MODELING DISPERSAL FOR GRID LANDSCAPES: AN EXAMINATION OF THE ECOLOGICAL CONSEQUENCES OF FOREST FRAGMENTATION IN THE GEORGIA PIEDMONT

by

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(Under the Direction of Kathleen C. Parker and Marguerite Madden)

ABSTRACT

The forests of the Georgia Piedmont have undergone periods of deforestation and reforestation since the time of European Settlement. The removal of forests to make space for agricultural fields reduced forest landcover throughout the Georgia Piedmont until the early 20th century, when broad agricultural abandonment resulted in widespread reforestation. This trend of reforestation has reversed in recent decades due to the growth of the city of Atlanta. In addition to the loss of forest cover, significant fragmentation of forests occurred. In the counties surrounding Atlanta, initial forest fragmentation was replaced with decreases in the numbers of forest fragments due to the elimination of forest fragments from the landscape. The core counties in the Atlanta metro area have more fragments in a size class that is larger than the other metro counties and the core metro counties also have also experienced greater losses of the proportion of total forest cover in the largest size class than the other counties in the Atlanta metro area. These findings differentiate the core metro Atlanta counties from the other counties in the metro area and possibly foreshadow the forest trends for the non-core metro counties in coming decades.

The spatial and genetic structures of forests are functions of the processes of pollen and seed dispersal. Modeling how dispersal occurs in landscapes helps researchers understand the links between patterns and processes over space. The sum of curve points model is the best method to model dispersal for grid landscapes when conceptual integrity and mathematical simplicity are the evaluation criteria. The isotropic modeling of dispersal using the sum of curve points model develops null model of dispersal than can be altered to better represent the factors in landscapes that alter the dispersal of pollen and seeds from a directionally even distribution over space.

INDEX WORDS: Georgia Piedmont, Atlanta, forest, fragmentation, urban expansion, landscape genetics, dispersal, grid, landcover, modeling.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Forest fragmentation is known to have numerous negative ecological and genetic consequences for species associated with the forest fragments (Saunders et al. 1991, Fahrig and Merriam 1994, Ehrlich 1996). What is less well known is how the process of dispersal is impacted by forest fragmentation (Ellstrand 1992, Austerlitz et al. 2004, Sork and Smouse 2006). The fragmentation of forests is one of the consequences of modern urban expansion and is a concern for the conservation of biodiversity in temperate forests (McKinney 2002, Nowak and Walton 2005). The city of Atlanta, Georgia has experienced tremendous urban expansion in recent decades, and is projected to continue to expand through the first half of the 21st century (Lo and Yang 2002, Yang 2002, Hu 2007). Understanding the conservation implications of Atlanta's urban growth requires an examination of the trends of forest cover and forest fragmentation in Atlanta's physiographic region, the Georgia Piedmont. In turn, understanding the impacts that forest fragmentation of the region has on dispersal first necessitates the development of conceptual model of dispersal that can be applied to landscapes. This dissertation examines the modern trends of forest fragmentation in the Georgia Piedmont and examines the application of conceptual models of dispersal to landscapes.

Biogeography, as an integrative discipline that considers both the physical and human influences in landscapes, is uniquely positioned to bridge more narrowly focused disciplines. The recent emphasis on landscape dynamics by biogeographers corresponds temporally with the rise of landscape ecology (Cowell and Parker 2004). Landscape ecology has grown dramatically since the mid-1980's and is arguably the most visible discipline that deals explicitly with patterns and processes in landscapes (Forman and Godron 1986, Turner 2005). This focus has led landscape ecology to embrace geographic information systems (GIS) as important tools in landscape analysis (Turner 1989, Turner 2005). The development of spatial analysis techniques by landscape ecologists has led some to suggest that biogeographers need to be more active in landscape ecology (Kent 2007). In addition to being well versed in spatial analysis techniques, biogeographers can contribute a holistic approach to landscape ecology that examines how humans impact the patterns and processes observed in landscapes. Biogeographers can thus maintain an integrative role among disciplines as it is positioned to do for the new discipline of landscape genetics.

Landscape genetics is a discipline that combines the analysis of landscape patterns and processes with the population and individual relationships developed by population geneticists (Manel et al. 2003, Holderegger and Wagner 2008). The spatial nature of landscape genetics makes biogeographers natural partners in this new discipline (Storfer et al. 2007); however, the visibility and popularity of landscape ecology has led the discipline to be defined as a collaboration of landscape ecologists and population geneticists (Manel et al. 2003, Sork and Smouse 2006, Holderegger and Wagner 2006). Although the collaborations between landscape ecologists and population geneticists are beginning to appear in the literature, biogeographers have been involved in genetic studies for some time and are exploring ways to examine the spatial aspects of population genetics (e.g. Parker et al. 2001). It is important for biogeographers to establish themselves as valuable contributors to landscape genetics in order to develop a position for their interdisciplinary work within this emerging field. This involvement will help link landscape patterns with the underlying ecological and genetic processes responsible for those patterns.

Habitat and species conservation is a primary focus of studies of temperate forest fragmentation (Fahrig and Merriam 1994, Ehrlich 1996). Forest fragmentation explicitly refers to the spatial patterns of forests in landscapes, and thus, are of concern to both biogeographers and landscape ecologists. Although the spatial analysis of forest fragmentation is important for understanding the habitat patterns that exist in landscapes, a deeper examination of the causes of forest fragmentation and how the fragmentation of habitats impacts dispersal processes in the landscapes is necessary to understand the past and future trends of the forests. Biogeographers are uniquely equipped to explore these complexities due to their integrative objectives and skill in GIS.

STUDY OBJECTIVES

This dissertation first examines the broader trends of forest cover and forest fragmentation at the county scale for the Georgia Piedmont from 1974 to 2005, then focuses on the counties of metro Atlanta for a closer examination of how the sizes of forest fragments have changed at the county scale during the same time period. Through these studies, this dissertation provides insights to the future of the biodiversity and ecological health of a region that is experiencing significant urban expansion. The final study of this dissertation proposes three conceptual models of dispersal that can be applied to real landscapes to model the potential movement of pollen and seeds in fragmented landscapes. These models provide a spatially explicit way to examine dispersal in real landscapes and analyze the potential genetic isolation of forest fragments.

The first two studies, chapters 2 and 3, examine the history of forest cover, forest fragmentation, and forest edge trends over three time periods in the Georgia Piedmont from 1974 to 2005. Of specific concern is change in forest extent and its complex relationship to forest fragment geometry as urban sprawl around Atlanta has progressed over the last three decades. Chapter 2 examines the entire Georgia Piedmont at the county level to determine how the modern forest trends correspond to historical forest trends and inform possible future trends. Chapter 3 is an examination of forest fragmentation in the Atlanta metro area. This study looks at the counties most heavily impacted by the modern growth of the city of Atlanta to determine how suburbanization has impacted the forests of the Georgia Piedmont. The future trends of forest fragmentation and forest cover for the counties of the Atlanta metro area are discussed with regard to modern forest trends. Both of these studies note how examinations of forest fragmentation are linked to landscape genetics.

The third study, chapter 4, develops methodologies for modeling dispersal in a GIS. While chapters 2 and 3 deal empirically with fragmentation in the Georgia Piedmont and qualitatively discusses implications for dispersal, chapter 4 examines dispersal modeling and its application to fragmented landscapes. Chapter 4 links with the first two studies through the processes of fragmentation and dispersal associated with temperate forest tree species. Both pollen and seeds move through landscapes by the process of dispersal, which is of particular importance in fragmented landscapes for maintaining the genetic structure of populations in landscapes. This study examines how the process of dispersal has been studied in the literature of temperate forest tree species and how the concept of dispersal can be modeled in a GIS to understand the relationships between patterns and processes in an ecological context. It develops three conceptual models of dispersal that can be applied to real landscapes. Models are compared in terms of their assumptions, strengths, and limitations; and their application to real-world situations is discussed. Furthermore, a framework is built upon which landscape geneticists can examine how landscape patterns impact observed genetic structures.

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CHAPTER 2

TRENDS AND CONSEQUENCES OF MODERN FOREST COVER AND FRAGMENTATION CHANGES IN THE GEORGIA PIEDMONT[1]

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INTRODUCTION

The forests of the southeastern United States experienced extensive cutting and agricultural expansion from the time of European settlement up to the early 20th century (Bond and Spillers 1935, Hartman and Wooten 1935, Brender 1952, Brender 1974, Sharitz et al. 1992). Although the activities of Native Americans, especially the use of fire (Van Lear and Waldrop 1989), likely modified the landcover of the southeastern United States from the patterns and compositions produced by natural forces prior to European settlement, the modern landscapes of this region are predominantly a reflection of the activities of the settlers (Brender 1974, Johnson and Sharpe 1976, Sharitz et al. 1992, Cowell 1998). Subsistence agriculture gave way to cash crops through the 19th century until land depletion and economic forces spurred land abandonment in the late 1800's and early 1900's (Brender 1974, Johnson and Sharpe 1976). The landcover of the Georgia Piedmont through the middle of the 20th century was largely shaped by the reforestation that occurred since the 1930's subsequent to cropland abandonment (Brender 1974, Johnson and Sharpe 1976). By the 1970's and early 1980's 60-70% of the Georgia Piedmont landcover had returned to forest (Brender 1974, Turner and Ruscher 1988).

The reforestation of the Piedmont increased the sizes of forest fragments and increased forest connectivity (Turner and Ruscher 1988). The trends of increasing forest landcover and decreasing fragmentation in the Georgia Piedmont were countered in the 1990's by studies of the Southeastern Piedmont ecoregion (Loveland et al. 2002, Griffith et al. 2003, Brown et al. 2005), and the Atlanta metro area (Yang and Lo 2002, Lo and Yang 2002, Madden et al. 2009), which found increasing urbanization as the cause of decreasing forest cover and increasing forest fragmentation. Understanding the modern trends of forest cover and fragmentation in the Georgia Piedmont and the impacts of expanding urban areas on forests is important for conserving the biological integrity of the forest ecosystem (Sharitz et al. 1992, McKinney 2006, Burton and Samuelson 2008). This study examines changes in forest cover, fragmentation, and fragment edges for the Georgia Piedmont for three different time periods from 1974 to 2005 at both the regional and county scale. Understanding the landcover trends associated with the urbanizing landscapes in the Georgia Piedmont is fundamental for examining the associations between ecological processes and genetic patterns.

Landscape genetics is the term currently applied to research that examines spatiotemporal processes that affect the genetic composition of populations (Manel et al. 2003, Storfer et al. 2007, Holderegger and Wagner 2008). There is increased appreciation for the ways in which landscape fragmentation influences gene exchange (Sork et al. 1999, Manel et al. 2003, Sork and Smouse 2006). Fragmented landscapes are usually conceptualized through island biogeography theory (MacArthur and Wilson 1967), which considers each fragment to be a unit of habitat that individuals of a particular species exist within and move between. Habitat fragmentation heavily impacts gene movement by altering the movement of individuals or changing how ecological processes function in a landscape. For plant species in the Georgia Piedmont, changes in pollen and seed dispersal can impact the genetic structure of forest fragments. Defining the landscape composition, configuration and matrix is a fundamental prerequisite for examining how landscape context affects gene movement (Storfer et al. 2007). Only by understanding the extent of species habitat loss and subsequent fragmentation can the impacts on species gene movement be examined and predicted. The examination of forest fragmentation trends in the Georgia Piedmont in this study will shed light on possible ecological and genetic consequences of changes in landcover for the future of this urbanizing region.

Urbanization has been implicated in the loss of forest habitat and increasing forest fragmentation in the American Southeast in recent years (Wear 2002, Griffith et al. 2003, Brown et al. 2005, Radeloff et al. 2005, Zhang et al. 2008). Urbanization is an ecological concern due to the negative impacts that it can have on biological diversity and environmental quality (Sharitz et al. 1992, Czech et al. 2000, McKinney 2002) and the potential for induced biotic homogenization (McKinney and Lockwood 1999, McKinney 2006). Conservation strategies for temperate forests have suggested that reducing habitat loss, habitat fragmentation, and associated edge effects may be effective approaches to limiting negative anthropogenic impacts (see: Soule 1991, Ehrlich 1996, Harper et al. 2005). While the temperate forests of the Georgia Piedmont should be considered as targets for conservation because they are habitats for numerous species, the overstory trees that make up the forest have their own individual responses to fragmentation that often differ from those of other temperate forest species, especially in regards to genetics.

Habitat fragments are areas of a type of habitat that are derived from a larger continuous area of habitat. In order for an area of habitat to be fragmented, separations must develop within the habitat area. These separations are most commonly spatial separations formed by the removal of areas of habitat. The existence of species within the habitat fragments is a function of the ability of individuals to move between the fragments and the number of individuals that can exist in each fragment (Templeton et al.

1990, Saunders et al. 1991, Fahrig and Merriam 1994, Ehrlich 1996, Young et al. 2006, Harper et al. 2005). For plant species, the genetic effects of habitat fragmentation are functions of longevity, generation time, gene dispersal though pollen and seeds, reproductive systems, and interactions with dispersal agents (Loveless and Hamrick 1984, Ellstrand and Elam 1993, Young et al. 1996, Ghazoul 2005), though gene dispersal is considered to be a major factor determining the distribution of genetic variation among plant populations (Loveless and Hamrick 1984, Hamrick et al. 1989, Fore et al. 1992, Ghazoul 2005). While habitat fragmentation is generally considered detrimental to gene flow and maintaining the genetic diversity of species, overstory trees may be buffered from the negative consequences by high pollen movement and longevity (Ellstrand 1992, Hamrick 2004, Ghazoul 2005); they may even experience increased gene flow with fragmentation (Fore et al. 1992, Young and Merriam 1994). Approaches to understanding these complex impacts of fragmentation on the population and genetic structures of species within a landscape are currently being developed through an integration of landscape ecology and population genetics (Sork et al. 1999, Manel et al. 2003, Sork and Smouse 2006). This study highlights geography and GIS as valuable contributors to discussions concerning the links between fragmentation and genetic structure.

METHODS

The forest cover of the Georgia Piedmont was determined from the Georgia Land Use Trends (GLUT) Land Cover layers for 1974, 1985, 1991, 2001, and 2005. These layers were produced by the Natural Resources Spatial Analysis Laboratory (NARSAL), currently at the College of Agriculture and Environmental Science within The University of Georgia (http://narsal.uga.edu/).

The GLUT land cover layers are derived from Landsat imagery at 60-meter resolution for the 1974 and 1985 layers, and 30-meter resolution for the 1991, 2001, and 2005 layers. The land cover was classified into 13 types of cover (Table 2.1). Ancillary data consisting of railroads, utility swaths, and airports assisted the land cover classification. Urban and suburban classes were assessed by a regression tree modeling method that classified impervious surfaces. Random patches of land cover classes were stratified by ecoregion and land cover class to conduct the accuracy assessment. Comparisons of land cover classifications with county-wide aerial photography mosaics of approximately 3,000 points per layer were performed to assess the classification accuracy. The overall accuracies listed for all of the data layers are between 80-90%.

The Georgia Piedmont was selected from the GLUT land cover layers by extracting the 57 counties (Figure 2.1) associated with the Piedmont as a selection mask using ESRI's ARCMAP version 9.1 (2004). The deciduous forest, evergreen forest, mixed forest, and forested wetlands classifications were reclassified as forest, and all other land covers were reclassified as other (Table 2.1). Each of the 57 Georgia Piedmont counties was clipped from the raster Piedmont forest layer. The forest cover, fragmentation, and edge lengths for each county were determined using the landscape metric program FRAGSTATS, Version 3 (McGarigal et al 2002). The FRAGSTATS analysis was performed at the class level using the Arc GRID format for the county raster layers and the four cell neighbor rule, which considers horizontally and vertically adjacent cells but not diagonally associated cells. All outputs were organized in

Microsoft Excel (2003) spreadsheets, and Pearson product-moment correlation coefficients between county-level fragmentation and forest cover across the 57 counties were calculated with Microsoft Excel functions for each of the five years studied. All maps were created using the ArcMap software (ESRI 1999-2009).

RESULTS

Although forest cover declined in conjunction with increases in forest fragmentation and forest edge over the past thirty years in many counties of the Georgia Piedmont, other counties showed a more complex relationship among these three variables. The Georgia Piedmont declined in forest cover overall and increased in the number of forest fragments for every year examined, while the amount of forest edge increased from 1974 to 1985 but declined from 1991 to 2005 (Table 2.2). The period from 1974 to 1985 seemingly experienced a loss of forest area similar to the period from 1991 to 2001, but the earlier period gained far fewer fragments (Table 2.3). Because the data layers from 1974 and 1985 have a different resolution than 1991, 2001 and 2005, it is prudent to examine the trends of forestation and fragmentation between time steps of the same resolution and not directly compare the 1974 to 1985 period with the others. While 1974 to 1985 showed an increase in the amount of forest edge, 1991 to 2001 experienced a significant decline in the total amount of forest edge, despite showing a loss in forest area and an increase in the number of fragments, running contrary to the standard associations between forest cover, fragmentation, and forest edge (Table 2.3). The period from 2001 to 2005 showed the same trends as 1991 to 2001; declining forest area and edge with increase fragmentation, only the number of fragments created is dwarfed by the 1991 to 2001 time period (Table 2.3). This trend holds true even as fragmentation is examined on an annual basis. The number of fragments created per year was significantly less from 2001 to 2005 than from 1991 to 2001 (Table 2.4). The decline in fragment size was also less per year in 2001 to 2005 and the decrease in forest edge per fragment per year was greater when compared to 1991 to 2001 (Table 2.4).

