

A spatial model to estimate habitat fragmentation and its consequences of long-term survival of animal populations.

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Abstract

The increasing proportion of the landscape used by humans has led to important decreases of the surfaces occupied by natural areas. Conversion of the land for agricultural purposes as well as urbanization, has turned large continuous unbroken patches of wild habitat into numerous small patches, isolated from each other among a matrix of inhospitable land-uses. In these modern landscapes, habitat fragmentation, disabling gene transfer between populations as well as stopping their spread to new habitats, appears as a major threat to the survival of numerous plant and animal species.

This study was conducted, as part of the Land use Evolution and impact Assessment Model (LEAM) with the objective of creating a general model, adaptable for a specific species, that would assess the degree of fragmentation of a landscape and investigate the capacity of the species to move between suitable patches of habitat. For practicality purposes, the model was set for a fictitious species, assumed to be a territorial, exclusive, forest specialist, requiring a minimum home range of 5 ha of low edge habitat to survive. This species was assumed capable of moving over distances of 300 meters through non-forested habitat, but unable to cross highly altered land-use cells such as residential, commercial and highway cells.

The method used, to assess fragmentation and patch connectivity, combines GIS analysis of a landscape (30m*30m) land-use map (using the NLCD 21 land-use classification) with spatial dynamic modeling. The first step of the analysis was to identify all patches of potentially suitable habitat (forest), in the land-use map, and calculate the perimeter and area of each patch. Suitable patches of habitat were then selected if their ratio area/perimeter was superior or equal to the minimal ratio of a 5 ha circular habitat (presenting minimum edge). These selected polygons were merged with the initial land-use map to form a suitable habitat map, which was then used in a spatial dynamic model, to determine patch connectivity. From the habitat map, maximum carrying capacity of each polygon was deduced, by dividing its area by home range size. A selective diffusion STELLA™ model was created to investigate movement of species between habitat patches. When run under the Spatial Modeling Environment (SME), using the suitable habitat map as input, this model produced around each polygon of suitable habitat, a buffer zone, corresponding to the maximum distance at which the species can disperse outside suitable habitat. This buffer map was imported into GIS and overlaid with the suitable habitat map. We considered that every polygon located inside the same buffered zone could potentially exchange populations with the other, and therefore were connected and could allow gene flow to occur between

populations. By summing the respective area of all polygon located within the same buffer zone and dividing by the home range area, we obtained the maximum genetic pool available in the connected area. We then compared the genetic pool with what is considered minimum viable genetic population for the considered species and determined which habitat patch might host populations in risk of extinction due to inbreeding.

The model was run over three of land-use change scenarios, provided by the LEAM group, and showed different responses, indicating that minor changes in land-use could have important repercussion on habitat fragmentation and therefore on the long term survival of species. The model map output also appeared to provide important information on the spatial distribution of patches and their importance as gene sources. The model could therefore have potential applications in land-use planning, for the establishment of natural corridors to connect isolated patches and restore viable genetic populations.

Introduction

The increasing proportion of the landscape used by humans is leading to an important decrease in the surfaces available for natural habitats. Conversion of land for agricultural and urban development has turned large continuous unbroken patches of wild habitat into numerous small patches, isolated from each other among a matrix of inhospitable land-uses. This phenomenon, of habitat fragmentation has been recognized as a major threat to biological diversity and is considered to be the primary cause of the present species extinction crisis (Wilcox and Murphy 1985, Schimiegelow and Mönkkönen 2002, Gibb and Hochuli 2001). Urbanization is considered a major cause of habitat fragmentation, and threatens the survival of many species worldwide (Tigas et al. 2002).

Numerous research projects are underway to assess the future evolution in landscapes as a response to human activity and needs, and particularly resulting from urbanization. However, most studies focus on “human oriented” interests and very few take into account the environmental consequences of these modified landscapes. This study, as part of the Land use Evolution and impact Assessment Model (LEAM) has for objective to create a general model, adaptable for a specific species, that would determine habitat suitability for a certain species and assess the degree of connectivity between patches that can host populations.

This method, applied to changing landscape provides indications on changes in species specific connectivity between patches and determine the impact of land-use change on population isolation and therefore on population fragmentations, which could be used as an indicator of habitat fragmentation.

Habitat fragmentation and its impact on species population

The process of habitat fragmentation involves three factors, which have important repercussions on plant and animal species that originally occupied large continuous areas of wild habitat (Schimiegelow and Mönkkönen 2002, Gehring and Swihart 2002).

First, fragmentation leads to the breaking of large patches into numerous smaller, resulting in a net habitat loss. This results in a decrease in the amount of resources and shelter areas available to wild species and therefore leads to a general reduction in the number of individuals that can be hosted.

Second, by opening core areas, fragmentation of continuous habitat patches, leads to a dramatic increase in edges (Sih et al. 2000). Edges present distinct micro-climatic conditions from the core and therefore might become less suitable for species. These edges also lead to higher predation rates by favoring generalist predator influx (Schmiegelow and Mönkkönen 2002), which in turn greatly impacts the population of resident species.

