecological disciplines, few studies have tested in which systems and under what conditions connectivity is important in determining ecological dynamics. Understanding the rules governing the importance of connectivity is crucial for developing a general theoretical framework for ecology and for our ability to predict ecosystem response to environmental change.

Our results support the hypotheses that potential connectivity, in addition to environmental conditions, is important in determining the spatial distribution of sudden oak death (hypothesis 1) and that the importance of connectivity is more apparent when measured using biologically meaningful metrics that account for the effects of landscape structure on potential movement (hypothesis 2). Models including a metric of connectivity calculated with simple Euclidean distance performed worse than models with environmental variables alone and models including a metric of connectivity calculated with effective distances (i.e. Euclidean distances modified to account for how landscape structure can influence dispersal or spread). Many studies have also demonstrated that measures of connectivity using effective distances perform better than Euclidean-based measures (Sutcliffe et al. 2003, Koscinski et al. 2009) and that results often depend on how connectivity is calculated (Moilanen and Nieminen 2002, Magle et al. 2009). Broadly, these studies indicate that the answer to the question of when connectivity is important may depend not only on the system, but also on how connectivity is measured. This in turn suggests that it would be prudent to consider multiple measures of connectivity in future tests of the importance of connectivity.

While connectivity may be important in determining the spatial pattern and severity of sudden oak death, results also suggest that environmental variables may have a slightly stronger effect than connectivity. This result does not support our original hypothesis that the relative importance of environmental variables and connectivity is approximately equal (hypothesis 3), but is consistent with studies demonstrating that plant pathogens are often highly sensitive to environmental conditions (Agrios 2005) and that spatial

Table 1. Model selection results and the relative importance of variables in each model for each cost scenario. Models A and B did not include the connectivity term. Models 1, 2, 3 and 4 included the connectivity term calculated with effective distances. λ = connectivity, C = canopy cover class (1–4), RH = average number of daily hours at optimal relative humidity for growth of *P. ramorum* (> 95%), PSI = potential solar radiation, TMI = topographic moisture index, T = average number of daily hours at optimal growth temperature for *P. ramorum* (10–25°C), and H-DBH = total DBH for all *P. ramorum* hosts.

Model ID	Variables and their relative importance based on standardized regression coefficients	Friction value for non-host land cover
A	RH > CC > PSI	NA
B	RH > CC > PSI > TMI	NA
1	RH > CC > PSI > λ	all friction scenarios
2	RH > CC > PSI > λ > T	5, 60, 80, 100, 150, 200
	RH > CC > λ > PSI > T	10, 20, 40
3	RH > CC > PSI >λ > H-DBH	all friction scenarios
4	CC > RH > PSI > λ > T > H-DBH	5
	RH > CC > λ > PSI > T > H-DBH	10,20,40
	CC > RH > λ > PSI > T > H-DBH	60, 80, 100, 150, 200

spread of plant diseases may be determined more by the ability of the pathogen to become established than by dispersal ability (Aylor 2003). Thus, in this system, spatial pattern of disease is determined by connectivity in the sense that highly connected locations have a more continuous path of suitable habitat between them, permitting the survival and gradual spread of pathogen.

Though not specifically tested here, results also provide information about the nature of dispersal in this system. If the friction value of non-host land cover was statistically 100 times higher than that of host land cover, then virtually all least-cost pathways would be confined to host land cover. The best-fit model identified in this study included the connectivity term when the friction value of non-host land cover was statistically 40 times higher than the friction of host land cover. This suggests that least-cost pathways had a higher tendency to pass through host land cover, but did occasionally pass through non-host land cover. Thus, while connectivity is important and the disease tends to travel through host land cover, long-distance dispersal and traveling through (or over) non-host land cover does occur in this system. These results are consistent with previous studies indicating that dispersal of *Phytophthora ramorum* is primarily local (i.e. within ~5 m of an infected host) (Condeso and Meentemeyer 2007, Mascheretti et al. 2008) and that medium to long-distance dispersal (~1500–10 000 m) may occur via strong winds and possibly human movement (Davidson et al. 2005, Mascheretti et al. 2008, Meentemeyer et al. 2008a), but is relatively rare (Mascheretti et al. 2008).

Although results demonstrate the potential importance of connectivity in determining disease dynamics, there are several limitations to our approach. First, the landscape was greatly simplified by defining only two land cover types. Evidence suggests that these two classifications are appropriate in this system (Condeso and Meentemeyer 2007), but several other landscape features may also influence the spatial dynamics of sudden oak death (e.g. differences in forest age or structure, and the presence and location of geographic features). Second, least-cost path analysis gives information about the potential overall resistance between locations, but does not give any specific information about actual dispersal pathways in the landscape (Adriaensen et al. 2003). Although our methods were based on empirical knowledge of the biology of the system, we have no empirical data to confirm that least-cost path analyses captured the true manner in which disease spread occurs. Lastly, we were unable to validate the model. While we have recent estimates of most of the predictor variables, we have not been able to obtain recent estimates of canopy cover, which is likely to change due to tree mortality associated with sudden oak death. We hope to validate the model when these data become available.

Conclusions and significance

Although connectivity studies typically focus on animal systems and diseases transmitted via vectors and hosts with active movement, our results demonstrate that connectivity can also be important in plant pathogen systems where movement is passive via wind-driven rain. This result highlights the importance of examining connectivity in systems characterized by different types of movement (e.g. land vs air, short vs long range, random vs selective) or, in the case of disease, different modes of transmission (e.g. vector-, host-, water-, rain-, air-borne) to more fully understand when connectivity is important in determining ecological dynamics. In addition, our results demonstrate that the manner in which connectivity is measured may govern our ability to detect its importance. This can have important consequences for modeling and predicting disease dynamics. The more simplistic commonly-used measures of connectivity that are based on Euclidean distances between locations could generate models that over- or under-estimate connectivity and the force of infection in disease models (Fig. 1c). If disease models are used to inform management, then misrepresentations of the force of infection could generate inaccurate models, which can compromise our ability to control and manage diseases.

Acknowledgements - We thank all members of the Center for Applied GIS at UNC-Charlotte for their helpful comments on the manuscript. We also thank Dave Rizzo and all of the members in his lab for their comments and continued support, the team of researchers at Sonoma State Univ. that helped set up the SOD plot network and collect data, and T. Emiko Condeso for all her previous work that made this study possible. This research was supported by grants from the National Science Foundation (EF-0622677), USDA Forest Service (State and Private Forestry-Pacific Southwest Region), and the CSU Agricultural Research Initiative.

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Supplementary material (available online as Appendix 017918 at <www.oikos.ekal.lu.se/appendix>) Appendix 1.

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