In every time period, most counties experienced a loss of forest cover and an increase in the number of forest fragments (Table 2.5). Only 5 out of 57 counties have a net gain in forest cover for the three time periods 1974 to 1985, 1991 to 2001, and 2001 to 2005 (Table 2.5). Despite deforestation and increasing fragmentation predominating throughout all three time periods, the correlation between the two variables becomes weaker in the more recent time periods. The Pearson’s correlation coefficient relating fragmentation to changes in forest cover declined from -0.79 in the 1974 to 1985 time period, to -0.69 for 1991 and 2001, to -0.37 for 2001 and 2005; all significant at $p<0.01$ (Table 2.6). This weakening negative correlation clearly shows that forest cover and forest fragmentation can have complex relationships.

The spatial trends of forest cover in the Georgia Piedmont from 1974 to 1985 showed the counties surrounding Atlanta experiencing the greatest loss (Figure 2.2a). This trend continued from 1991 to 2001 (Figure 2.2b) and expanded from 2001 to 2005 (Figure 2.2c) to include more counties surrounding Atlanta. The cumulative effects of the three time periods showed Atlanta as the center of the greatest loss of forest cover in the Georgia Piedmont, and 4 out of the 5 counties that gained forest cover clustered in the central southern part of the region (Figure 2.2d).

Fragmentation in the Georgia Piedmont did not occur evenly throughout the region from 1974 to 1985. The greatest fragmentation of the Georgia Piedmont from 1974 to 1985 was in the counties around Atlanta, while the rest of the region experienced mild positive fragmentation or negative fragmentation (Figure 2.3a). Negative fragmentation in this study is the reduction of the number of fragments in counties. This can be caused by either the elimination of fragments or the connecting of fragments into larger habitat areas. The counties around Atlanta continued to experience strong fragmentation between 1991 and 2001 and most of the rest of the Georgia Piedmont experienced mild to moderate fragmentation (Figure 2.3b). The trend reversed from 2001 to 2005 as the counties around Atlanta showed strong declines in the number of forest fragments as the rest of the Georgia Piedmont shows mild positive or negative fragmentation (Figure 2.3c). The net results of the three periods are increased fragmentation in the counties around and to the north of Atlanta, decreased fragmentation in some counties to the south and the southwest of Atlanta, and mixed positive and negative fragmentation in the eastern counties of the Georgia Piedmont (Figure 2.3d).

DISCUSSION

The trends of increasing forest cover and decreasing fragmentation in the Georgia Piedmont prior to the 1980’s (Brender 1974, Turner and Ruscher 1988) have reversed dramatically, especially for the counties surrounding Atlanta. Forest cover has decreased for 52 out of 57 of the counties in the Georgia Piedmont from 1974 to 2005 and forest fragmentation skyrocketed from 1991 to 2001. The tremendous amount of forest fragmentation is due to the removal of forest by low-density housing developments in the counties surrounding Atlanta. The rapid growth of the city of Atlanta from 1991 to 2001 caused the extensive loss of forest cover and increased the number of forest fragments in the region. Urbanization of the counties surrounding Atlanta (Yang and Lo 2002, Lo and Yang 2002) has become a dominant force shaping the forests of the Georgia Piedmont, and its effects are expanding to more counties as the Atlanta Metropolitan Area develops.

While the trend of declining forest cover is likely to continue in the counties around Atlanta, the number of forest fragments had started to decline in the early 2000's, in sharp contrast to the strong fragmentation that occurred from 1991 to 2001. The initial deforestation trend of the counties is strongly related to the creation of forest fragments. As the Atlanta area has continued to develop, the small forest fragments that were created from the urbanization of the region in the 1990's are likely being removed, thus lowering the number of forest fragments relative to the total area of forest and reducing the amount of forest edge per fragment, the rate of decline of fragment size per year, and the correlation between the change in forest cover and the number of fragments. While habitat fragmentation is broadly considered to be detrimental to the survival of species, the reduction in the number of forest fragments around Atlanta is not due to the reconnection of habitat fragments, but rather the elimination of fragments. Studies that look broadly at the number of habitat fragments need to keep in mind the trends of the total amount of habitat in an area in addition to the number of fragments in order to distinguish the loss of fragments from the uniting of fragments. Continued development in areas on the edge of the Atlanta Metropolitan Area will likely cause declines in forest cover and initial increases in forest fragmentation followed by decreases in the number of forest fragments.

The predicted genetic consequences for plant species within increasingly fragmented landscapes include increased genetic drift, more inbreeding, and reduced interpopulation gene flow (Ellstrand and Elam 1993, Young et al. 1996). These impacts have been of increasing importance in the Georgia Piedmont, especially around Atlanta, through the past thirty years. The specific impacts on forest fragments, particularly in urbanizing areas, can be complicated by the types of species being considered, the metapopulation structure of the fragments, and the history of forest cover in the area. Some temperate forest tree species might experience increased gene flow due to fragmentation (Fore et al. 1992, Young and Merriam 1994), while other species within the fragments become more isolated. Changes in metapopulation structure may produce complex inter-fragment gene flow relationships that are difficult to evaluate (Harrison and Hastings 1996, Sork et al. 1999).

The history of forest fragmentation in an area is of tremendous importance because it structures the genetic landscape that is observed in modern times. Around Atlanta, forests are more likely to exist on steeper slopes that are less favorable for housing development (Lo and Yang 2002). These areas are also less likely to have been removed in the past to clear land for agricultural purposes. This raises the potential for the current deforestation due to urbanization around Atlanta to be removing the progeny of the individuals on the steeper slopes that repopulated the area since the agricultural abandonment of the late 1800's and early 1900's. Further analysis of the forest cover and fragmentation of the Atlanta Metro Region is required to understand how the genetic landscape of the region is changing due to the modern trend of increasing urbanization.

Numerous negative ecological (Sharitz et al. 1992, Czech et al. 2000, McKinney 2002, McKinney 2006) and genetic (Templeton et al. 1990, Saunders et al. 1991, Fahrig and Merriam 1994, Ehrlich 1996, Young et al. 2006, Harper et al. 2005) impacts can be expected in the Georgia Piedmont due to the recent trends of deforestation and fragmentation. The ways in which the overstory trees of the region are able to withstand the consequences of fragmentation are not well known. More studies into the extent of physical separation between fragments that overstory trees can bridge through pollen or seed movement, or can withstand through longevity, are needed. Integrated approaches are required to examine how patterns of fragmentation impact ecological processes and subsequently structure patterns of genetic diversity in species. Chapter 4 takes a step in this direction by developing and comparing conceptual models of pollen and seed dispersal through real landscapes.

The modern trends of deforestation and forest fragmentation in the Georgia Piedmont, as well as the complex relationship that Atlanta's urban expansion has with surrounding forests, serve as both a regional case study of the broader land-use trends in the continental United States (Riitters et al. 2002, Brown et al. 2005) and a predictor of future forest cover and fragmentation trends in areas of urban expansion (Nowak and Walton 2005). The anticipated expansion of Atlanta in the Georgia Piedmont (Lo and Yang 2002) will likely extend the complex trends of forest fragmentation associated with urban expansion into counties farther from Atlanta's core. The forests of the Georgia Piedmont associated with the city of Atlanta are thus of both regional and national interest, particularly for areas with increasingly fragmented forests.

This study highlights the dominant trend of deforestation and the complex relationship between urbanization and forest fragmentation in the Georgia Piedmont. It identifies the counties surrounding Atlanta as the primary areas of changes in forest cover and fragmentation. These conclusions suggest that more regional planning and forest management are required in the Georgia Piedmont to mitigate the ecological consequences of urban expansion. Future work in the region is needed to examine the potential for species existing within urbanizing landscapes to withstand the detrimental effects of spatial disassociation that occurs with habitat fragmentation.

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Table 2.1. GLUT land cover classifications and reclassification for this study.

Forest Categories	**Other Categories**
Deciduous forest	Beaches/dunes/mud
Evergreen forest	Quarries/strip mines/rock outcrops
Mixed forest	Open water
Forested wetland (salt water)	Low intensity urban
Forested wetland (freshwater)	High intensity urban
	Clearcut/sparse
	Row crops/pasture
	Non-forest wetland

Table 2.2. Georgia Piedmont forest areas, number of forest fragments, and total forest edges.

Year	Area forest (ha)	Number of fragments	Total edge (km)
1974	3210737	12514	115480
1985	3021254	15570	121233
1991	2929067	196219	325436
2001	2753370	240422	315687
2005	2661904	243800	312359

Table 2.3. Changes in Georgia Piedmont forest areas, number of forest fragments, and total forest edge.

Years	Forest area change (ha)	Fragment number change	Total edge change (km)
1974-1985	-189483	3056	5753
1991-2001	-175697	44203	-9749
2001-2005	-91466	3378	-3328

Table 2.4. Average yearly changes in Georgia Piedmont forest areas, number of forest fragments, average fragment sizes, total forest edge, and total forest edge per fragment.

Years	Forest area per year change (ha)	Fragment number per year change	Average fragment size per year change (ha)	Total Edge per year change (km)	Total Edge per fragment per year change (m)
1974-1985	-17226	278	-63	523	1883
1991-2001	-17570	4420	-3	-975	-221
2001-2005	-22867	845	-0.5	-832	-985

Table 2.5. Changes in the percent of county forest cover, the cumulative changes in county forest cover, and number of fragments in the Georgia Piedmont. Positive values in bold.

County	Forest cover change 1974-1985	Forest cover change 1991-2001	Forest cover change 2001-2005	Forest cover change 1974-2005	Fragment change 1974-1985	Fragment change 1991-2001	Fragment change 2001-2005
Baldwin	-3.59	-4.59	-1.67	-9.85	**18**	**833**	**8**
Banks	-0.58	-10.02	**1.40**	-9.20	-6	**946**	-193
Barrow	-3.60	-7.02	**0.19**	-10.44	**61**	**710**	**13**
Bibb	-0.65	-8.77	-3.84	-13.26	**6**	**709**	-780
Butts	**0.47**	**2.15**	**1.72**	**4.34**	**5**	-19	-221
Carroll	-3.97	-6.21	-2.33	-12.51	**131**	**2183**	**404**
Cherokee	-4.36	-4.64	-7.93	-16.92	**79**	**2443**	**881**
Clarke	-4.63	-7.98	-2.51	-15.12	-6	**328**	-243
Clayton	-6.45	-9.66	-7.51	-23.62	**49**	**557**	**18**
Cobb	-12.28	-14.28	-7.51	-34.07	**288**	**3689**	-1262
Columbia	**1.68**	-8.15	-1.07	-7.53	-37	**973**	**194**
Coweta	-3.81	-3.21	-5.14	-12.16	**84**	**1030**	**835**
DeKalb	-13.16	-10.75	-4.71	-28.62	**111**	**1342**	-399
Douglas	-0.94	-8.83	-6.96	-16.74	**9**	**1470**	**441**
Elbert	-10.64	**1.72**	**0.87**	-8.05	**120**	**135**	**23**
Fayette	-1.49	-5.49	-5.71	-12.68	**31**	**1685**	**315**
Forsyth	-4.53	-6.39	-8.81	-19.74	**47**	**1510**	**619**
Franklin	-2.51	-1.66	**0.30**	-3.87	**66**	**594**	**33**
Fulton	-9.60	-10.05	-6.94	-26.60	**212**	**1764**	-38
Green	-5.34	-4.11	**2.41**	-7.04	**15**	**859**	-154
Gwinnett	-13.53	-14.76	-7.50	-35.80	**415**	**3677**	-741

Hall	-2.60	-9.20	-2.88	-14.68	**58**	**2242**	**231**
Hancock	-4.07	-1.40	**1.63**	-3.85	**71**	**154**	-44
Haralson	-4.20	-6.17	-1.44	-11.81	**53**	**957**	**141**
Harris	-5.35	-3.69	-2.14	-11.18	**107**	**994**	**542**
Hart	-6.44	**1.83**	**0.76**	-3.85	**59**	**376**	-116
Heard	-8.94	-4.78	-3.21	-16.93	**90**	**463**	**535**
Henry	-0.78	-6.43	-8.17	-15.38	**1**	**1887**	**934**
Jackson	**1.19**	-7.12	-0.63	-6.56	-9	**1246**	**92**
Jasper	-1.26	-2.69	**4.29**	**0.34**	**8**	**750**	-538
Jones	**0.56**	-3.46	**0.80**	-2.10	**22**	**765**	-152
Lamar	**2.04**	**3.33**	-0.61	**4.76**	**4**	-303	**45**
Lincoln	-3.23	-4.76	**1.38**	-6.61	**31**	**405**	**54**
Madison	-5.47	-0.52	-0.33	-6.32	**71**	**373**	**95**
McDuffie	**0.53**	-4.26	-0.01	-3.75	-16	**642**	-94
Meriwether	-7.66	**0.28**	-3.09	-10.47	**65**	**292**	**478**
Monroe	**1.33**	-2.63	**1.84**	**0.55**	-32	**87**	-73
Morgan	-5.07	-1.22	**2.08**	-4.21	**57**	**192**	-265
Muscogee	-13.38	-5.87	-4.27	-23.51	**79**	-2242	**262**
Newton	**0.48**	-5.09	-1.30	-5.90	-13	**840**	**155**
Oconee	**1.18**	-4.51	**0.01**	-3.32	**23**	**604**	**44**
Oglethorpe	-6.44	**2.07**	**2.53**	-1.85	**84**	-141	-123
Paulding	-3.86	-1.65	-8.20	-13.71	**108**	**1132**	**1165**
Pickens	-1.24	**0.42**	-7.52	-8.35	**1**	**444**	**370**
Pike	-0.20	**2.43**	-4.38	-2.15	-4	**71**	**247**

Polk	**7.78**	**0.38**	**0.24**	**8.41**	-66	**791**	-565
Putnam	-7.91	-4.81	**2.41**	-10.31	**110**	**1098**	-340
Rockdale	-2.90	-4.47	-7.65	-15.02	-2	**788**	**41**
Spalding	-2.37	**2.70**	-4.23	-3.90	**22**	-164	-14
Stephens	-0.71	-4.48	**1.77**	-3.41	**8**	**871**	**5**
Talbot	-7.67	**3.59**	-0.70	-4.78	**79**	-613	**139**
Taliaferro	-3.12	-1.51	**0.08**	-4.56	**16**	-41	**106**
Troup	-10.42	-4.95	-3.06	-18.44	**199**	**1089**	**405**
Upson	-4.79	**8.08**	-4.64	-1.35	**47**	-795	**176**
Walton	-0.91	-4.40	**1.99**	-3.32	-3	**1186**	-186
Warren	**1.16**	-0.78	-0.40	-0.01	-3	**296**	-69
Wilkes	-2.63	**0.39**	**1.13**	-1.11	**33**	**49**	-58

Table 2.6. Pearson's correlation coefficient r between change in percent of county forest cover and number of county forest fragments across all 57 counties of the Georgia Piedmont.

Years	Pearson's r	p-value
1974-1985	-0.79	p<0.01
1991-2001	-0.69	p<0.01
2001-2005	-0.37	p<0.01

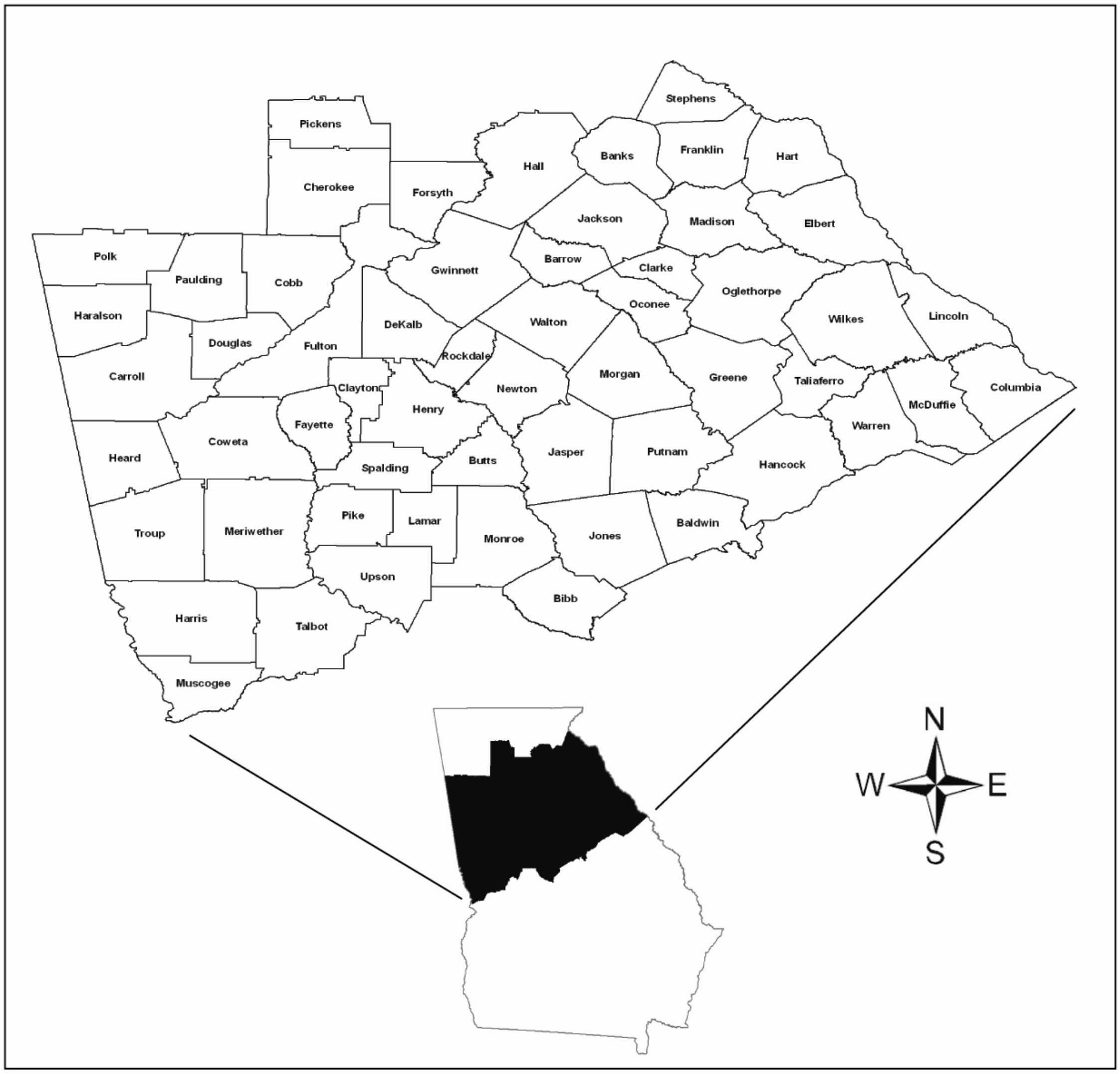

Figure 2.1. Counties of the Georgia Piedmont.