Third, habitat fragmentation results in the geographic isolation of “islands” of habitat among a matrix of urban or agricultural land-uses. This might greatly restrict the mobility of certain organisms (Andreassen et al. 1996), and thereby isolate some populations. However, small isolated populations can be threatened by inbreeding, which represents a serious problem for their survival and could lead, in case of severe inbreeding, to population extinctions (Templeton et al. 1990, Schmitt and Seitz. 2002). Moreover, small populations are more sensitive to stochastic events, such as fires or epidemic outbreaks that could drive local population to extinction.

Finally, as the isolation of habitat patches increases, the probability that they be recolonized decreases (Parker and Nally. 2002). Therefore, long-term survival of isolated populations cannot be assumed in any case. Nonetheless, not all species have the same sensitivity to habitat fragmentation. Naturally rare, sedentary species, with specialized in habitat requirement show an important decline whereas abundant mobile generalist species are less affected (Nally et al. 2000) or even favored, in the case of edge specialists (Tscharntke. 1992, Gehring and Swihart. 2003). Also the degree of isolation of habitat patches might depend on the migration capacity of each species living within them. As a consequence, habitat fragmentation cannot be generally described, and should be specified for every individual species.

This study focused on a fictitious animal species, the “fraggle”, which was assumed to be sensitive to fragmentation. As stated by Akçakaya (2001):” methods that ignore demographic factors are not likely to give realistic assessment of species threatened by human impact”. Therefore present model does not pretend to provide a very accurate indicator of population response to habitat fragmentation, but provides information concerning the maximum carrying capacity and maximum number of individuals that are connected together within habitat patches and therefore can exchange genes. These data will be used, as bases, in a spatial dynamic population model that will be the subject of a future publication.

Methods

A combination of GIS analysis of a landscape land-use map with a spatial dynamic model was used to investigate landscape fragmentation for a considered species.

This study, contrary to most of the previous work on habitat fragmentation did not involve artificial computer generated landscapes (Schumacker 1996) but was based on real land-use maps and on predicted land-use map provided by the Land use Evolution and impact Assessment Model (LEAM) group. The advantage of this approach is that it is not based on a random destruction of natural habitat (performed in most models), but rather uses socio-economic drivers to determine land-use change and urbanization and therefore provide a more accurate estimation of future potential landscape changes. This approach also integrated life history characteristics of a considered species, but could be parameterized for potentially any terrestrial organism. We considered three different scenarios, present land-use, business as usual with development limited to facility planning area and high

economic growth scenario with development limited to facility planning area and investigated the repercussions on Fraggie populations.

Study area

This study considered the landscape of the Peoria Tri county area, in Illinois, USA, composed of Peoria, Tazewell and Woodford counties. The 1995 NLCD land-use map at a resolution of 30*30 meters was overlaid the road network (Illinois ISGS). The dataset we considered was composed of 2522 rows and 3042 columns, representing a surface of 690473 ha (Fig. 1).

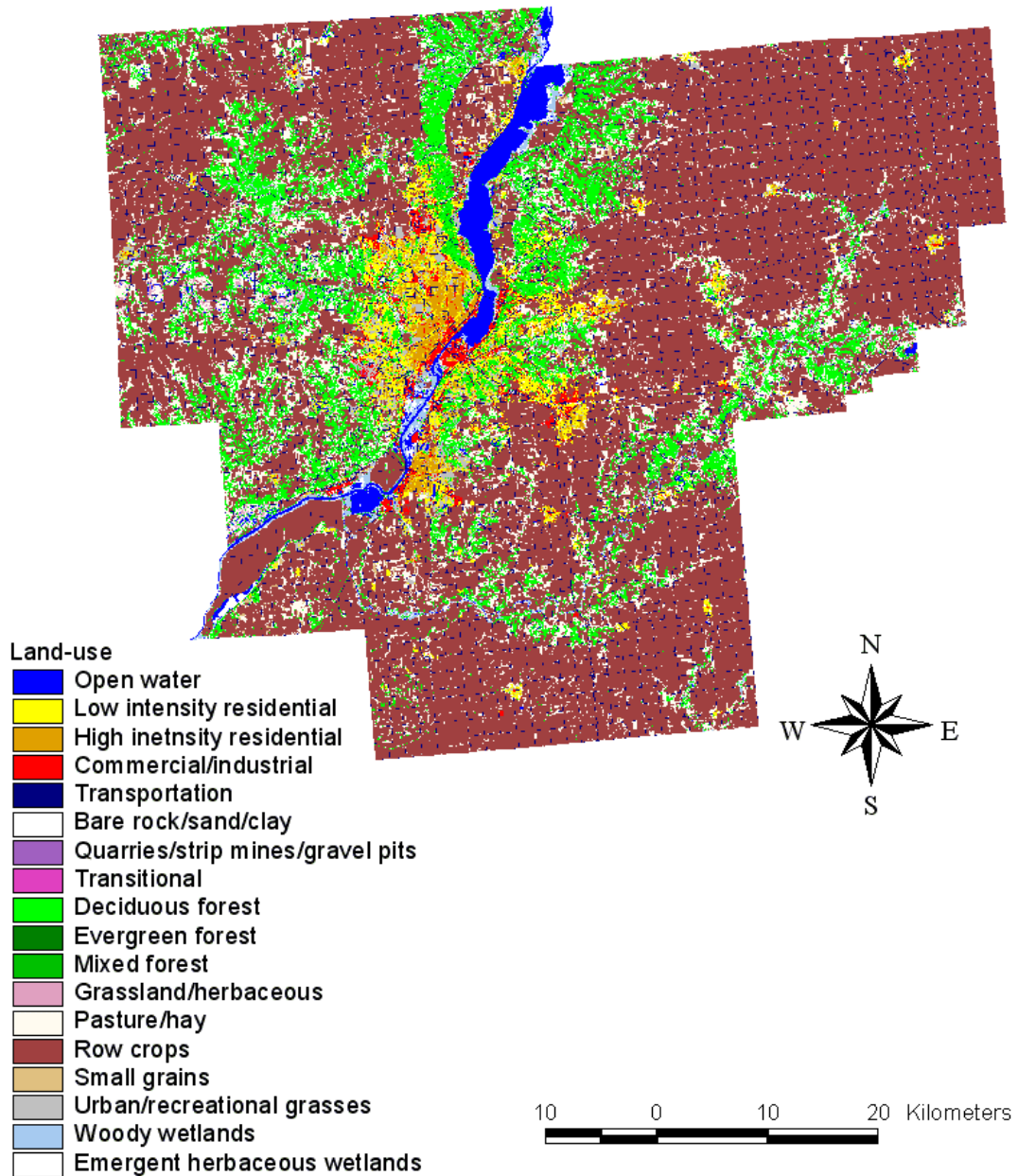
Three different maps were considered:

- (1) The initial 1995 Peoria Tri county land-use map, among which 60554 ha were occupied by forested area
- (2) The land-use map predicted, in 30 years, in case of business as usual and development limited to facility planning area (fpa), among which 54457 ha were occupied by forested area
- (3) The land-use map predicted in 30 years in case of high economical scenario and development limited to facility planning area (fpa), among which 51278 ha were occupied by forested area.

The two 'predicted' maps were provided by the LEAM group and were obtained from runs of the pLEAM model (2003).

Figure 1: Peoria Tri-county land-use map

NLCD land-use in Peoria Tri-county, IL



Species considered

For practical purposes, this model was calibrated for a fictitious species (the fraggle), assumed to be a territorial, exclusive deciduous forest specialist, requiring a minimum home range of 5 ha of low edge habitat to survive. This species was considered the equivalent of a small mammal, unable to fly from one habitat patch to the other, and thus required to physically cross land-use cells in order to disperse through the landscape.

Fraggles were assumed to move freely inside suitable patches of habitat and within connected patches and allow gene flow. As suggested by Tschardtke (1992), A population size of 500 individuals was assumed sufficient to maintain genetic variation and long-term survival. Fraggles were assumed to be able to migrate through some non-forested land-uses (Table 1) to reach other suitable patches. The movement of fraggles through the landscape was assumed to be non-random and certain land-uses could be crossed whereas others acted as barrier (Table 1).

The selection of crossable habitats, was performed considering an avoidance of “human occupied” landscapes by Fraggles and their incapacity of to swim across rivers. The dispersal of fraggles was limited to a distance of 300 meters, considering the fact that fraggles outside of their preferred habitat are subjected to higher predation rate and is unable to find food or shelter.

Table 1: Land-use selection for Fraggles dispersal

Crossable land-uses	Barrier land-uses
24: roads	11: open water
31: bare rock/sand/clay	12: perennial ice and snow
33: transitional	21: low intensity residential
41: deciduous forest	22: high intensity residential
42: evergreen forest	23: commercial
43: mixed forest	25: large roads such as state and national highways
51: shrubland	32: quarries, strip mines
71: grassland/herbaceous	61: orchards
81: pasture/hay	85: urban, recreational grasses
82: raw crops	
83: small grain	
84: fallow	
91: woody wetland	
92: emergent herbaceous wetland	

Data manipulation and habitat selection

The AscII data obtained from the pLEAM runs were georeferenced by copying the first line of the NLCD land-use AscII file. These data were then converted into grid format using ESRI ArcView 3.3. Our model operates in three successive steps:

- (1) Selection of the species “specific habitat” land-uses;
- (2) Determination of suitable habitat patches, that can sustain at least one individual;
- (3) Estimation of connectivity between patches and determination of the maximum gene pool they can host.

Selection of forested habitat

We considered Fraggles as exclusive forest specialists and selected, using ArcView 3.3, from each of the three land-use maps all forested cell. We then converted the selected grid file into a shapefile in order to remove boundaries between cells of the same type and create habitat patches. We defined a habitat patch as any collection of 30*30 meter cells occupied by forest that touched at either their side or corners. However, fraggles require a certain home range of forested habitat, large enough to provide them with the necessary food and shelter for their survival. Therefore not all forest patches can be considered as suitable to host fraggle populations.

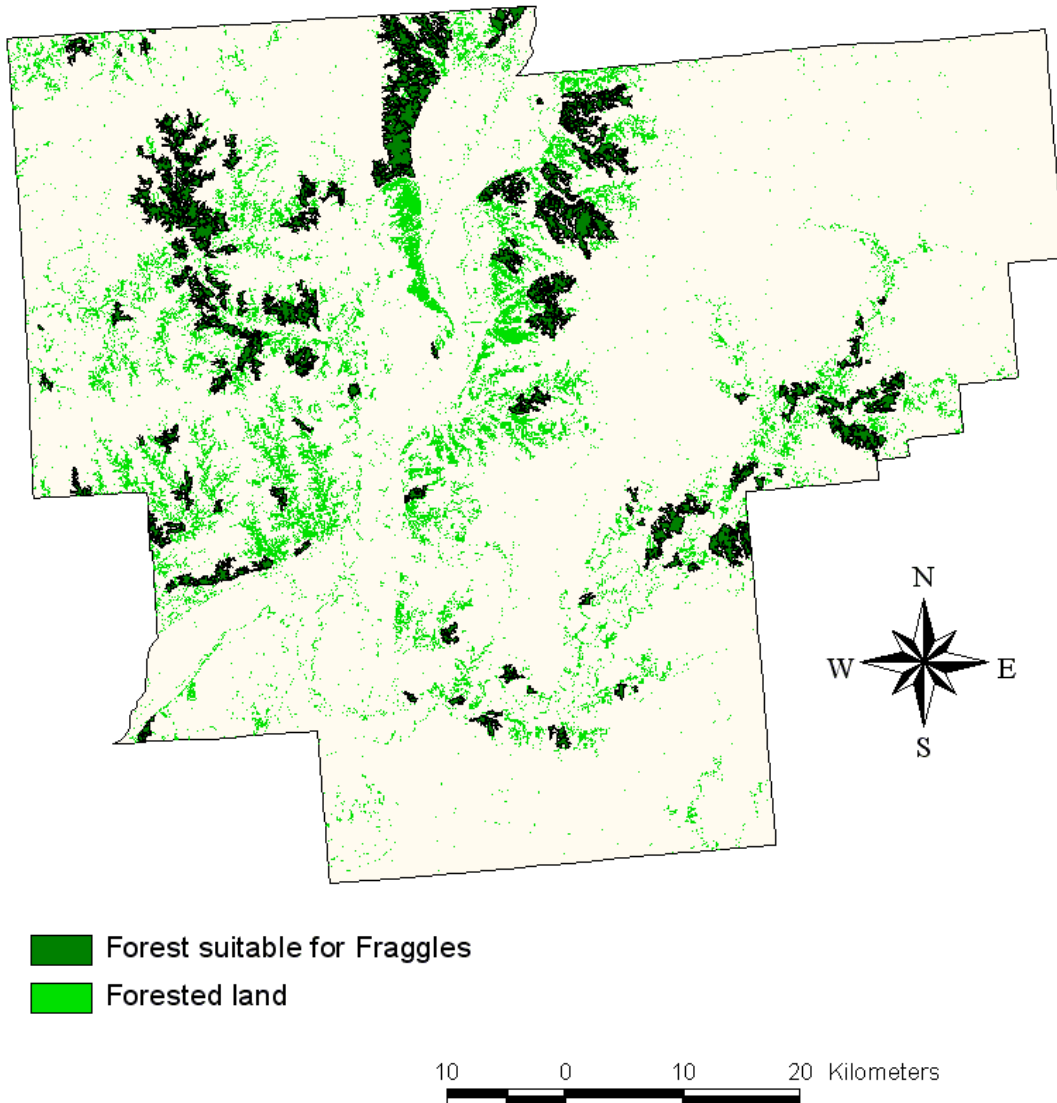
Selection suitable habitat patches that can potentially host fraggle population

Fraggles were considered sensitive to fragmentation and unable to survive in highly fragmented habitat. Due to the uncertainty existing in the literature concerning the extent to which edges reach into core habitat (from 8 to 240 meters (Schumaker 1996)), we decided to use the area/perimeter ratio, showed by Schumaker (1996) to be correlated with habitat quality, to determine habitat suitability for fraggles.

We defined fraggles as requiring a minimum home range of 5 ha. Therefore a patch of habitat with the highest possible area/perimeter ratio and a surface of 5ha should be the smallest suitable possible patch to sustain an individual. Circular shapes present the highest area/perimeter value therefore, we defined the lowest area/perimeter ratio necessary to sustain an individual as $R^2 / 2$ $R = R/2$, which for a 5 ha circle is approximately equal to 63 meters. We calculated, the area/perimeter ratio for each forest patches of the 3 land-use maps an selected, using ArcView 3.3, all patches with at ratio superior or equal to 63 as a suitable patch to sustain a fraggle metapopulation (Fig. 2). The polygons of suitable area were then converted back to grid format, reclassified, and merged with the original land-use map and with the reclassified grid corresponding to restricted access roads (representing highways and interstates). This “habitat” map was used in the last step of the model to determine connectivity between patches of suitable habitat.