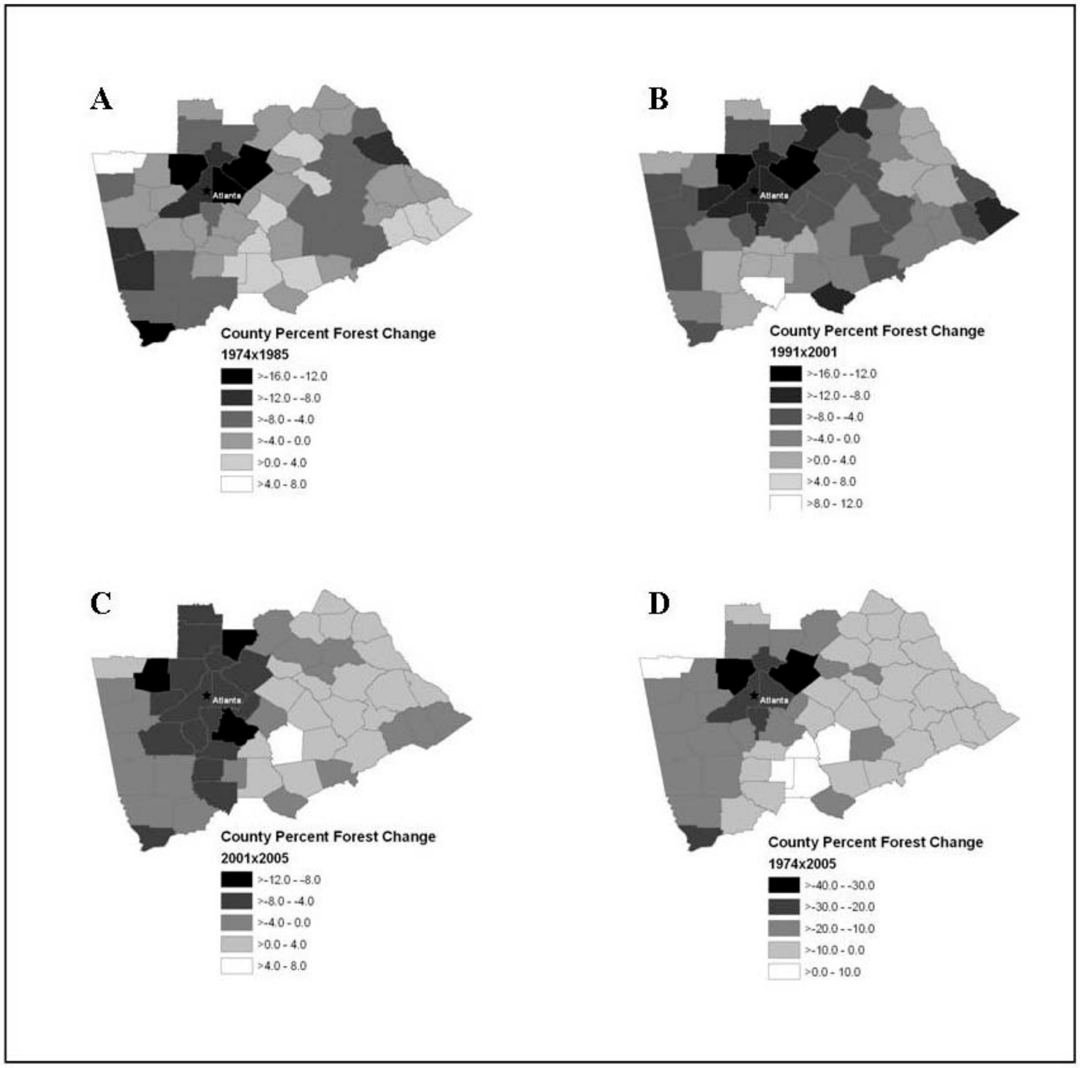

Figure 2.2. Percent change of total county area covered with forest from 1974 to 1985 (a), 1991 to 2001 (b), 2001 to 2005 (c), and 1974 to 2005 (d).

Figure 2.3. Change in the number of forest fragments in each county for 1974 to 1985 (a), 1991 to 2001 (b), 2001 to 2005 (c), and 1991 to 2005 (d).

CHAPTER 3

THE IMPACTS OF ATLANTA'S URBAN SPRAWL ON FOREST COVER AND FRAGMENTATION[1]

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[1] Miller, M.D. 2009. The impacts of Atlanta's urban sprawl on forest cover and fragmentation. To be submitted to *Southeastern Geographer*.

INTRODUCTION

Urban sprawl is a term used to describe low density development around urban areas, often necessitating significant automobile use by individuals for transportation. The lack of centralized planning is usually blamed for allowing urban sprawl to occur around cities, but the demand of individuals to live in settings that seem closer to nature drives the development of sprawl landscapes (Brown et al. 1997, Kaplan and Austin 2004). Unfortunately, the desire to be closer to nature can cause the destruction and fragmentation of natural environments (Soule 1991, Theobald et al. 1997, McKinney 2002, McKinney 2006). The relative tranquility of low density housing developments among the fragments of formerly cohesive forests comes at ever-farther distances from the urban areas where the employment opportunities that finance the suburban American Dream exist. Until the negative consequences of urban sprawl, both environmental and social, exceed the perceived benefits of existing on the periphery of urban areas, the expansion of urban sprawl is inevitable. This study examines the impacts that urban sprawl has had on forest area and fragmentation around the American poster-child of urban sprawl, Atlanta, Georgia. Understanding the impacts of urban sprawl on the forests surrounding large metropolitan areas like Atlanta enables the prediction of future forest area and fragmentation trends, including the genetic and ecological consequences of human impacts on the future forest patterns.

In the first half of the twenty-first century, the United States is projected to continue the trend of significant expansion of urban areas at the expense of contiguous forestland that occurred at the end of the twentieth century (Brown et al. 2005, Nowak and Walton 2005, Zhang et al. 2008). Urbanization of the matrix between the forest fragments (Jules and Shahani 2003) further complicates the already difficult conservation of fragmented ecosystems (Saunders et al 1991, Fahrig and Merriam 1994, Ehrlich 1996). This scenario is increasingly prevalent around Atlanta, Georgia where the metro area is expected to continue its rapid growth through at least 2030 (Nelson 1999, Rao 2007). This growth will require a lot of land for new housing development. The land surrounding Atlanta has experienced significant reforestation since the extensive farm abandonment in the Georgia Piedmont in the first few decades of the twentieth century (Brender 1974, Johnson and Sharpe 1976, Turner and Ruscher 1988) and it is these new forests that will be removed and fragmented to make space for the housing developments that support the growing metro Atlanta area population (MacDonald and Rudel 2005; see chapter 2).

The negative ecological consequences of habitat fragmentation include decreased habitat area, increased physical separation of species, and degraded habitat quality (Fahrig and Merriam 1994, Ehrlich 1996). As urban areas expand, they occupy space that was previously habitat for a range of species. The impacts that urban expansion has on ecosystems suggest that conservation efforts and land-use planning need to be required for urban and urbanizing area (Soule 1991, Savard 2000, McKinney 2002). The rapid modern expansion of the city of Atlanta highlights the forests associated with the surrounding urbanizing counties as being at risk for considerable ecological damage.

The fragmentation of forests can have serious genetic consequences for the plant species that constitute the bulk of the biomass and biodiversity of forests (Templeton 1990, Ledig 1992, Young et al. 1996). The spaces separating forest fragments may constitute barriers to gene movement within the landscape and may result in the loss of genetic diversity or even the local extinction of species (Ellstrand and Elam 1993, Young et al. 1996, Koenig and Ashley 2003). Even though forest fragmentation has been shown to have many negative ecological and genetic impacts, some species, such as the larger overstory tree species, may be able to withstand temporary fragmentation (Hamrick 2004, Ghazoul 2005), or even experience increased gene flow (Fore et al. 1992, Young and Merriam 1994). More work is needed to address how forest fragmentation affects gene movement in landscapes and what it means for the connectivity of species (Sork et al. 1999, Sork and Smouse 2006).

The trends of reforestation and increasing forest connectivity in the Georgia Piedmont that occurred in the mid 20th century (Brender 1974, Johnson and Sharpe 1976, Turner and Ruscher 1988) reversed at the end of the 20th century, particularly in the counties surrounding the city of Atlanta (Yang 2002, Yang and Lo 2002, Lo and Yang 2002). Atlanta's population growth since the 1960's accelerated at the end of the 20th century and caused the rapid suburbanization of counties surrounding Atlanta. The expansion of suburban developments around Atlanta in the 1990's increased forest fragmentation and decreased the forest cover of the region (Yang 2002, Yang and Lo 2002, Lo and Yang 2002; see chapter 2). Lo and Yang predicted that as Atlanta continues to grow in population and expand in area, more forest fragmentation and loss of forest cover will occur (Yang and Lo 2002, Lo and Yang 2002). The spatially explicit mapping of Atlanta's expansion at the expense of forests and other categories of landcover has been examined using both cellular automata and logistic regression (Lo and Yang 2002, Hu and Lo 2007). While the specific locations of future urban development around Atlanta vary based on the predicted growth patterns of the region and demographic, econometric, and biophysical variables, the trends of deforestation and increased forest fragmentation are consistently predicted for the region.

This study expands on chapter 2 and examines more closely changes in forest cover and forest fragmentation in the metro counties surrounding Atlanta to determine how the process of urban expansion impacts the number and sizes of forest fragments. Specifically, the number and area of forest fragments in each country are computed from land cover maps for five different years between 1974 and 2005; from these statistics, changes in forest classification are calculated for three different time spans within this broader period to quantify landscape change. These trends will help inform the futures of forests in metro Atlanta counties in terms of gene movement and other ecological processes.

METHODS

The majority of the city of Atlanta lies in Fulton county, with a small portion within Dekalb county. The recent extensive growth of Atlanta (Figure 3.1) has led to a dispersed settlement of the region that requires the inclusion of numerous counties surrounding Atlanta in studies of the impacts of urban sprawl. The Atlanta Metro Area is defined in this study as the thirteen counties used by C.P. Lo, Xiaojun Yang, and Zhiyong Hu in their studies of Atlanta land-use, land-cover changes and urban growth (Yang 2002, Yang and Lo 2002, Lo and Yang 2002, Hu and Lo 2007) (Figure 3.2). These studies include the counties within the planning area of the Atlanta Regional Commission (ARC) and Coweta, Forsyth, and Pauling counties. Together, these counties comprise the jurisdiction of the Georgia Regional Transportation Authority (GRTA).

The landcover layers used for this study are the Georgia Land Use Trends (GLUT) data layers, produced by the Natural Resources Spatial Analysis Laboratory (NARSAL) (http://narsal.uga.edu/) and available from the Georgia GIS Clearinghouse (http://data.georgiaspatial.org/). These layers are derived from Landsat imagery and classified using a classification and decision tree method that includes boosting and cross-validation procedures that incorporate road, elevation, hydrology, and wetland data into the pixel classification process. The 1974 and 1985 layers have a spatial resolution of 60-meter pixels and the 1991, 2001, and 2005 layers have 30-meter resolution. The thirteen landcover classes were reclassified into "forest" or "other" classes, with deciduous forest, evergreen forest, mixed forest, and forested wetland classifications becoming "forest". The thirteen counties of the Atlanta Metro Region were isolated by selecting pixels based on county boundaries.

The forest/other data layers were input to ArcMAP 9.2 (ESRI 1999-2009), to determine the number and area of forest fragments in each county for each year. ArcMAP's raster calculator was used to determine the pixel changes in forest classification for the time steps of 1974 to 1985, 1991 to 2001, and 2001 to 2005. Forest area and fragmentation trends between 1985 and 1991 are not shown due to the difference in pixel resolution and potential conflicts in pixel classification.

RESULTS

The metro Atlanta counties experienced heavy deforestation and fragmentation from 1974 to 2005 (Figure 3.3), which is in line with, albeit at an accelerated pace, the other counties in the Georgia Piedmont (see Chapter 2). Forest cover for every metro

Atlanta county declined for all of the time periods examined: 1974 to 1985, 1991 to 2001, and 2001 to 2005. Forest fragmentation increased for every county during the time periods 1974 to 1985 and 1991 to 2001, except for Rockdale from 1974 to 1985 which experienced a decrease of 2 fragments. This trend of fragmentation continued for the peripheral metro counties from 2001 to 2005; but the core Atlanta counties of Cobb, Gwinnett, Fulton, and Dekalb experienced decreases in the number of forest fragments within their boundaries, despite declining forest areas (Figure 3.3).

Cobb, Gwinnett, Fulton, and Dekalb counties also distinguish themselves from the other metro Atlanta counties in the percentages of forest fragments within different size classes for all of the years examined (Figure 3.4). These counties showed an increased percentage of fragments in the second smallest size class, 0.36-1.44 hectares, whereas other metro counties generally showed a peak in the <0.36 hectare class and declined until the large class consisting of all fragments >29.16 hectares. This trend was most prominent for the years 1991, 2001, and 2005. These same years showed the core metro counties Cobb, Gwinnett, Fulton, and Dekalb losing fragments in the small size classes above 0.36 hectares and an increase in the smallest fragment size class (Figure 3.4). Their fragment size distribution curves have are to the non-core metro Atlanta counties, with the smallest fragment size class containing the greatest number of fragments and a decline in the number of fragments within each larger class up to the greater than 29.16 hectares class.

In all counties, the >29.16-hectare fragment class contained the majority of forest area within the county (Figure 3.5). Most of the peripheral counties showed only minor decreases in the percentage of forest area in the largest size class from 1974 to 2005. In contrast, the core metro counties of Cobb, Gwinnett, Fulton, and Dekalb, along with Clayton county, showed steep declines in the percentage of forest area in the largest class from 1991 to 2005 (Figure 3.5). All other size classes seemed to benefit from losses in the largest classes, with the second smallest size class (0.36-1.44 hectares) showing the most notable gain. This contrasts with the decline in the percentage of forest fragments in that class during the same time period (Figure 3.4).

A visualization of the urban areas of metro Atlanta becomes clear once the areas of retained forest for the time periods 1974 to 1985, 1991 to 2001, and 2001 to 2005 are mapped (Figure 3.6). The deforestation of metro Atlanta counties is shown as the areas that change from the forest classification to “other”; the core metro counties of Cobb, Gwinnett, Fulton, and Dekalb were most dramatically deforested from 1974 to 1985, and the peripheral counties, from 2001 to 2005 (Figure 3.6). In 1974-1985, the pixels that changed to the forest classification were relatively evenly distributed, while in 2001-2005, that land-cover transition was more prominent in the outer counties of the metro region. These past and current trends are all products of the urban sprawl associated with growth of the city of Atlanta and provide a glimpse into the future for the forests for the peripheral counties of the Atlanta metro region, and the counties just beyond their borders.

DISCUSSION

The modern growth of Atlanta has been distributed among the counties in the metro Atlanta area as suburban sprawl. The loss of forest area and the fragmentation of forests experienced by the metro Atlanta counties from 1974 to 2005 are common results of the expansion of urban areas (Medley et al. 1995, Theobald et al. 1997, McKinney 2002, Novak and Wang 2004, Radeloff et al. 2005, Robinson et al. 2005). Within the Atlanta metro area, contrasts between the core urban counties and peripheral counties in the pattern of deforestation and fragmentation are evident. Cobb, Gwinnett, Fulton, Dekalb, and Clayton counties have experienced an earlier change from forest to other categories (Figure 3.6); they have also seen a more dramatic conversion of large forest fragments to smaller classes (Figure 3.5) compared to the other metro counties. This expanding sphere of forest fragmentation reflects continued development of areas outside the city of Atlanta, and is likely to continue in the peripheral metro counties as housing developments push beyond the area that currently serves the spatial requirements of the suburban lifestyles desired by those working in Atlanta. The complex relationships between income and housing location may even exacerbate the urban sprawl around Atlanta. The suburban developments that serve the wealthy may be pushing individuals in the middle class who want to live outside the city of Atlanta to seek out more affordable housing developments on the outskirts of Atlanta (Lo and Yang 2002, Hu and Lo 2007). This increased demand for development on the limited space within counties drives the deforestation of the region.