Figure 2: Patches suitable for fraggle survival

Forest patches suitable to support Fraggle populations in Peoria Tri-county, IL



Estimation of connectivity between suitable habitat patches

Schumaker (1996) suggested that habitat connectivity and animal dispersal should be considered using animal natural history, more than mathematical formulas. Therefore, in order to estimate the complex movements of fraggles across the landscape we chose to

couple a cellular selective diffusion model created with STELLA™ modeling software, with the Spatial Modeling Environment (SME) developed at the University of Maryland (Maxwell et al. 1999). This approach enables us to model the spread of fraggles, over a spatial grid, outside of suitable patches, by incorporating fraggle selection criteria to cross land-use cells (Table 1).

Movements of fraggles outside of suitable forest patches were simulated using a selective diffusion model. This model, created under STELLA™, was through the spatialization process allowed by SME introduced in all of the 30*30 meter grid cell of the “habitat” map. It modeled the behavior of a fraggles moving outside of its suitable habitat, by selectively crossing “crossable” cells and avoiding “barrier” cells (Table 1) At every time step, the eight cells surrounding each cell of suitable habitat were considered and “crossable” (Table 1) cells were given a value identical to the value for suitable habitat whereas “barrier” cells were given a value of zero.

The selective diffusion equation allowed us to consider all potential fraggle dispersal (in eight directions) from every suitable habitat cell. This process enabled us to consider the impact of each specific land-use type surrounding suitable forest habitat on the dispersal pattern of fraggles. We limited the dispersal of fraggles out of their suitable habitat by allowing them to move during 10 time steps outside of their suitable habitat, which represents a dispersal distance of 300 meters. We therefore obtained a grid “migration map” corresponding to the maximum surface matrix that could potentially be reached by fraggles while they migrate outside of their suitable habitat (Fig. 3).

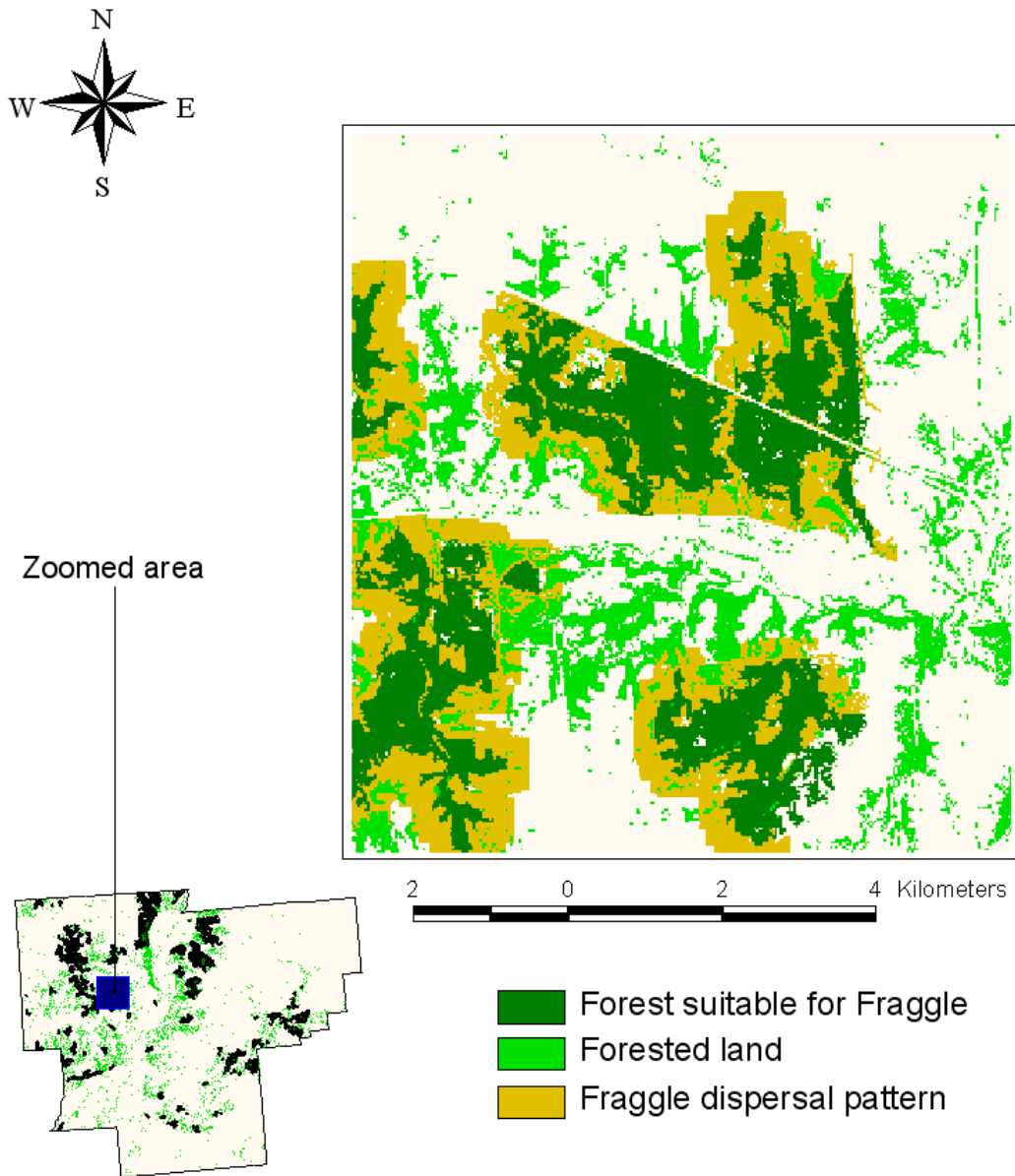
We considered that each cell, defined as “crossable” could be crossed with a probability of one, whereas in reality, migration over different types of land-uses could certainly lead to important variations in the death rate of individuals and therefore have a significant impact on the probability of fraggle to reach a certain location. However, these considerations are outside of the scope of this model (but will be investigated in a population model to be run in parallel with the habitat model).

The goal of this model is to investigate potential gene flow between patches, rather than the actual probability of migration success of fraggles. This approach was performed to take into account the idea, stated by Templeton et al. 1990 and Simberloff and Cox. (1987), that limited exchanges of individuals between metapopulations could increase their genetic diversity and decrease their chance of inbreeding depression.

To determine connectivity between patches, the “migration map” was overlaid in ArcView 3.3 and converted to polygon with the polygons corresponding to suitable habitats for fraggles (fig. 3). We considered that every polygon of suitable habitat located within the boundaries of the same “dispersal area”, were connected together and could potentially exchange population and therefore form a “genetically connected entity”. For this purpose, we used an ArcView script that attributed to each polygon of suitable habitat, the identification number of the “dispersal area” polygon in which they were included. We used Microsoft Excel to edit the data table corresponding to the “suitable habitat” shapefile and calculate, for each “genetically connected entity” the total area of suitable fraggle habitat they contained.

Figure 3: Movements of fraggles outside suitable habitat

Connectivities between suitable patches of habitat



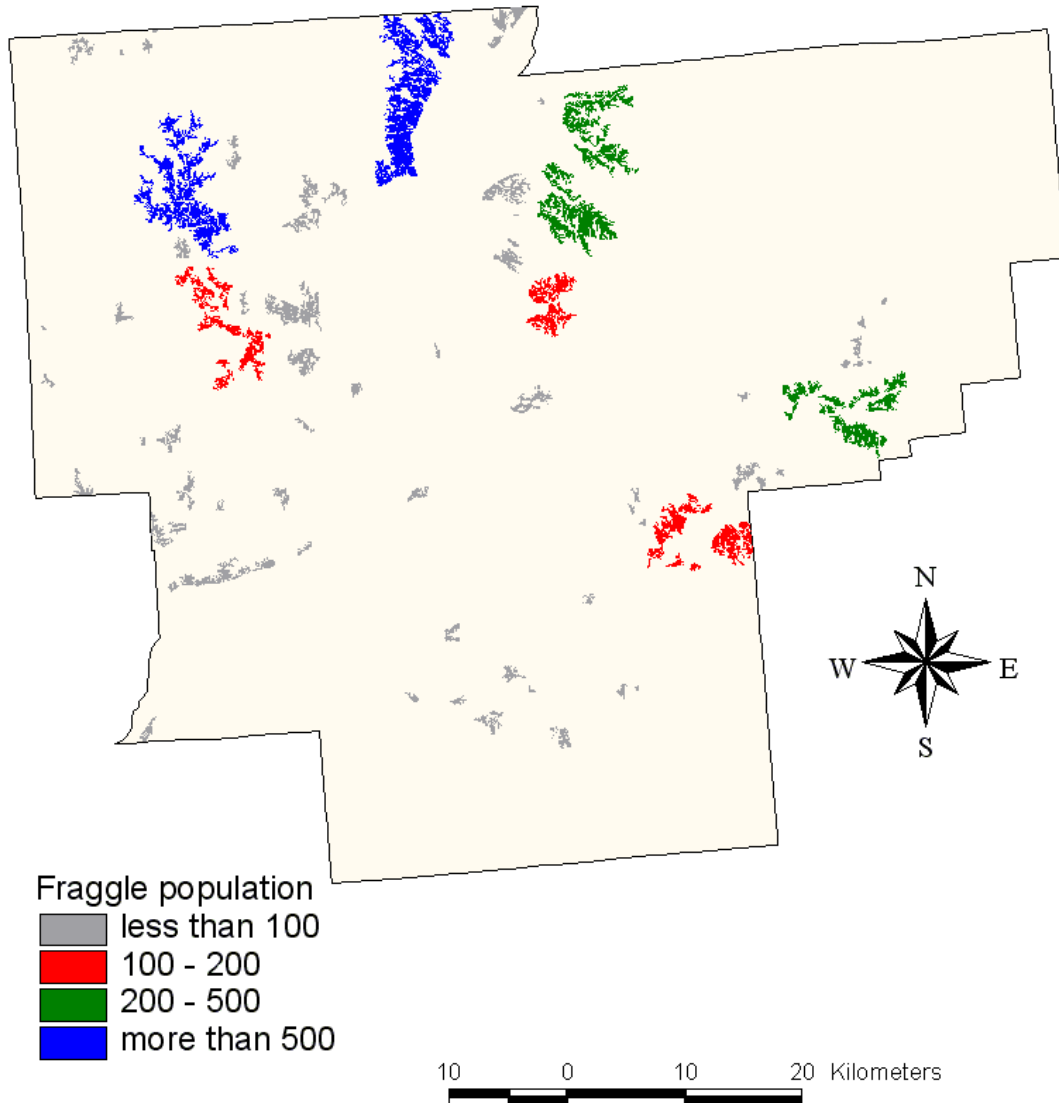
Estimation of maximum carrying capacity and maximum connected gene pool