The decrease in the number of forest fragments in the core metro Atlanta counties from 2001 to 2005 counters the expected trend of increased forest fragmentation with the continued urban expansion of Atlanta (Yang and Lo 2002, Lo and Yang 2002). This result indicates that there is a point at which continued urban growth begins to consume the forest fragments that were created by earlier urban development. A more in-depth examination of the extent of urbanization in the core metro Atlanta counties through time may permit development of predictions for when the fragmentation of the forests in the peripheral metro counties surrounding Atlanta will reach this transition point.

An interesting contrast is the lower proportion of forest fragments in the smallest size class in Cobb, Gwinnett, Fulton, and Dekalb counties than in all of the other metro counties (Figure 3.4). A natural assumption is that urban infill had already removed many of the smallest forest fragments from the highly developed urban area (Ji et al. 2006). It is more difficult to explain the recent shift in forest fragment size proportions from the second smallest class to the smallest class in 1991, 2001, and 2005. It could be that urban infill is reducing fragments in the intermediate size classes to patches that fit in the smallest class. The rapid fragmentation of more continuous forest areas due to new low density housing developments could also cause the shift. Either cause makes the forest fragment size class distributions of the core metro counties look more similar to the distributions of the peripheral metro Atlanta counties in the later part of period analyzed.

Although the classification accuracy of all the counties examined in this chapter was > 80% (see Chapter 2), the results of this study are products of the spatial resolutions of the GLUT data layers and may not capture the totality of the forest cover in the counties studied. Even the finer 30-meter resolutions of the 1991, 2001, and 2005 data layers likely fail to identify some small patches of forest, thus underestimating the amount of forest cover and the number of forest fragments. The underestimation of forest fragmentation may be countered by an overestimation of fragmentation due to the erroneous disruption of narrow strips of forest cover by other landcovers. This study also treats forest cover as a binary; pixels are either forest or not forest. This does not account for changes in forest density and composition. Higher resolution data layers might be able to more clearly define forest edges, identify small patches of forest, and possibly detect changes in forest density and composition. Despite the limitations of the GLUT data layers used in this study, the observed trends of forest cover and forest fragmentation are likely robust enough to be observed at both greater and lesser spatial resolutions.

The rapid growth of the city of Atlanta through the past 50 years was not caused by the coincidence of unmanaged factors, but rather was aggressively promoted by the city government and local business leaders (Hartshorn et al. 1976, Nelson 1999, Jaret 2002). The economic and demographic growth of Atlanta is expected to continue in the foreseeable future (Nelson 1999, Rao 2007), increasing the spatial extent of the sprawl in the counties surrounding Atlanta and exacerbating the social and environmental problems with which sprawl is associated. The organization tasked with developing management strategies for Atlanta, ARC, has little actual power to enact the strategies they propose as the local governments control most land-use decisions (Nelson 1999, Rao 2007). This dispersal of power over development limits the impacts that regional development plans can have to reign in sprawl. A notable exception is the GRTA, which has the authority of approval over county transportation plans and some large developments. Given that the GRTA was only established in 1999 in response to the loss of federal funding for road and highway construction for 13 counties that violated federal air quality standards, and only has authority over those counties (Jaret 2002), few changes in the development of the counties around Atlanta will likely occur without significant economic incentives.

The extensive urban development surrounding Atlanta compromises the integrity of the fragmented forest ecosystems. The fragmentation of species habitats degrades the quality of habitats in each fragment and impedes the movement of individuals to areas with more favorable conditions (Saunders et al. 1991, Ehrlich 1996, Theobald et al. 1997, Czech et al. 2000, McKinney 2002). A major issue regarding the existence of ecosystems in newly fragmented landscapes is the replacement potential of the overstory plant species of the fragments. The long generation time of temperate forest tree species gives them more permanence in the vegetation structure of forest fragments (Hamrick 2004), but if future generations of these species are unable to develop within the fragments, the vegetation of the fragments is destined to gradually change composition, lose overstory components, or become managed landscapes that may not represent the natural vegetation of the region.

The ability of species to move between fragments is also a major concern for the genetic viability of those species within the landscape (Templeton et al. 1990, Ellstrand 1992, Fahrig and Merriam 1994). If species are unable either to move between or disperse their progeny between fragments, the replacement of individuals within fragments will come from the limited gene pool that exists within each fragment. This would cause extensive inbreeding of species within each fragment and the loss of genetic diversity for both the fragments and the region, due to the genetic drift of the small populations (Templeton et al. 1990, Ellstrand and Elam 1993, Young et al. 1996). These processes of genetic degradation mean that even if the forest fragments produced by the continued low-density development of counties surrounding Atlanta are able to resist the immediate ecological damage done by fragmentation, the persistence of a fragmented landscape will erode the fundamental genetic integrity of species in the fragments and potentially weaken their ability to resist pathogens, withstand environmental changes, and produce healthy offspring.

The ecosystems of the fragmented forests surrounding Atlanta will likely experience significant detrimental ecological impacts from the continued sprawl developing around the city. One possible positive consequence of the expansion of the city of Atlanta lies in the social impact of having a large population exposed to elements of nature. The drive to live in low-density developments is partly attributable to the desire to be closer to nature (Kaplan and Austin 2004). This appreciation of nature may ultimately help place conservation and environmental awareness in the social consciousnesses of individuals that live in the heavily fragmented landscapes surrounding Atlanta (Savard et al. 2000, Kaplan and Austin 2004). The emotional and spiritual connections to nature that are fostered by the presence of forest fragments in the urbanizing areas around Atlanta can increase support for conservation efforts outside of the Atlanta region. Threatened ecosystems outside the metro Atlanta area may find supporters from within the degraded ecosystems of the Atlanta metro area due to suburbanite’s attachment to the nature in their backyards.

The trend of expanding urban areas will cause the loss and fragmentation of many forests that are currently on the fringes of cities in the United States (McKinney 2002, Nowak and Walton 2005). Forest fragmentation as a result of urban expansion has been observed both regionally (Griffith et al. 2003) and for major urban centers outside of the American Southeast (Robinson et al. 2005). The recent decline in forest fragmentation due to the complete removal of small forest fragments from landscapes in the core metro Atlanta counties may foreshadow the forest fragmentation trends of other expanding urban areas, as was found in Rhode Island from 1985 to 1999 (Novak and Wang 2004). Other urbanizing areas may reach the same threshold of urban development where the elimination of forest fragments in a landscape outpaces the creation of forest fragments. The ecological impacts on these forests will threaten their viability as self-sustaining habitats for plants and animals that they currently support. The sprawl of development around Atlanta has impacted the forests of numerous surrounding counties in this manner, and these effects will likely expand to counties even farther from Atlanta if the city continues to grow as predicted. The growth of Atlanta is a function of demographic, econometric, and biophysical forces; changes to which can alter both the rate and spatial structure of urban expansion and the subsequent trends of forest cover and forest fragmentation around Atlanta (Hu and Lo 2007). It is important that the trends of forest fragmentation continue to be monitored in this region to better understand how modern urban sprawl will impact the ecosystems around the metro Atlanta area and other expanding urban centers.

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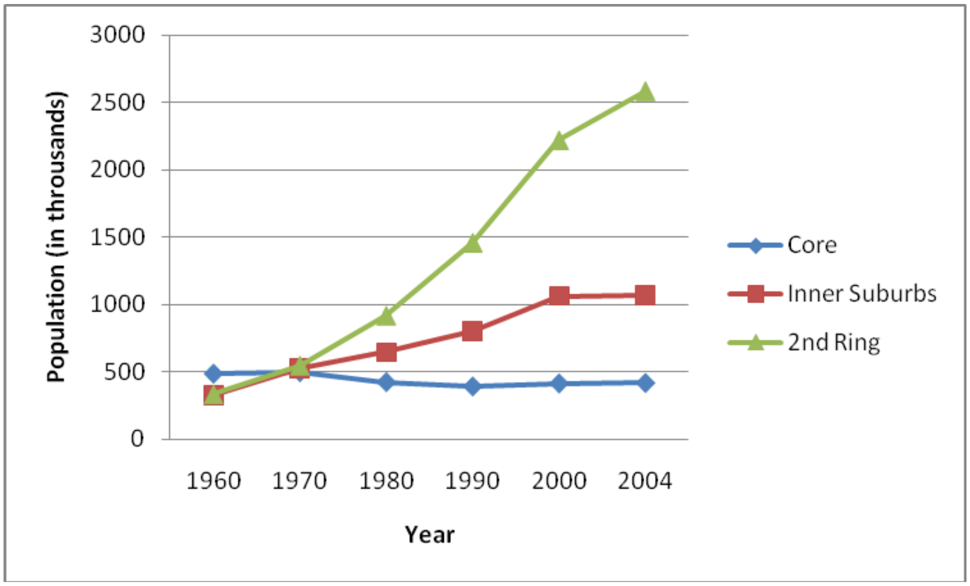

Figure 3.1. Atlanta's population growth from 1960-2004. Atlanta's core is defined as within the city boundaries, the inner suburbs as consisting of DeKalb and Fulton counties (excluding Atlanta's core), and Atlanta's 2nd ring as consisting of 13 surrounding counties (excluding the core and inner suburbs) (Demographia 1994-2005).

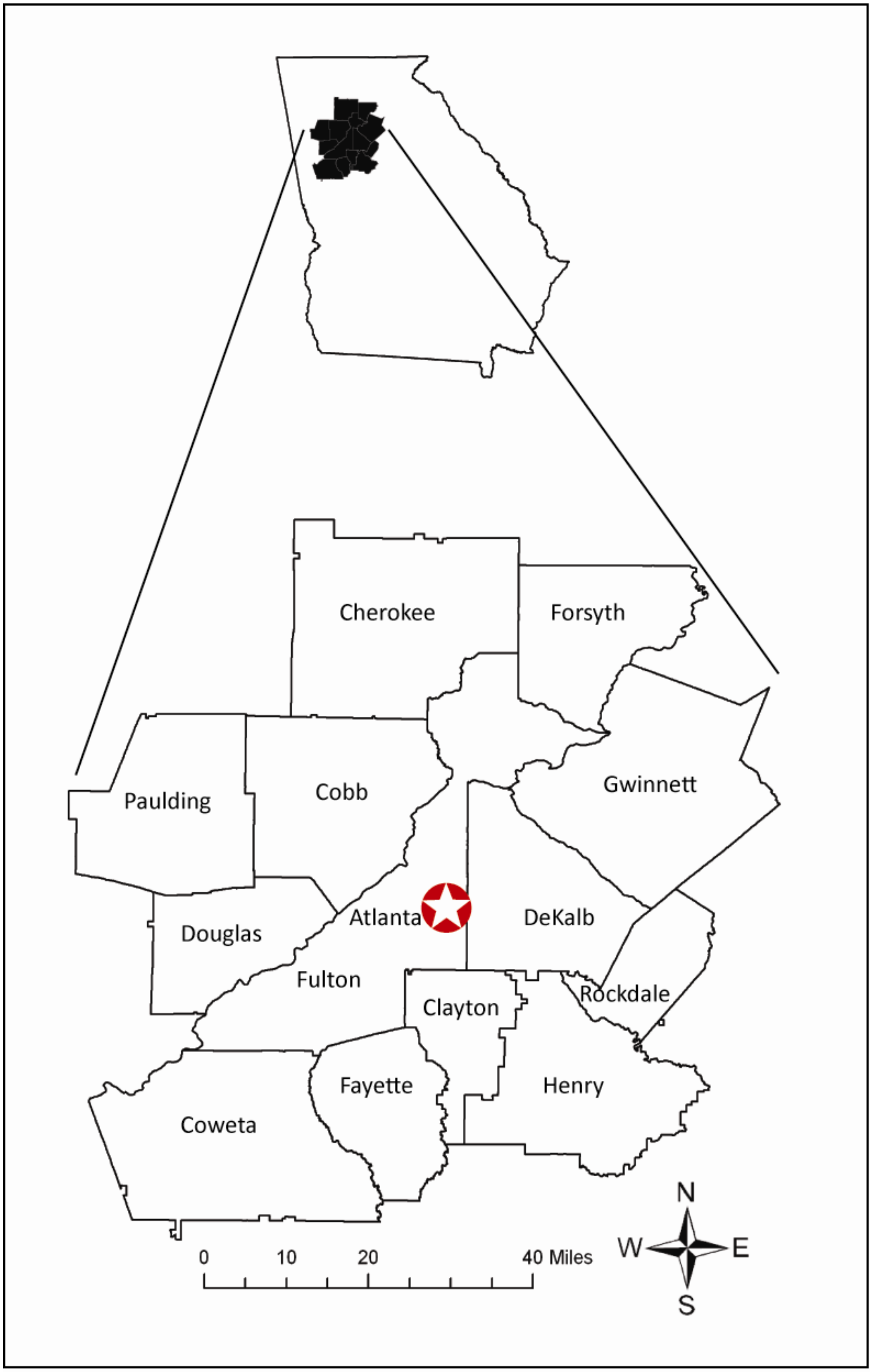

Figure 3.2. Metro Counties of Atlanta, Georgia.

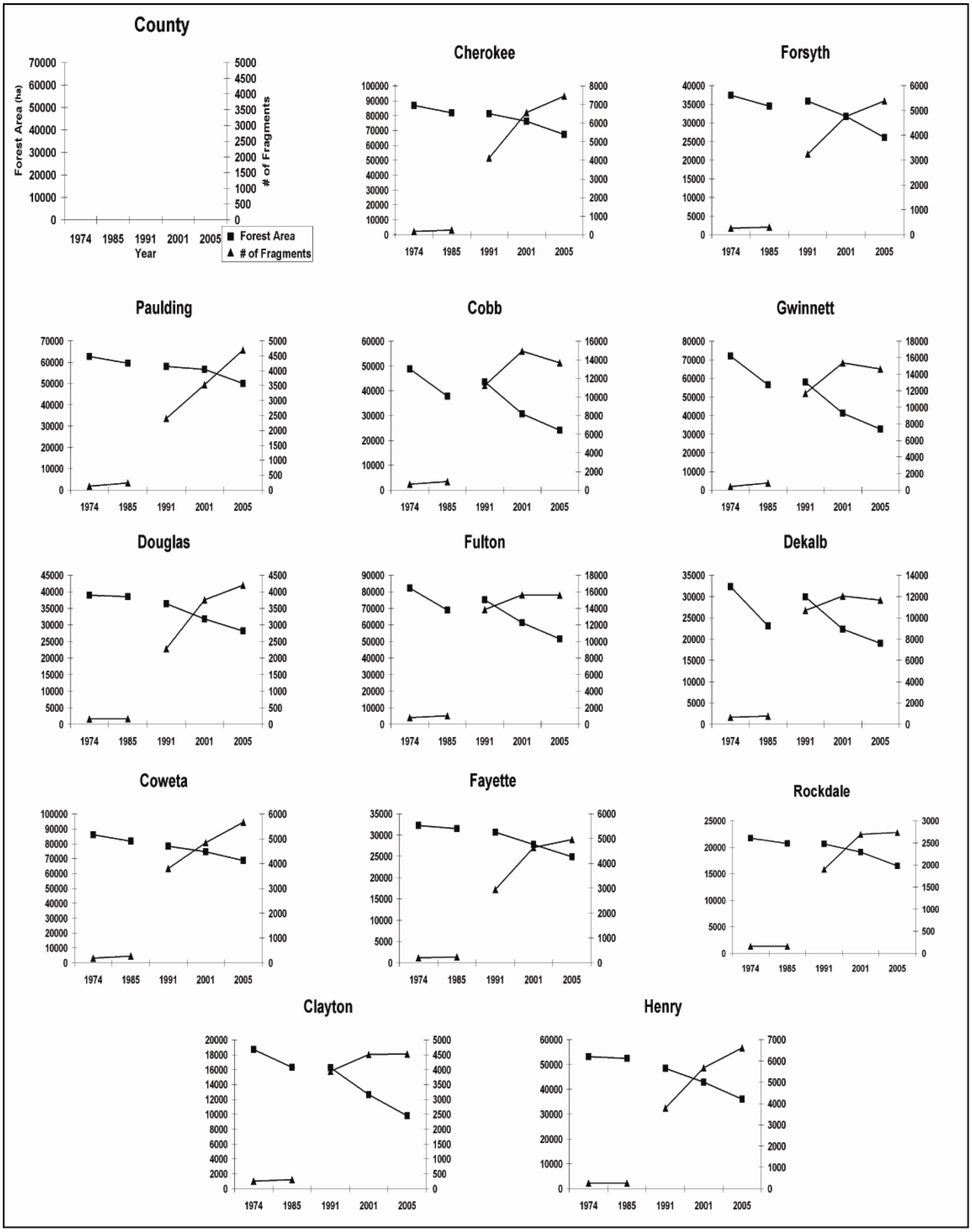

Figure 3.3. Forest Area and Fragment Trends for the Atlanta Metro Counties, 1974-2005.

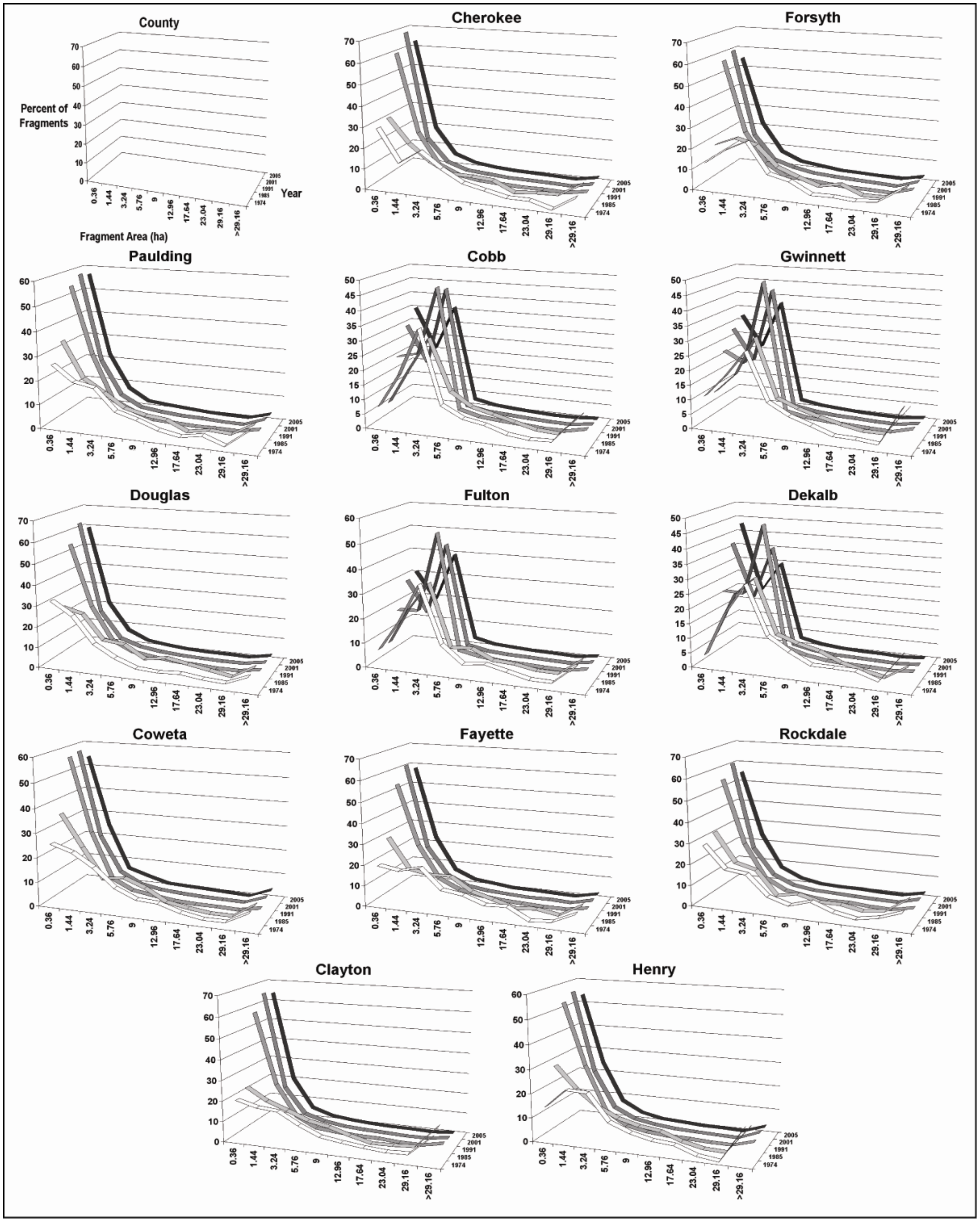

Figure 3.4. Forest Fragment Size Class Distribution for the Atlanta Metro Counties, 1974-2005.

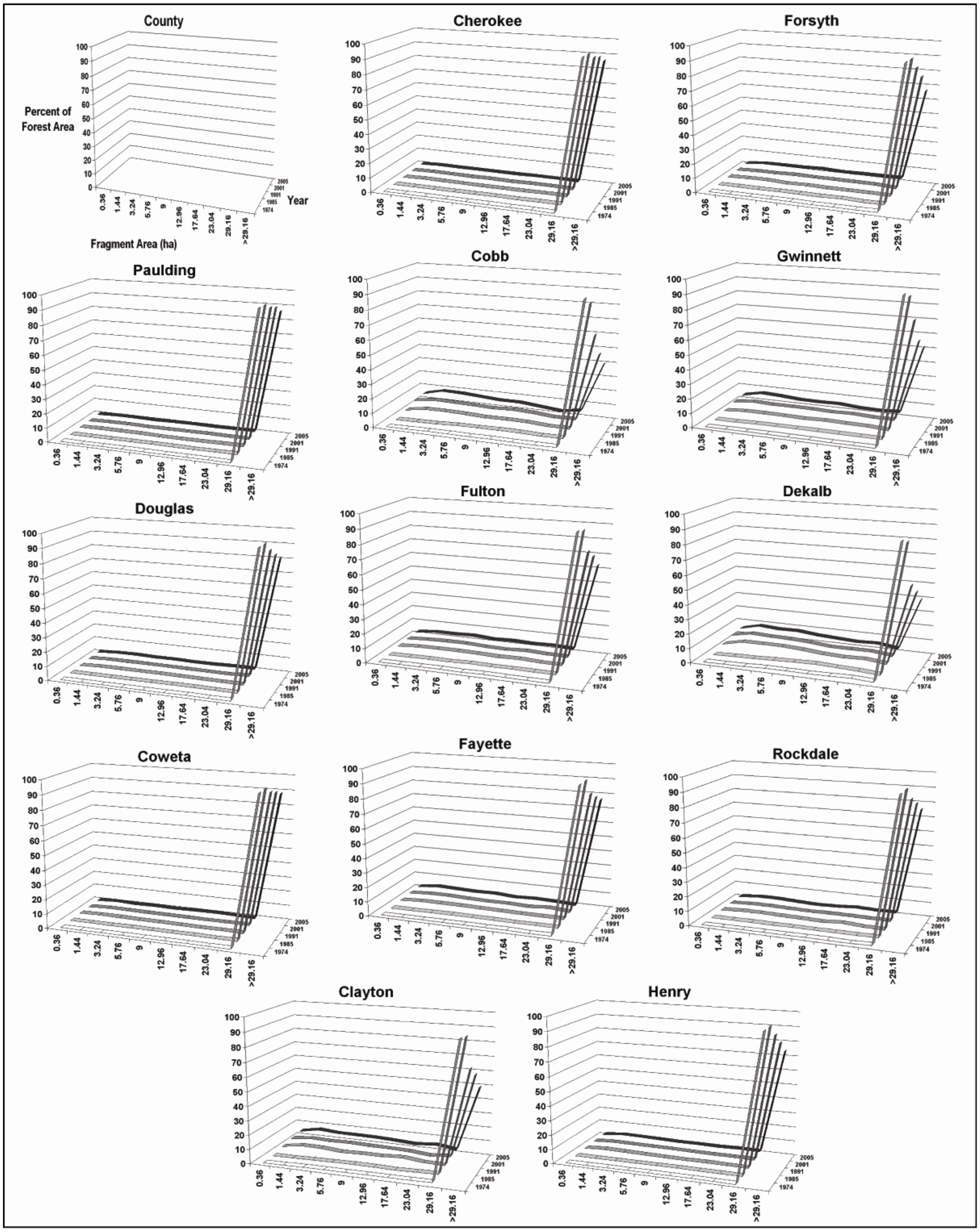

Figure 3.5. Percent of County Forest Area per Fragment Size Class for the Atlanta Metro Counties, 1974-2005.

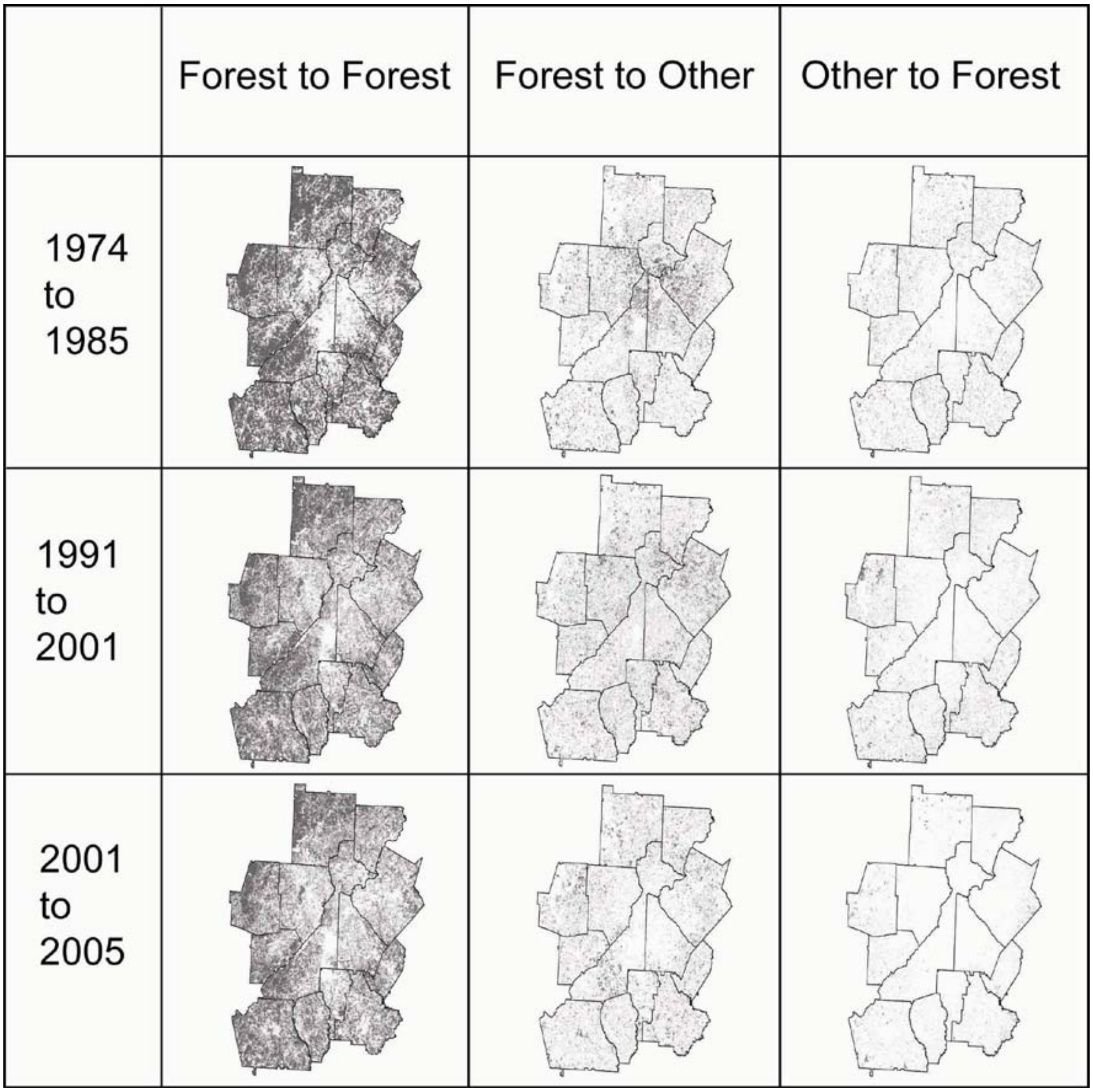

Figure 3.6. Forest Landcover Changes for the Atlanta Metro Counties, 1974-2005.

CHAPTER 4

MODELING DISPERSAL FOR GRID LANDSCAPES[1]

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INTRODUCTION

The modern examination of the spatial aspects of population genetics requires contributions from geneticists, ecologists and geographers. The field of landscape genetics has recently developed in response to these interdisciplinary lines of inquiry. While landscape genetics is most often framed as an amalgamation of population genetics and landscape ecology (Sork et al. 1999, Manel et al. 2003, Sork and Smouse 2006, Holderegger and Wagner 2006, Holderegger and Wagner 2008), the expertise of geographers is essential to the spatial considerations inherent in the ecological processes involved with the genetic structuring of populations (Storfer et al. 2007). The process of dispersal has a vast literature in both population genetics and landscape ecology, particularly for the dispersal of pollen and seeds. This study examines how dispersal can be spatially modeled in a geographic information system (GIS) and demonstrates the importance of geography as a contributor to the field of landscape genetics.

The estimates of pollen and seed dispersal distances vary widely, even between species in the same genus. Estimates of pollen dispersal for pine species range from well under a hundred meters to many thousands of meters (Table 4.1). Pine seeds also have a considerable range of dispersal distance estimates (Table 4.2). These wide ranges of dispersal distances suggest that the landscape contexts of the studies may be important factors in the observed characteristics of dispersal. In order to understand dispersal at the landscape level, the estimates of pollen and seed dispersal, as modeled with mathematical representations of dispersal (Figure 4.1), need to be applied to representations of landscapes. GIS provides the platform which can apply models of dispersal to landscapes and help integrate the process of dispersal with the patterns of species locations in landscapes. This chapter develops conceptual models of dispersal, which is a prerequisite to the use of GIS to model dispersal through real landscapes (such as those examined in chapters 2 and 3).

Most studies of pollen and seed dispersal follow one of three methodologies: ecological observation, genetic analysis, and dispersal modeling. Ecological observation studies have included using pollen and seed traps (Wright 1952, Wang et al. 1960, Nathan et al. 2000, Hewitt and Kellman 2002), tracking dispersed items (Iida 1996, Pons and Pausas 2007), and observation of dispersers and offspring (Johnson 1988, Lindgren et al. 1995, Gomez 2003). Genetic analysis studies of dispersal use the relationships between individuals to develop estimates of dispersal curves and distances for pollen and seeds (Shen et al. 1981, Dow and Ashley 1998, Streiff et al. 1999, Gonzalez-Martinez et al. 2002, Grace et al. 2004, Austerlitz et al. 2007). Dispersal modeling studies broadly examine mathematical representations of dispersal and how they can be impacted by various environmental factors (Okubo and Levin 1989, Malanson and Armstrong 1996, Meahger et al. 2003, Smouse and Sork 2004, Schueler and Schluznen 2006, Williams et al. 2006, Kuparinen et al. 2007, Snall, et al. 2007).

Ecological observation studies look directly at the dispersed objects (e.g. Wright 1953, Iida 1996, Vander Wall 2003) or evidence of object movement, such as pollination due to the transport of pollen grains (Lindgren et al. 1995). These types of studies typically describe dispersal through the development of dispersal curves (Wright 1952, Wright 1953, Wang 1960, Johnson 1988, Nathan et al. 2000), or distance-based descriptions of movement (Lindgren et al. 1995, Iida 1996, Hewitt and Kellman 2002, Vander Wall 2003, Pons and Pausas 2007). The dispersal curves provide a quantification of the dispersed objects along a distance axis (with the height of the curve representing the amount of dispersant transported a certain distance from the point of origin; e.g., Figure 4.1), while the studies with distance-based descriptions typically only provide an average distance of dispersal and observed dispersal distance limits; e.g., Tables 4.1, 4.2). Even though the distance-based descriptions help conceptualize the limits of dispersal over space, the dispersal curves are more useful for modeling how a total amount of dispersal objects is partitioned to the space around the origin of dispersal. Conceptually, the dispersal curves model an even dispersal of objects based on a mathematical equation, while distance based descriptions are used to describe clumped or uneven dispersal, such as the dispersal of seeds by birds or rodents that cache many seeds at a specific location (Iida 1996, Gomez 2003, Vander Wall 2003).

Studies of dispersal based on genetic analysis generally use models of parentage (Shen et al. 1981, Burczyk et al. 1996, Dow and Ashley 1998, Streiff et al. 1999, Gonzalez-Martinez et al. 2002, Burczyk et al. 2004, Dutech et al. 2005, Valbuena-Carabana et al. 2005) or maternity exclusion analysis (Grace et al. 2004) to determine how pollen and seeds move over space. The spatial information gained from these types of studies can be used to develop dispersal curves to model the movement of pollen and seeds in landscapes (Austerlitz et al. 2004, Austerlitz et al. 2007). In contrast to ecological observation-based dispersal curves that model the total dispersal of pollen and seeds from a dispersal point, genetically derived dispersal curves are based on sampled seedling or adult populations. Just because a seed or pollen grain is dispersed does not mean that it will result in the development of a progeny of the dispersal source. Genetic analysis studies therefore develop dispersal curves that reflect the dispersal of only successful pollen and seeds.

Studies that model dispersal are extremely varied in their methodologies. Approaches include modeling based on the following: atmospheric processes responsible for pollen and seed transport (Schueler and Schlunzen 2006, Kuparinen et al. 2007), statistically partitioned parentage (Smouse and Sork 2004, Robledo-Arnuncio et al. 2006), dispersal in complex landscapes (Malanson and Armstrong 1996), and dispersal based on mathematical probability (Okubo and Levin 1989, Tufto et al. 1997, Meagher et al. 2003, Meagher and Vassiliadis 2003, Williams et al. 2006, Snall et al. 2007). While the objective of these studies is to model dispersal over space, only Malanson and Armstrong (1996), Tufto et al. (1997), and Meagher et al. (2003) take the totality of the landscape into consideration. The methodological and objective specificity of dispersal modeling studies limits their applications beyond the parameters defined by the authors. The examination of conceptual dispersal models in this paper presents a framework of spatial dispersal modeling for grids that can be broadly applied to various scenarios, including the movement of inanimate ecological items, biological pathogens, and energy. This study uses pollen and seed dispersal for examples.