Fragmentation was showed to have effects on the shape, but not extend, of species home range, and no differences in population density and survival were observed (Harper et al. 1993). We assumed that the home range of a fraggle could encompass only one patch of habitat, and that only habitat patches larger than the minimal home range size could host fraggles. The selection of suitable patches using the habitat area/perimeter ratio allowed us to choose patches that can host fraggle population (at least one individual) but provided no information on the total population that could be hosted in each patch. For each suitable habitat patch, its maximum fraggle carrying capacity was determined, by dividing the surface of the patches by the minimum species home range (5 ha). The species, being assumed territorial, only one individual was considered to live in each home range. The obtained values for each patch represent an overestimation of the real population that could be hosted, since the proportion of core and edge habitat varies within habitat polygons. Therefore these values should be considered as indicators of maximum potential population.

We applied the same method to each “genetically connected entity” to determine the maximum potential number of individuals present in a group of connected patches, therefore representing the available gene pool. The gene pool data were then entered in the suitable habitat data table and plotted, for each genetic entity, in the maximum fraggle population map (Fig. 4).

Figure 4: Maximum possible fraggle population per genetic entity.

Maximum Fraggle population hosted in Peoria Tri-county, IL



Results and discussion

We observe, in Figure 5 that different land-use change scenarios resulted in different impacts on the geographical distribution of fraggles and on the available gene pool in each “genetically connected entity”. The results in Table 2 indicate that development in the two considered scenarios leads to a decrease in the total forested area as well as in the total surface suitable for the survival of fraggles. However, contrary to what might intuitively be deduced, we remark, in table 2 and Figure 5, that the scenario leading to the highest decrease in surfaces covered by forests (high economy fpa) provides more hectares of suitable habitat for fraggles than does the business as usual scenario, even though it preserves more forest.

Table 2: Changes in the forested surfaces

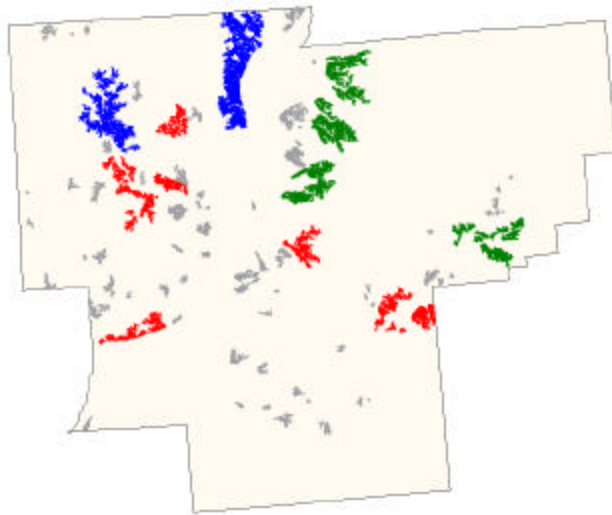
Scenario	Total forested area (ha)	Total area of suitable patches (ha)
Initial	60554	24728
Business as usual fpa	54458	20348
High economy fpa	51279	20370

We therefore deduce that the spatial distribution of the patches of forested habitat removed by urbanization is a very important factor to be considered. This consequently justifies our approach and emphasizes the necessity to investigate the effect of land-use change spatially through the landscape and by incorporating life history parameters of the considered species. We conclude that considerations of forest preservation at the cellular level only do not represent a suitable technique to manage for fraggle populations.

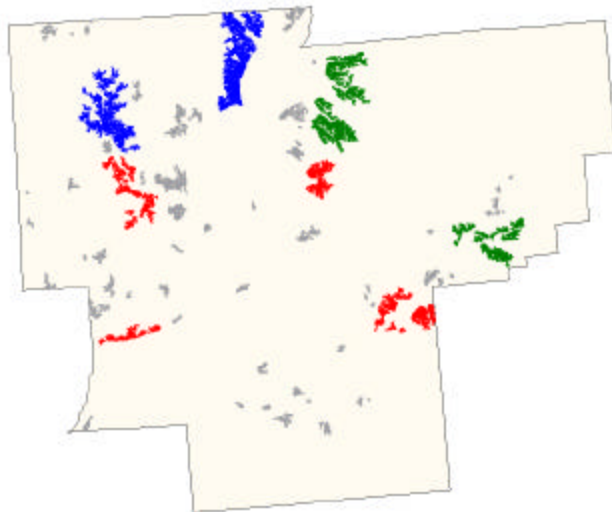
However, considerations of the total area of suitable patches are not sufficient to provide a tool to manage fraggle population in the long term. Most of the suitable habitat patches are presently isolated in the landscape (Fig. 5) and therefore represent “genetic islands”. If the number of individuals in the metapopulation hosted in these patches becomes too small, they might suffer from inbreeding depression and in the long term could face extinction (Simberloff and Cox. 1987). By looking at Figure 6, we observe, for each scenario, that only a small proportion of fraggles (approximately 30%) are located in “genetically connected entities” that can host more than 500 individuals and should not be threatened by inbreeding (Tschardt 1992). We also observe that, for this category of patches, the high economy scenario, although leading to more destruction of forested areas, allows to maintain a higher number of fraggles within non-inbreeding threatened populations. However, if we consider populations moderately at risk of inbreeding, with more than 100 individuals per metapopulation, we observe that the trend is reversed and that the business as usual scenario allows to sustain more fraggles (2898 against 2863) than the high economy scenario.

Therefore, depending on the threshold number considered necessary to avoid inbreeding, the interpretation on the impact of different scenarios on fraggle population varies. Finally, if we consider the spatial distribution of the various “genetically connected entities” (Fig.5), we observe that several small patches are located in the vicinity of larger one. If these patches could be connected together, the genetic pool shared within these habitat patches would increase and therefore could decrease the extinction risk of the fraggle population they host. Consequently, similar type of outputs could be useful to help decision making for the selection of habitat corridor locations, by accessing their potential impact on the long-term survival of species.

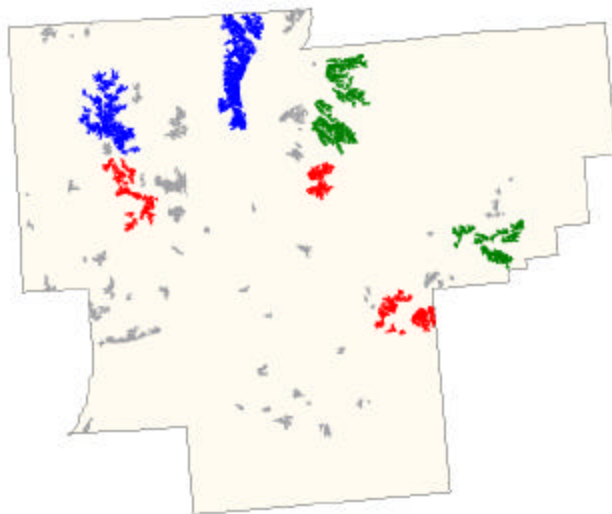
Figure 5: Map of the maximum fraggle genetic pool for three scenarios



1. Initial land-use



2. Year 30 business as usual FPA



3. Year 30 high economy FPA

Legend





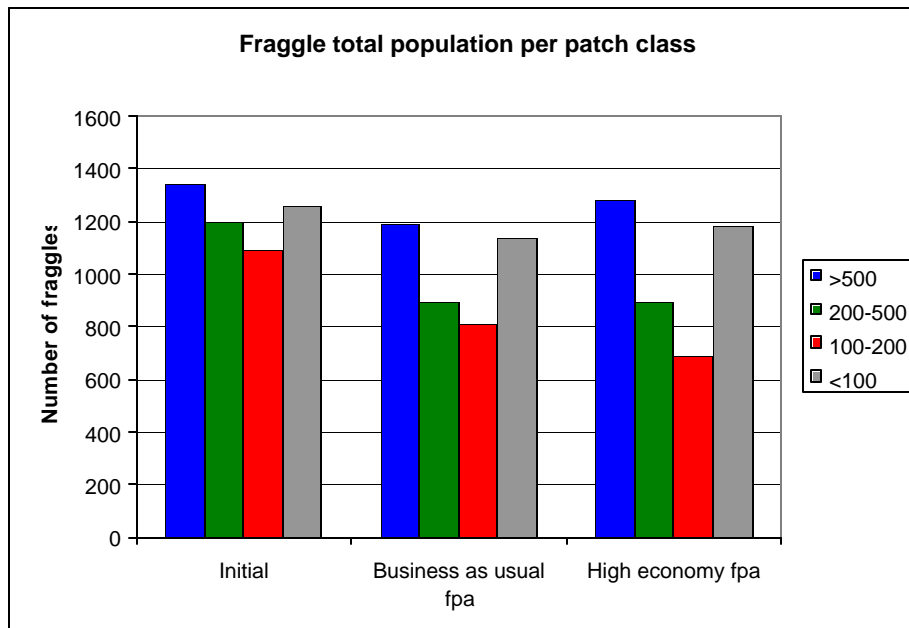
-  less than 100
-  100-200
-  200-500
-  more than 500

Figure 6: Total number of fraggles present per “gene pool” category



Conclusion

We developed, as part of the Land use Evolution and impact Assessment Model (LEAM), a general method to assess, based on land-use maps, the suitability of habitat patches, for a selected species and the degree of habitat connectedness, by considering the spatial arrangement of habitat cells. We showed that this approach, adaptable for various terrestrial species, provided more pertinent results than the pure consideration of total surface of habitat cell and could be potentially useful to provide indication on the impact of land-use change on habitat sensitive species. The results of this model could also serve as input for more specific dynamic population models to provide better estimation of the population dynamic variation triggered by land-uses change. Finally, we indicated the potential usefulness of the habitat map outputs in the developments of effective habitat corridors to increase habitat patches connectivity.

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