The objective of a study determines which of these three approaches, ecological observation, genetic analysis, or dispersal modeling, is most appropriate for the analysis of dispersal in a particular instance. Total pollen and seed dispersal is most accurately described by ecological observation studies. Transport of pollen that results in fertilization and dispersal of seeds to effective germination sites is best analyzed through genetic data obtained from the sampling of seedlings and adults; i.e., the results of successful dispersal. Both types of studies can be preformed for the same individuals in a landscape, but the resulting dispersal curves will reflect the respective methodologies, and will potentially give different representations of dispersal. Because the number of individuals in a landscape is often enormous, and the costs to obtain information on each individual in a population can be prohibitive, using dispersal curves developed from a population sample is an important tool for modeling the occurrence of dispersal within a landscape.

There are numerous factors that can impact dispersal to alter an isotropic (directionally even) pattern of dispersal to an anisotropic pattern (directionally uneven) (Wagner et al. 2004, Dutech et al. 2005, Austerlitz et al. 2007), or that can otherwise alter the structure of dispersal (Malanson and Armstrong 1996, Wiens 2001, Malanson 2003, Ghazoul 2005). The directionally uneven flow of air, patterns of animal movement, and topography can cause pollen and seeds to have anisotropic distributions. Inherent to models of anisotropic, or otherwise altered, dispersal patterns are conceptual null models of dispersal; these provide an isotropic starting point for the development of more complex models (e.g., that represent anisotropic landscapes or dispersal that is somehow altered from a simple case). This study develops these null models of dispersal that can be used to model the basic patterns of dispersal in landscapes.

While the dispersal of pollen and seeds has been extensively studied using a wide variety of techniques, the spatial aspects of dispersal are usually oversimplified. Most studies model dispersal as following some decaying curve with distance on the x-axis. This is a one-dimensional consideration of space that fails to consider how the decay curve can be applied to actual landscapes from which the data used to develop the curves were obtained. These studies distill information from spatial landscapes that are at least two-dimensional into a single spatial dimension (i.e., distance from the dispersal origin). Modeling dispersal with only one spatial dimension implicitly assumes that dispersal is isotropic. Models with one dimension of space assume that dispersal is even for all directions, while anisotropic dispersal includes directional dependence. Thus, applying modeled dispersal curves to landscapes naturally assumes isotropic dispersal. Extending one-dimensional dispersal curves to landscapes with two spatial dimensions is an important step to understanding how the movement of pollen and seeds occurs at the landscape level. This study examines methods of modeling dispersal for grid landscapes.

A fundamental issue with applying data modeled from points to landscapes is how to partition the landscape into units. Within an area where dispersal occurs, there is an infinite number of points that can receive pollen or seeds. Modeling the area as a grid, which is the structure of raster data layers, creates a usable surface, with grid centroids that are compatible with point values obtained from a dispersal curve. This study proposes the following three models to conceptualize the application of dispersal curves to grid landscapes.

1. The point values of the decay curve can be applied to each cell in the grid landscape based on each cell’s distance from the dispersal cell (*sum of curve points model*).

2. The area under the curve can be partitioned to cell centroids that are within defined distance ranges from the origin of dispersal (*area of distance range model*).

3. In a similar manner, if the decay curve is rotated around the y-axis to create a three-dimensional object of dispersal, the volumes above the distance ranges can be partitioned out to the cell centroids within the distance ranges (*volume of distance range model*).

This study first develops these three conceptual models of dispersal in a grid landscape, defines assumptions associated with each, and explores how they compare to each other. It then examines how the models are influenced by varying forms of a decay curve. Finally it discusses strengths and limitations of the different models and recommends which one is the most appropriate for modeling dispersal. Dispersal initially is modeled from a single point in a landscape and builds to dispersal from multiple points to improve our understanding of how dispersal can be modeled in two spatial dimensions. The results of this study will help researchers apply their dispersal curves recursively to the landscapes from which they were developed. This interdisciplinary area of study will help geographers engage with population geneticists and landscape ecologists to develop a greater understanding of the spatial aspects of pollen and seed movement. This work can also be applied beyond the field of landscape genetics to any discipline that utilizes the concept of dispersal.

METHODS

This study models separately dispersal from a single cell, as well as from multiple dispersal cells, in a grid to all grid cells within a defined distance limit. The single dispersal cell landscape shows how different conceptualizations of dispersal and different forms of the negative exponential curve affect dispersal from one cell to all the cells in the landscape that are within a defined distance limit. The multiple dispersal cell landscape is similar except that it depicts dispersal from multiple points and, consequently, is more representative of dispersal occurring within natural spatial patterns of plants. Because dispersal can occur across borders, the analysis area of the multiple dispersal cell models must be buffered by the defined distance limit of dispersal to ensure that the impacts of dispersal cells outside of the analysis area are considered. This larger grid allows the dispersal of a single dispersal cell in the analysis area to be modeled beyond the border of the analysis area, which shows the total impact of the dispersal cell within the defined distance limit of dispersal.

The analysis area for the single dispersal cell models contained all cells whose centroids are within 100 units of the 10 x 10 unit dispersal cell's centroid, which resulted in a 21 x 21 grid. The analysis area for the multiple dispersal point landscape was defined as a 10 x 10-cell grid, with a cell resolution of 10 units. In order to examine dispersal to and from all the cells in the analysis area, a buffer of at least 100 units around the analysis area is required. A 30 x 30-cell raster layer was created to ensure the dispersal of cells outside of the center 10 x 10-cell analysis area to cells within the analysis area was considered. The raster layer was converted into a text file and imported into ArcMAP 9.2 (ESRI 1999-2009) in an ASCII GRID format. The raster file was converted into a point shapefile with the points representing the centroids of the raster cells. The software program Hawth's Tools (Beyer 2004) was used to create a distance matrix for all 900 points. Manipulations of the distance matrix to examine how the negative exponential curve, $y=e^{-\lambda x}$, can be modeled for grids were preformed in Microsoft Excel 2007.

The dispersal distributions from a single cell were examined using the distances from a cell in the center analysis area to all cells in the matrix for the forms of the curve λ = 0.001, 0.01, 0.1, and 1.0. Only cells within 100 units of the analysis cell were included in the analysis; all cells more distant from the source cell were omitted. Three ways of conceptualizing dispersal were modeled for the cell: the sum of all points on the dispersal curve for all cells in the dispersal radius (*sum of curve points*) (Figure 4.2), the partitioning of the area under a dispersal curve to the cells in the dispersal radius (*area of distance range*) (Figure 4.3), and the partitioning of the volume under the rotated dispersal curve (*volume of distance range*) (Figure 4.4). For the *sum of curve points* dispersal, the values of y in the negative exponential curve for every distance (x) from the dispersal cell were calculated and the proportion of the total dispersal was applied to the cells. The number of cells within each progressive 10-unit distance range from the dispersal cell was determined for the *area of distance range* and *volume of distance range* models. The area under the dispersal curve for each distance range was distributed evenly to the cells in the distance range (including the dispersal cell in the 0 to 10 unit range) for the *area of distance range model*. The same partitioning was used for the volumes under the negative exponential curve for each distance range of the *volume of distance range* model. The integration of the negative exponential curve required to find the areas and volumes under the curve was performed using Wolfram's Online Integrator (Wolfram Research Inc. 2010).

The hypothetical landscape pattern used to model multiple cell dispersal was patterned after a reclassified landcover layer that represented forest cover in an area of Gwinnett County, Georgia, USA. This pattern was used because it represented a moderately fragmented landscape with dispersal agents native to the data layer. The use of this pattern is not meant to tie the models in this study to a particular ecological context. The pattern merely acts as a non-random, multiple cell dispersal landscape for the purpose of showing how the type of model and the form of the dispersal curve influence the occurrence of dispersal in landscapes. A 30 x 30-cell grid of the landcover pattern, where cells of forest cover were considered dispersal cells, was created with the 10 x 10-cell analysis area in the center. The same analysis procedures for the single pixel dispersal were used, except that multiple (rather than only single) dispersal source cells were taken into account. To create the dispersal matrix, the columns of cells that were not dispersal cells were removed from the matrix. The rows for all of the cells and their distances from the dispersal cells remained for analysis. As with the single cell dispersal models, λ values of 0.001, 0.01, 0.1, and 1.0 were used in the negative exponential curve for the *sum of curve points, area of distance range*, and *volume of distance range* models.

All three models, whether applied on a single-cell or multiple-cell dispersal basis, make a number of assumptions. These assumptions are:

1. Every dispersal cell disperses the same amount.
2. Every dispersal cell disperses according to the same dispersal curve.
3. There is a defined maximum distance at which dispersed items are considered. The negative exponential curve extends indefinitely on the x-axis so a distance limit to dispersal must be declared.
4. Dispersal is isotropic, as defined previously.

The evaluation of the models was based on logical coherence and ease of use. In this study, logical coherence is a reflection of how well the models represent the one-dimensional dispersal curve when applied in a two-dimensional landscape. Ease of use is evaluated through the mathematical complexity of the models.

RESULTS

SINGLE CELL DISPERSAL

The *area of distance range* model of dispersal most clearly shows the forms of the negative exponential curve, as this model simply partitions 10 unit sections of the curve to the cells whose centroids are within the distance ranges. As the λ values for the curve decrease, the curve flattens out and the distance ranges have increasingly similar parts of the curve out to the 100 unit limit (Figure 4.5). The *volume of distance range* model also partitions a defined total amount equally to the cells whose centroids are within each corresponding distance range. Where the *area of distance range* partitions the values of a two dimensional area that fall under a curve, one dimension of which is space, the *volume by distance range model* partitions a three dimensional volume, two of which are space. Unlike the *area of distance range* model, the *volume of distance* range model shows an increase in the amount of dispersal to the farther distance ranges for the lower λ values (Figure 4.5). The *sum of curve points* model behaves similarly to the *volume of distance range* model. The 0.001 and 0.01 λ values both show an increase in dispersal to farther distance ranges (Figure 4.5).

All of the models show the same result for the largest λ value, that dispersal is almost entirely limited to within 10 units of the dispersal point (Figure 4.5). The models differ on how that dispersal is partitioned out to cells. The *sum of curve points* model does not partition the total of the distance ranges, so the dispersal from the negative exponential curve with a λ value of 1 is contained within the cell from which the dispersal originated (Figure 4.6). The *area of distance range model* and the *volume of distance range* models partition the amount of dispersal evenly to the cells within the distance range, so the cells adjacent to the dispersal origin cell and the origin cell have the same amount of dispersal, just under the maximum of twenty percent of the total dispersal (Figure 4.6).

The increase in amount of dispersal to the farther distance ranges seen in the *sum of curve points* and the *volume of distance range* models is counterbalanced by the increasing number of cells in the more distant ranges and thus not apparent in the maps of dispersal. The *area of distance range* model has the slowest spread of dispersal as λ decreases while the *volume of distance range* model has the quickest spread of dispersal. At a λ value of 0.01, the *sum of curve points* model and the *volume of distance range* model have reached the limit of even dispersal within the defined 100 unit limit; only the *area of distance range* model has not. At a λ value of 0.001, all of the models have every cell within the defined dispersal limit of 100 units receiving between 2.5 and 0.02 % of the total dispersal (Figure 4.6).

MULTIPLE DISPERSAL CELL LANDSCAPE

The multi-point dispersal landscape has an initial structure of more dispersal cells above the center analysis area than below (Figure 4.7). Within the analysis area there are several small connected dispersal cell patches and two isolated dispersal cells.

When the negative exponential curve has a λ value of 0.001, the dispersal from cells within the analysis area is masked by the contributions from dispersal cells above the analysis area and within the 100 unit dispersal limit (Figure 4.8). All the dispersal models show a gradation of low reception in the lower left of the center area that increases progressively towards the upper right. This same pattern is present for a λ value of 0.01, with the a*rea of distance range* model showing a slightly more apparent local dispersal from the patch of dispersal cells in the upper left of the analysis area than the other models. Once the λ value is increased to 0.1, dispersal from cells within the analysis area dominates the dispersal pattern within the analysis area, and effects of dispersal from outside that focal area become less evident. The decay of the curve has become steep enough at this point that some isolated non-dispersal cells only have between 0 and 10 percent of their possible receipt (Figure 4.8). The isolated dispersal cells have also become distinguishable from their non-dispersal neighbors in the *sum of curve points* model. At a λ value of 1, the *sum of curve points* model show dispersal is over 90 percent contained to the dispersal cells. The *area of distance range* and *volume of distance range* models show a more complex dispersal pattern due to the partitioning of the dispersal within 10 units from the centroid of the dispersal to five cells. This partitioned dispersal makes it difficult to identify isolated dispersal cells for these models.

DISCUSSION

SINGLE CELL DISPERSAL

The *area of distance range* model most closely represents the concept of the dispersal curve with space occupying one dimension. It partitions the area under a single curve out to a defined dispersal limit to the cell centroids within distance ranges. This results in the *area of distance range* model retaining the identifiable shapes of the dispersal curves when the dispersal to each distance range is charted (Figure 4.5). Although the *area of distance range* model retains the form of the decay curve, it is less conceptually coherent than the other models of dispersal because the dispersal values based on one dimension of space are partitioned to points that represent an area with two spatial dimensions. This model forces the form of the dispersal curve on the total dispersal to each distance range.

The *volume of distance range* model is similar to the *area of distance range* model in that both models partition a total amount of dispersal with distance ranges to the cell centroids within the ranges. Despite this similarity, the *volume of distance range* is more closely related to the *sum of curve points model*. Because the *area of distance range* model is based on the area between one spatial dimension and the decay curve that is segmented into equal range distances, the only variable that changes the amount of dispersal to each distance range is the decay curve. The *volume of distance range* model is also based on equal distance ranges, but because the distance ranges are increasingly farther away from the dispersal point, the areas of the rings under the rotated dispersal curve become progressively larger. This results in the total dispersal to each distance range for the *volume of distance range* model producing similar results to the *sum of curve points* model. The *volume of distance range* model is the most conceptually accurate representation of dispersal in this study because it includes two spatial dimensions in the production of the dispersal values that are partitioned to the cell centroids within the distance ranges.

Conceptually, the *sum of curve points* model represents two spatial dimensions through the additive use of multiple dispersal curves that extend from the point of dispersal out to each cell centroid of the grid that is representing the study area. While the *sum of curve points* model is not as conceptually tidy as the *volume of distance range* model, it is mathematically simpler and easier to use.

Ideally, the *volume of distance range* model would be modified so that it attributed the volume above each cell and under the rotated dispersal curve to the cell centroids instead of partitioning the volumes of rings out to associated cell centoids. This model would consider two spatial dimensions in dispersal amount allotment to cell centroids and would allow each cell to represent only the volume of the rotated dispersal curve above the areas of the cells. Such a model would be very difficult to develop due to the complex shapes that the cells would cut from the slope of the rotated dispersal curve. While this model would seem to be conceptually preferable to the models described in this study, the *sum of curve points* model is actually closely related to this ideal volume model. Three-dimensional volumes are found through multiple integration, which are based on Riemann sum approximations. These Riemann sum approximations are simply the sum of the volumes of boxes under the surface curve. As the number of boxes increases, the approximation of the volume under the surface becomes more accurate. If we consider the value where the curved surface passes over each centroid as the heights of each of the boxes of a Riemann sum, and we cancel out the equal base areas of every cell, we are left with just the heights at the cell centroids representing the volumes of the boxes. This is equal to the *sum of curve points* model of dispersal in this study. Consequently, the *sum of curve points* model is equal to a Riemann sum approximation model of volume based dispersal.

All of the models in this study have their own advantages that influence which model is most appropriate for a particular situation. The *sum of curve points* model is mathematically the simplest model to apply to grid landscapes. It does not require calculus like the *area of distance range* and *volume of distance range* models. The *area of distance range* model preserves the form of the dispersal curve in a grid with two spatial dimensions. The *volume of distance range* model is the most conceptually coherent model because it partitions a volume based on two spatial dimensions to a grid that also has two spatial dimensions. Researchers need to determine which model is the most appropriate for their data based on these differences.

MULTIPLE DISPERSAL CELL LANDSCAPE

The modeling of dispersal in landscapes with multiple dispersal points requires several decisions about application of the dispersal curve to a landscape. Beyond deciding which model to use, the limit of dispersal needs to be considered. The influence of dispersal points outside of the analysis area must be factored into studies of landscape dispersal. By buffering the analysis area by a defined distance limit of dispersal, the contributions of dispersers just outside of the analysis area are included. Depending on how the curve is described, this procedure can be criticized as not taking long distance dispersal into account. The influence of long distance dispersal for the population genetics of plant species is an important and ongoing area of study (Cain et al. 2000, Bullock and Clarke 2000, Nathan et al. 2002) that should be the focus of future studies of dispersal modeling.

The methods of this study apply most directly to the counts of dispersed items from a source point. If the influence of the dispersed items does not correspond with the number of items dispersed over space, a readjustment of the dispersal curve is necessary to reflect this influence. This would be necessary if items dispersed from longer distances have more impact than locally dispersed items. This disparity is typified by the foci of the ecological observation studies (eg. Wright 1952, Iida 1996, Johnson 1988) and the genetic analysis based studies of dispersal (eg. Streiff et al. 1999, Gonzalez-Martinez et al. 2002, Austerlitz et al. 2004, Grace et al. 2004). The dispersal of seeds and pollen as modeled by ecological observation does not necessarily reflect the dispersal of progeny, as a large amount of pollen and seeds that are dispersed close to the dispersal origin are in a limited amount of space for the development of progeny. In models of dispersal that develop dispersal curves with one dimension of space (e.g. Okubo and Levin 1989, Meagher et al. 2003, Austerlitz et al. 2004), 10 distance units from the dispersal origin occupy the same amount of space as 10 distance units that start at any distance from the dispersal origin. When these curves are applied to two spatial dimensions, the 10 distance units become rings that increase in area as distance from the dispersal origin increases. While fewer items are dispersed to these distances, there is a greater area for progeny establishment. Genetic analysis studies are able to develop dispersal curves that reflect the ability of dispersed pollen and seeds to develop into progeny.

The dispersal of pollen and seeds is suspected to have anisotropic dispersal patterns based on varied local conditions that alter the dispersal from an isotropic pattern

(Wagner et al. 2004, Dutech et al. 2005, Austerlitz et al. 2007). This study developed methods to model isotropic dispersal. Factors that make dispersal anisotropic in landscapes can be accounted for through the manipulation of the dispersal matrix. Future studies will examine anisotropic modeling for grid landscapes. An interesting property of the modeled isotropic dispersal for multiple dispersal point landscapes in this study is that the dispersal from a dispersal cell to other dispersal cells is equal to the received dispersal from the other dispersal cells. This is because in an evenly partitioned landscape where all dispersal follows the same decay curve in an isotropic pattern, distance is the determining variable for how much dispersal occurs from one dispersal cell to another dispersal cell. Because two dispersal cells disperse based on the same distance to each other on the same decay curve, they disperse an equivalent amount to each other. This principle of isotropic equivalence results in no dispersal cell receiving more or less total dispersal than it disperses. Once dispersal is non-isotropic, this equivalence is broken.

The development of dispersal landscapes is an important step for landscape geneticists to understand how the dispersal curves that are generated for species can be applied to two-dimensional representations of space. Recent approaches to dispersal modeling in landscape genetics have conceptualized space without considering the entire landscape (Austerlitz et al. 2004, Dyer and Nason 2004, Dyer 2009), i.e., incorporating primarily the specific locations of individuals or populations sampled, without explicit information on the intervening landscape matrix. When individuals are aggregated into irregular shapes or represented by points that do not constitute regular components of a landscape, the spatial integrity of models is compromised. Within larger shapes, grouping individuals into populations can cause individuals to be represented by a center point that is spatially distant from their true locations. More work is required to understand the spatial considerations of dispersal within population genetics and how pollen and seeds move through actual landscapes composed of heterogeneous habitats. The contributions of geographers to this type of landscape modeling can enrich the understanding of how dispersal processes act over space. This area of research is especially critical given current efforts to develop software to model pollen dispersal (Sugita 1994, Sugita et al. 1999, Middleton and Bunting 2004). This study provides software developers with essential suggestions for modeling dispersal in two spatial dimensions. Further involvement of geographers with the spatial aspects of landscape genetics is essential for the development of this interdisciplinary field.

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Table 4.1. Selected studies and reviews of reported pollen dispersion distances for pine.

Study/Review	Species	Pollen dispersal distance (σD = standard deviation)	Methodology
Wright, J.W. 1952	*Pinus cembroides* var. *edulis*	σD = 17m	Pollen traps
Wang et al. 1960	*Pinus elliottii* Engelm.	σD = 67.8m	Pollen traps
Lindgren et al. 1995	*Pinus sylvestris* L.	10-400km	Phenological observations/ pollen capture
Marquardt and Epperson. 2004	*Pinus strobus*	σD = 30m	Microsatellite genetic analysis
Robledo-Arnuncio and Gil. 2005	*Pinus sylvestris* L.	Avg. = 135m 7% beyond 200m	Chloroplast/microsatellite paternity genetic analysis

Table 4.2. Selected studies of reported seed dispersal distances for pine.

Study/Review	Species	Seed dispersal distance (σD = standard deviation)	Methodology
Epperson and Allard 1989	*Pinus contorta* spp. *latifolia*	σD> 30 m	Allozyme genetic analysis
Nathan et al. 2000	*Pinus halepensis*	97% < 20 m Max = 95 m	Seed traps
Gonzalez-Martinez et al. 2002	*Pinus pinaster* Ait.	Patch size ~ 10 m	Microsatellite genetic analysis
Vander Wall 2003	*Pinus contorta,* *P. ponderosa,* *P. jeffreyi,* *P. lambertiana*	28 m, 25.6 m, 16.7 m, 13.4 m	Ballistic dispersal model
Grace et al. 2004	*Pinus palustris*	54% > 75 m	Allozyme genetic analysis
Williams et al. 2006	*Pinus taeda* L.	0.0011 > 1 km	Computer modeling

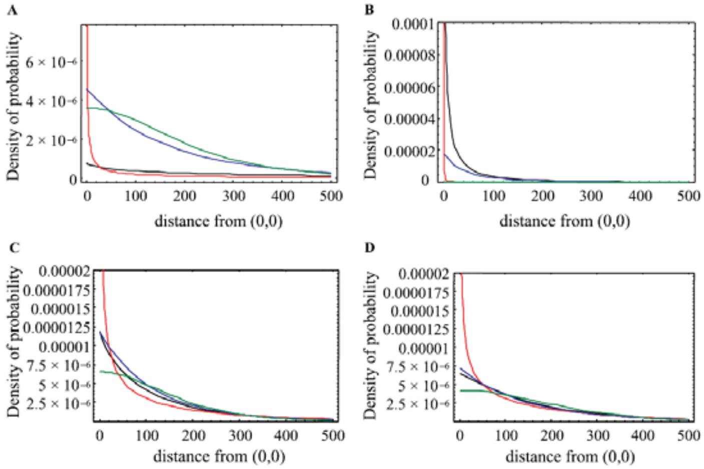


Fig. 2 Best fitting curves for the four experimental data sets, *Sorbus torminalis* 1999 (A) and 2000 (B), *Dinizia excelsa* (C) and *Quercus lobata* (D), for the four families of curves studied, exponential power (black line), Weibull (red line), geometric (blue line) and 2*Dt* (green line) They correspond to the case where the shape parameter (*b*) was set to a fixed value and density was jointly estimated (second line of Tables 4–7).

Figure 4.1. Dispersal curves for the pollen of three different species using four families of curves (source: Austerlitz et al. 2004).

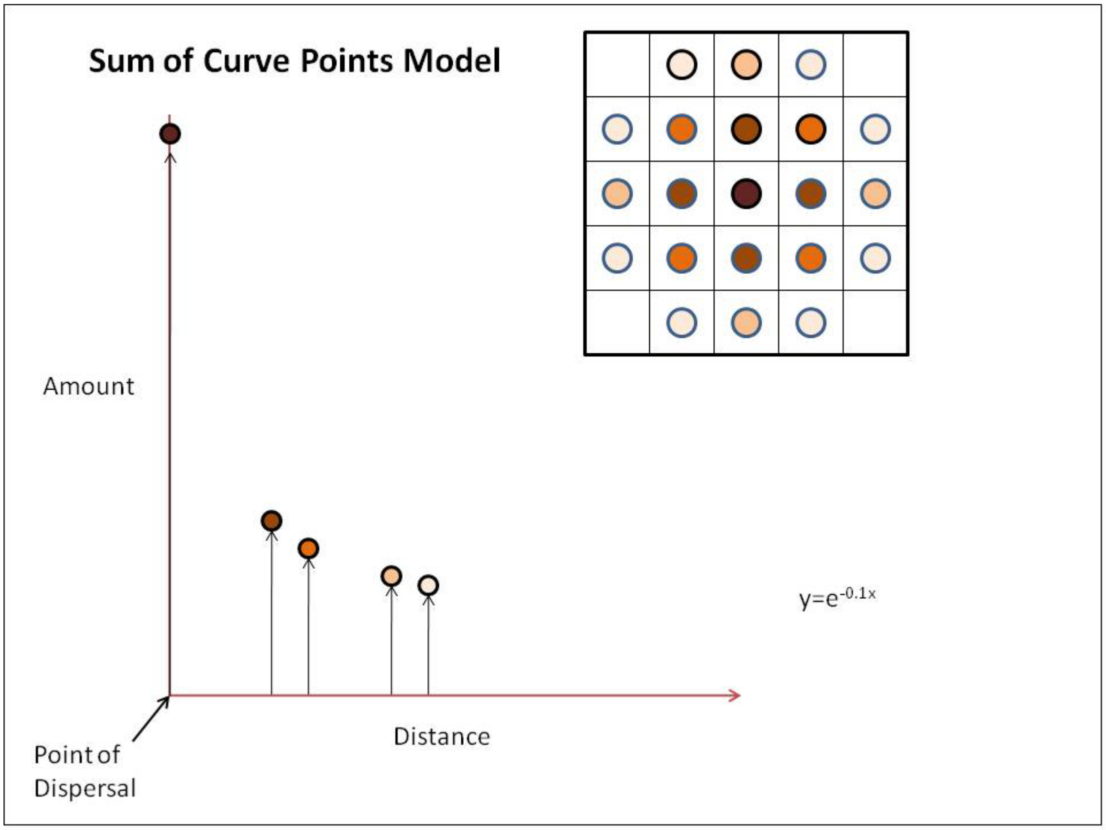


Figure 4.2. *Sum of curve points* model of dispersal for λ = 0.1. Black arrows represent values on the decay curve given to cell centroids based on their distances from the dispersal cell. The dispersal to each cell is determined by the point on the dispersal curve at the distance each cell is from the origin of dispersal (center gird cell). Each cell's dispersal amount based on the curve points is divided by the sum of the dispersal amounts of every cell within the defined limit of dispersal to find the proportion of dispersal to each cell.

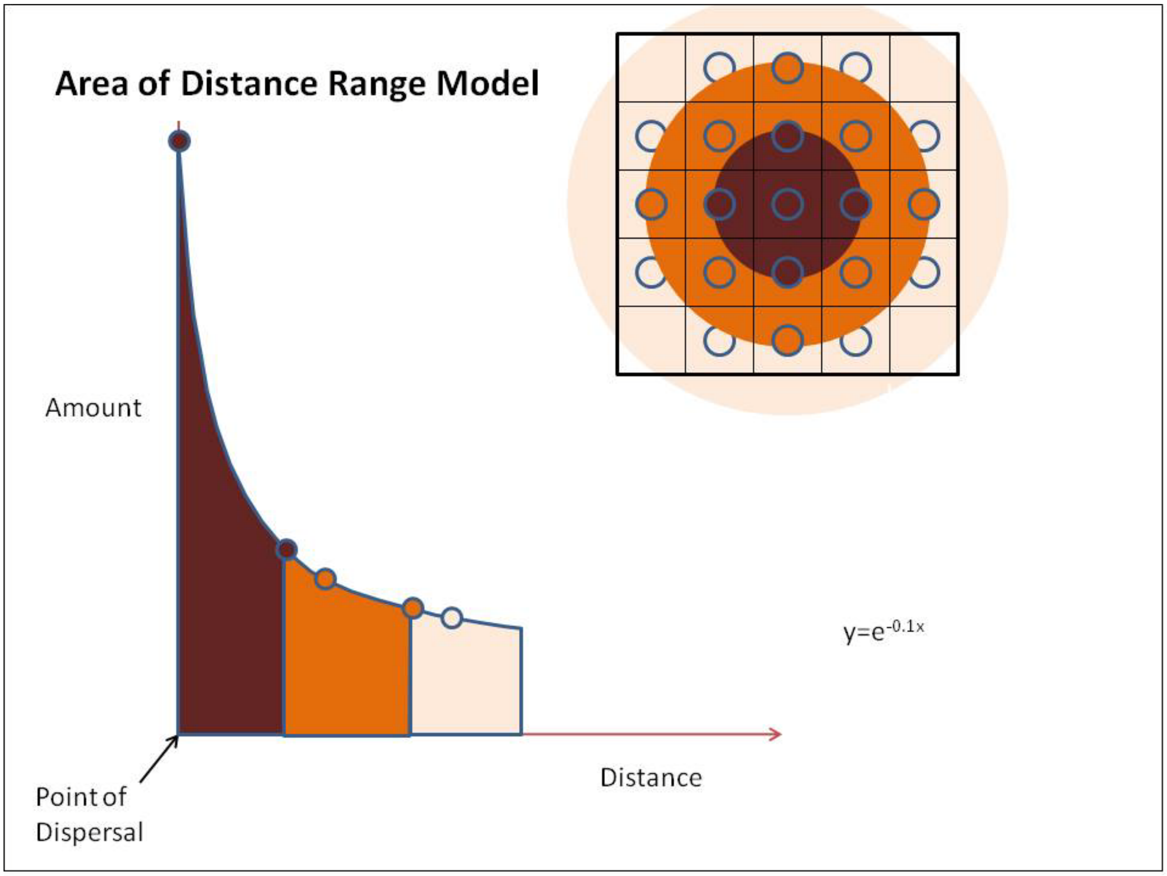


Figure 4.3. *Area of distance range* model of dispersal for λ = 0.1. Each colored area of the chart represents the area under the curve for each 10-unit distance range that is divided among the cell centroids within each distance range on the grid. Distance ranges include the cell centroids that fall on the outer range limits.

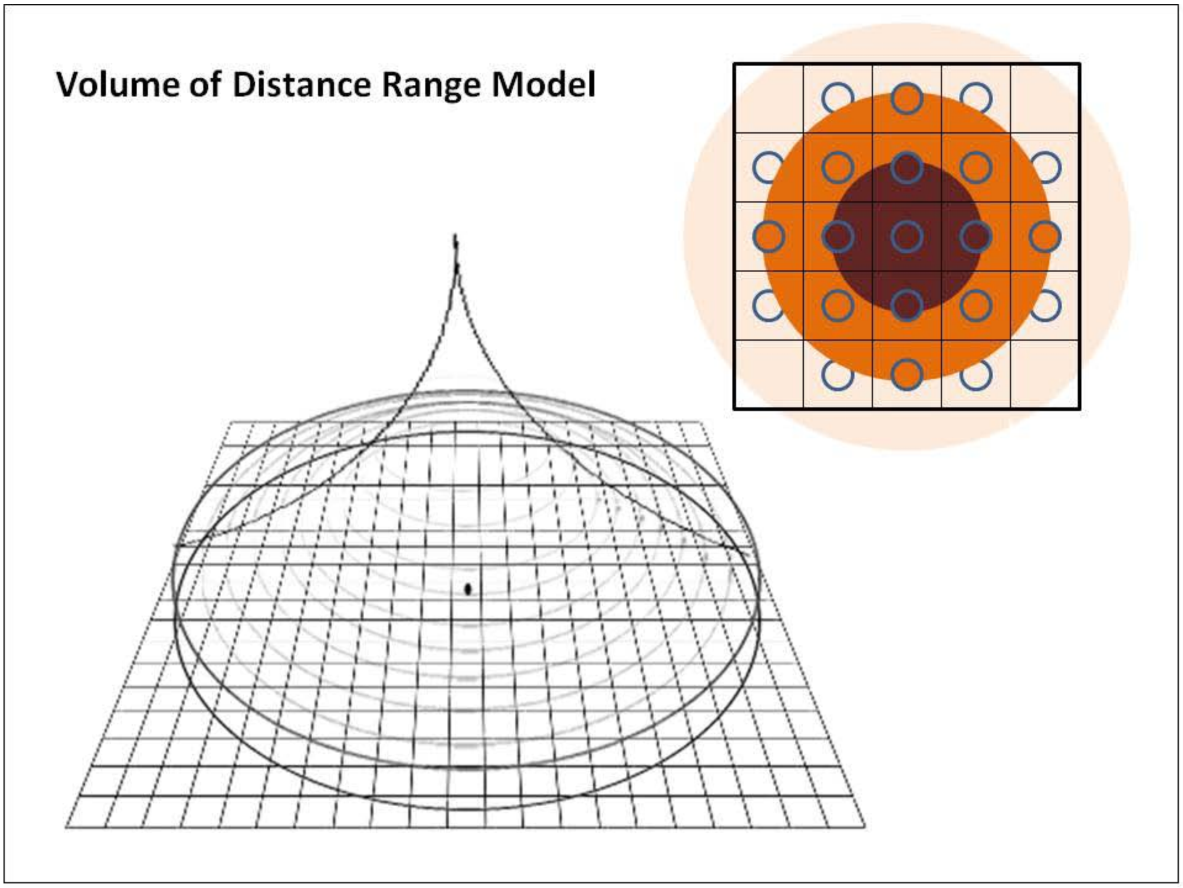


Figure 4.4. *Volume of distance range* model of dispersal. Colored rings represent the distance ranges under the curve surface for each 10-unit distance range whose volumes are divided among the cell centroids within each distance range. Distance ranges include the cell centroids that fall on the outer range limits. This model takes the areas of the distance ranges in the *area of distance range* model and rotates them around the axis of the origin of dispersal to make three dimensional shapes, with the volume of each defined by the annulus that constitutes its base and the height of the shape below the curve. Each volume is divided among the cell centroids within each distance range.

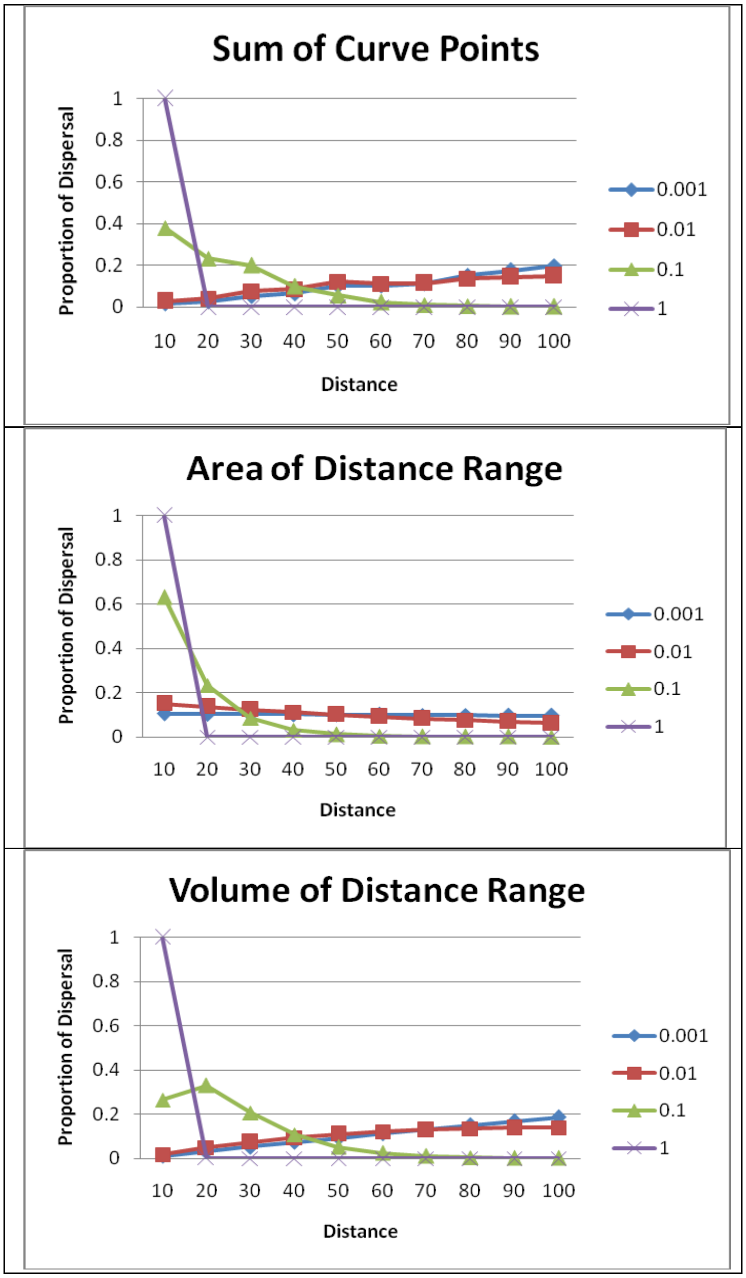
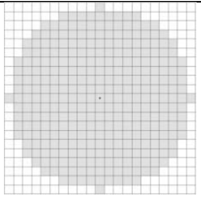
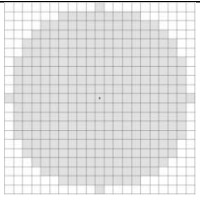
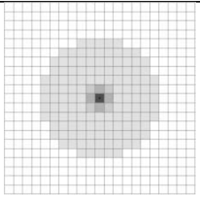
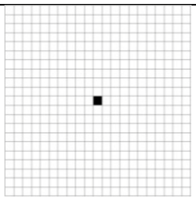
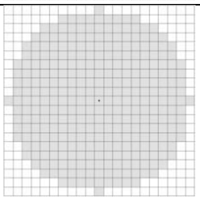
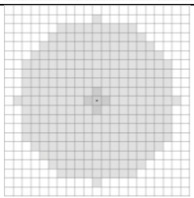
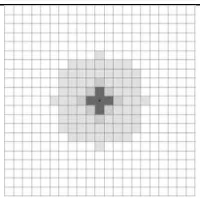
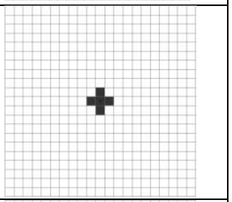
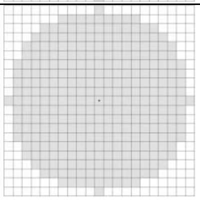
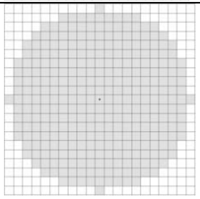
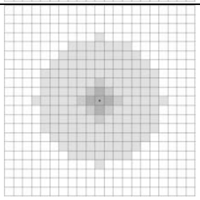
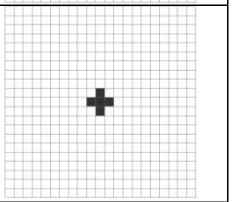


Figure 4.5. Three models of the distribution of the negative exponential dispersal curve to distance ranges for variable λ values. The proportion of a total dispersal amount of 1 is on the y-axis and 10 unit distance ranges are on the x-axis. The *sum of curve points* chart shows the sum of the proportion of dispersal of the cell centoids for each distance range. The *area of distance range* and *volume of distance range* charts show the proportion of dispersal to each distance range.

	$\lambda = 0.001$	$\lambda = 0.01$	$\lambda = 0.1$	$\lambda = 1$
Sum of Curve Points				
Area of Distance Range				
Volume of Distance Range				

□ 0 - <0.0002 ▨ 0.0002 - <0.025 ▨ 0.025 - <0.05 ▨ 0.05 - <0.075 ▨ 0.075 - <0.1

▨ 0.1 - <0.125 ▨ 0.125 - <0.15 ▨ 0.15 - <0.175 ▨ 0.175 - <0.2 ■ >0.9998

Figure 4.6. Three models of dispersal from a single dispersal cell to all cells within a defined dispersal limit of 100-units for λ values ranging from 0.001 to 1 in the dispersal curve $y=e^{-\lambda x}$. The shades of grey represent the proportion of a total dispersal value of 1 for each cell in the grid.

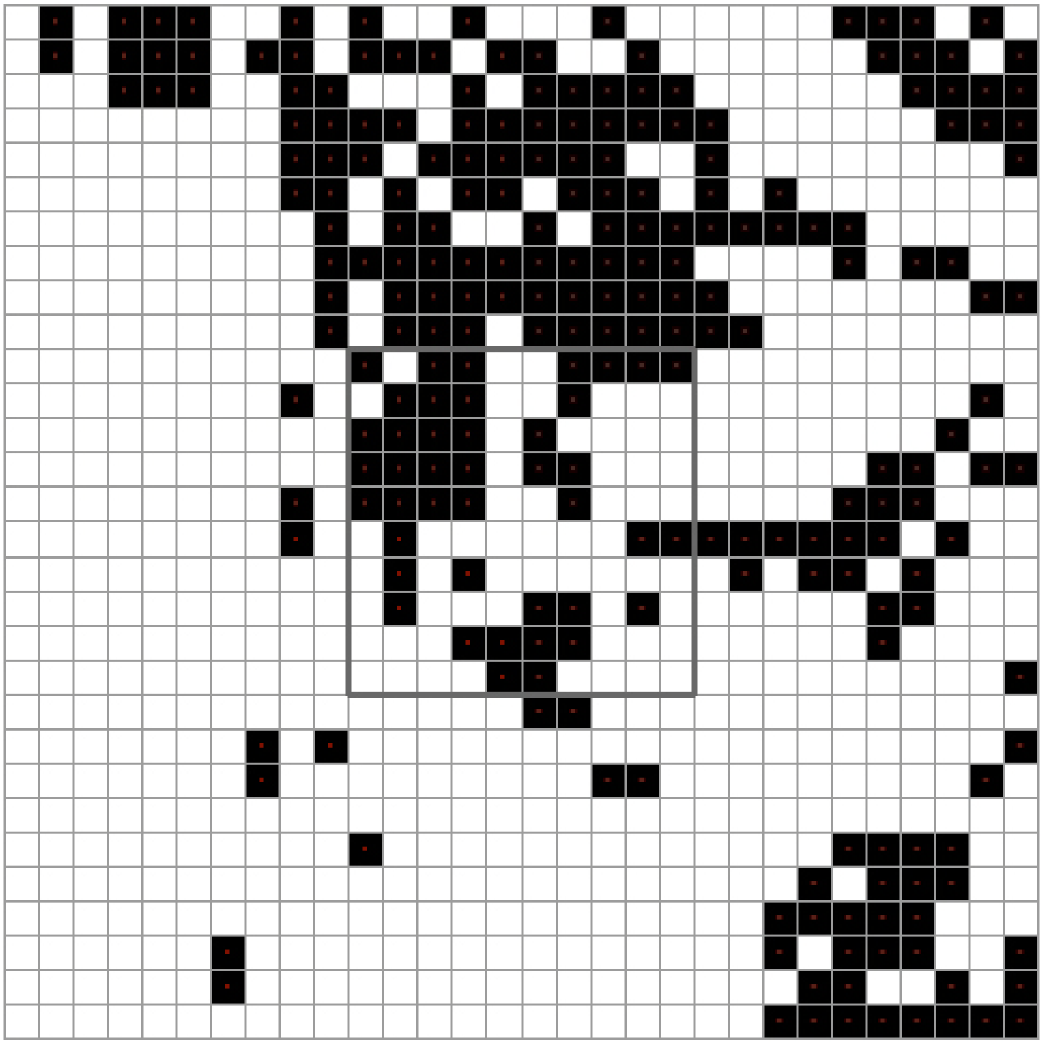
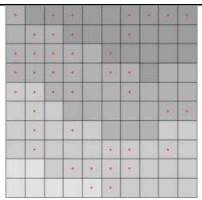
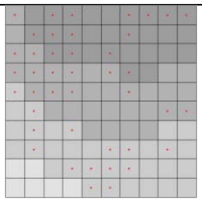
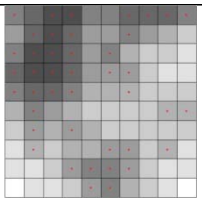
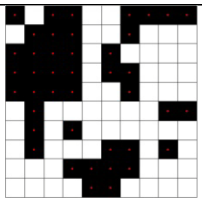
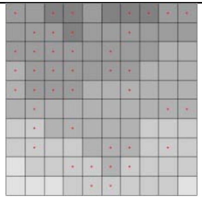
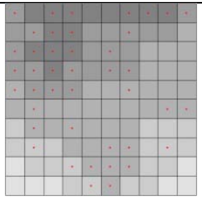
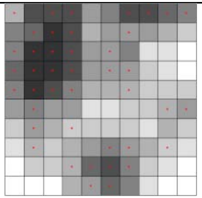
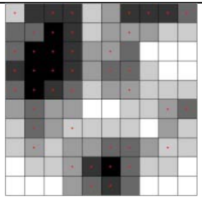
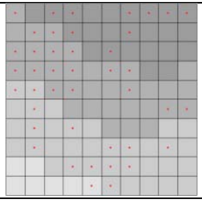
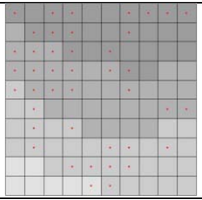
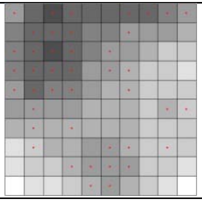
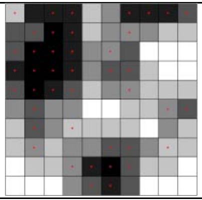


Figure 4.7. Multiple cell dispersal landscape with center analysis area highlighted in grey and dispersal cells in black with points for centroids. Cell sides are 10-units.

	λ = 0.001	λ = 0.01	λ = 0.1	λ = 1
Sum of Curve Points				
Area of Distance Range				
Volume of Distance Range				

□ 0 - <0.1 ▨ 0.1 - <0.2 ▨ 0.2 - <0.3 ▨ 0.3 - <0.4 ▨ 0.4 - <0.5

▨ 0.5 - <0.6 ▨ 0.6 - <0.7 ▨ 0.7 - <0.8 ▨ 0.8 - <0.9 ■ 0.9 – 1.0

Figure 4.8. Proportions of a total dispersal value of 1 to each cell within the analysis area for a multiple cell landscape for three models of dispersal based on variable λ values for the negative exponential curve $y=e^{-\lambda x}$. Analysis area includes the influences of cells within 100-units (the dispersal limit) of the analysis area. Dispersal cells are indicated by point centroids.

CHAPTER 5

CONCLUSIONS

This dissertation consists of three studies; an examination of the trends of forest cover and forest fragmentation in the Georgia Piedmont from 1974 to 2005 (chapter 2), a closer look at how the urban expansion of Atlanta has impacted the number and sizes of forest fragments in the metro Atlanta area (chapter 3), and a study that explores how to model dispersal in grid landscapes (chapter 4). Chapters 2 and 3 are linked through the use of a common data source, the GLUT data layers for Georgia, and their shared themes of trends of forest cover and forest fragmentation. Chapter 4 relates to chapters 2 and 3 through the examination of dispersal, which is a process that acts in the landscapes patterns of chapters 2 and 3. Each chapter is intended to be able to stand alone as a separate manuscript, though each chapter alludes to the broader themes of landscape processes and patterns.

The forests of the Georgia Piedmont rebounded strongly from the extensive deforestation that occurred from the time of European settlement through the early 20th century to be the dominant landcover in the Piedmont in the early 1970's (Bond and Spillers 1935, Brender 1974). Since the 1970's, however, forest cover has been declining in the Georgia Piedmont. The removal of forest cover up to the early 20th century was driven by the clearance of fields for agricultural purposes. This contrasts with modern deforestation in the Georgia Piedmont which is driven by the expansion of urban areas. The dominant urban area in the Georgia Piedmont is the city of Atlanta, which has been rapidly expanding in population and spatial extent since the middle of the 20th century. Atlanta's impacts on the forests are so great that the expansion of Atlanta is the primary driver of changes in forest cover and forest fragmentation in the Georgia Piedmont.

The traditional consequences of deforestation, besides the loss of forest, are increased fragmentation and increased forest edge. The second chapter of this dissertation shows how the expected consequences of deforestation can be complicated in a real world examination of deforestation by urban expansion. The modern expansion of the city of Atlanta initially produced the expected trends of loss of forest cover, increased fragmentation, and increased forest edge, but the continued growth of Atlanta eventually caused a loss of forest edge for the Piedmont and a decline in the number of forest fragments in the counties surrounding Atlanta. These results show that urbanization has more complicated impacts on forests than traditionally thought. Atlanta's urban expansion initially fragmented the surrounding forests but eventually began removing forest fragments. This transition reversed the trends of increased forest fragmentation and increased forest edge due to urban expansion, but serves as a warning that decreased forest fragmentation does not always indicate a healthier, more connected forest. Decreased fragmentation can also indicate the loss of forest fragments from landscapes.

Beyond the basic trends of increasing or decreasing fragmentation, the relationship between forest cover and forest fragmentation, the sizes of forest fragments, and the number of forest fragments in the counties surrounding Atlanta are strongly impacted by the growth of Atlanta. The third chapter of this dissertation examines how the spatial extent and numbers of different forest fragment size classes are impacted by the city of Atlanta at the county scale. The core metro Atlanta counties have different distributions of forest fragment sizes than surrounding counties. The second smallest fragment size class is the most prevalent size class in the core metro counties while the smallest fragment size class is the most prevalent size class in the surrounding counties. The core metro Atlanta counties are also losing forest area from the largest fragment size class while all the smaller fragment size classes are increasing in prevalence, which indicates that existing fragments are likely being further fragmented into smaller units with continuing urban development that is infilling the urban core. These trends in the core metro Atlanta counties are likely to occur in surrounding counties in the future as Atlanta's urban expansion extends ever farther from the center of the city.

The second and third chapters of this dissertation focus on the changing landscape patterns of forests in the Georgia Piedmont with a particular focus on the city of Atlanta. The fourth chapter looks at how ecological processes that occur in these landscapes can be modeled using a GIS. This approach integrates the themes of patterns and processes to develop an understanding of how processes occur based on real world landscape patterns. Both landscape ecology and biogeography have these themes as primary foci of their discipline (Turner 1989, Kent 2007). The ecological processes of pollen and seed dispersal are also intimately linked to population genetics as it is the movement of pollen and seeds that determines gene movement in landscapes and ultimately structures genetic variation of species. The field of landscape genetics has recently developed as an integrative field that studies the links between genetics and landscape patterns and processes (Manel et al. 2003).

The dispersal modeling of the fourth chapter shows how models of dispersal can be applied to grid landscapes and demonstrates the importance of considering the influence of dispersers outside the primary area of interest. It discusses the strengths and limitations of each model. The *sum of curve points*, *area of distance range*, and *volume of distance range* models all can be used to model dispersal in grid landscapes. The applicability of each model to studies of dispersal is contingent on how researchers want to apply dispersal curves to two spatial dimensions. These conceptual models can be applied to the dispersal curves developed by ecologists, biogeographers, and population geneticists to examine how dispersal occurs in landscapes. There are numerous factors that can influence how dispersal occurs in a landscape, but an isotropic null model of dispersal underlies all dispersal processes. This study developed the methods by which the null models of dispersal can be developed for any study. The factors that alter the null models of dispersal are specific to each study and can be applied to the null models developed in the fourth chapter of this dissertation.

The dispersal modeling in this dissertation is of great significance to the new field of landscape genetics as it allows information about dispersal process that impact genetic relationships to be modeled in grid landscapes that represent actual land cover or other physical characteristics. More work is needed to understand the fundamental relationships between dispersal process and landscape patterns, and biogeographers can be important contributors to this research. The knowledge of spatial modeling and expertise in GIS possessed by biogeographers position them as critical players in the interdisciplinary examination of the spatial aspects of genetic structure. This dissertation is an example of how biogeography can link the real world impacts of urban expansion on forest structure to the modeling of dispersal processes in fragmented landscapes and potential impacts on gene movement and genetic structure of species.

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