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3 **Lakeshore zoning has heterogeneous ecological effects: An application of a coupled**
4 **economic-ecological model**

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Abstract

Housing growth has been widely shown to be negatively correlated with wildlife populations, avian richness, anadromous fish, and exotic invasion. Zoning is the most frequently used public policy to manage housing development and is often motivated by a desire to protect the environment. Zoning is also pervasive, taking place in all 50 states. One relevant question that has received little research concerns the effectiveness of zoning to meet ecological goals. In this paper, we examined whether minimum frontage zoning policies have made a positive impact on the lakes they were aimed to protect in Vilas County, Wisconsin. We used an economic model that estimated when a given lot will be subdivided and how many new lots will be created as a function of zoning. Using the economic model, we simulated the effects of multiple zoning scenarios on lakeshore development. The simulated development patterns were then input to ecological models that predicted the amount of coarse woody debris (CWD) and the growth rate of bluegills as a function of residential density. Comparison of the ecological outcomes under different simulated zoning scenarios quantified the effect of zoning policies on residential density, CWD, and bluegill growth rates. Our results showed that zoning significantly affected residential density, CWD counts and bluegill growth rates across our study area, although the effect was less clear at the scale of individual lake. Our results suggest that homogenous zoning (i.e., for a county) is likely to have mixed results when applied to a heterogeneous landscape. Further, our results suggest that zoning regimes with a higher minimum shoreline frontage are likely to have larger ecological effects when applied to lakes that are less developed.

Keywords: biological-economic models, housing growth, human-natural systems, lakeshore development, landscape simulation, land use, policy, sustainability, zoning.

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INTRODUCTION

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The use of private land has critical importance for conserving ecosystem functions and services (Bean and Wilcove 1997, Wilcove et al. 1998, Daily et al. 2001, Rosenzweig 2003). In the United States, over 70% of land is privately owned, and more than two-thirds of the nation's threatened and endangered species are partially or fully dependent on privately owned habitat (Doremus 2003, Sanford 2006). Private land also supports habitat for more common species and generates a variety of ecosystem services (Daily 1997). The conversion of natural habitat on private land to more developed uses has broad-scale ecological impacts (Leu et al. 2008). However, ecosystem service benefits generated from private land accrue to a broader population than just the individual landowners themselves. Economic theory suggests that land-use policy can improve the efficiency of allocating land to habitat and developed uses when benefits are accrued by a larger public (Lewis and Plantinga 2007).

Policy attempts to preserve environmental benefits generated from private land take many forms in the United States. Regulations such as the Endangered Species Act and zoning are examples of direct government intervention concerning the allowable use of land. Other approaches use economic incentives, such as the Conservation Reserve Program, or the outright transfer of land to protected status through the purchase of development rights or in fee title. All these policy tools can and have been used to preserve the public good benefits derived from ecosystems located on private land. A relevant question concerns the effectiveness of such policy tools in securing ecosystem services, ecosystem function, and biodiversity.

The purpose of this study was to empirically quantify the ecological effects of minimum frontage zoning on lake shorelines in Vilas County, Wisconsin, USA. Our application is

70 implemented with a coupled economic-ecological model. An econometric model of private
71 landowner decisions (Lewis et al. 2009) was input to a land use simulation model of shoreline
72 development under varying zoning policies. The outcomes of the land use simulations were then
73 input into ecological models (Christensen et al. 1996, Schindler et al. 2000). Integrating the land-
74 use model directly with spatially-explicit landscape simulations and ecological models of
75 lakeshore habitat and sport fish growth rates allowed us to quantify the effects of zoning on
76 specific ecological metrics – thus, providing evidence concerning the efficacy of zoning to
77 preserve ecosystem function. Past studies have hypothesized that initial landscape
78 configurations have a large impact on the effectiveness of land conservation policies (Newburn
79 et al. 2005, Lohse et al. 2008). Therefore, we used our results concerning the effect of zoning on
80 ecological indicators to model how initial landscape conditions influence the impact of zoning.
81 Our results provide policy relevant evidence as to the types of lake shorelines in which zoning is
82 likely to be effective, and where it is likely to have little ecological effect.

83 Coupled economic-ecological models are often used to examine the effectiveness of
84 conservation policies because these models can quantify the trade-offs between ecological
85 indicators and economic returns. In forestry applications, coupled models have been used to
86 analyze maximum timber yields given certain ecological benchmarks (Nalle et al. 2004, Hurme
87 et al. 2007). At a broader scale, economic development has been weighed against the
88 preservation of a large assemblage of species and carbon sequestration (Polasky et al. 2005,
89 Nelson et al. 2008). In both the forestry and broad scale cases, the results have illustrated that,
90 with appropriate policy, economic returns and species preservation *can* be compatible.

91 A particularly important land conservation challenge is suburban and rural development
92 (Radeloff et al. 2005). While different types of development may have a variety of effects on

93 species (Lenth et al. 2006, Niell et al. 2007, Merenlender et al. 2009), the general trend is
94 widespread negative effects on wildlife habitat (Theobald et al. 1997), avian richness (Pidgeon et
95 al. 2007), anadromous fish (Lohse et al. 2008), and the likelihood of species invasions (Hansen
96 et al. 2005). The most widespread policy tool used to manage suburban and rural development is
97 zoning. Throughout the United States zoning is pervasive – all fifty states have enabling acts that
98 grant local governments the legal authority to implement zoning. Nearly all municipalities and
99 many rural areas have enacted zoning ordinances, and many ordinances have explicit
100 conservation goals. However, despite zoning’s prevalence and underlying conservation ethos,
101 little work thus far has focused on the basic question of whether zoning actually improves the
102 provision of ecosystem services from private land (however, see Langpap and Wu 2008 and
103 Lewis 2009 for two recent examples). In the last 12 years, only 11 articles have been published
104 in six leading conservation journals (Biological Conservation, Conservation Biology, Ecological
105 Applications, Ecological Monographs, Ecology, and Landscape Ecology) that match the topic
106 search for “conservation and zoning” but not marine (Web of Knowledge as of June 23rd 2009,
107 Appendix 1). None of these articles provide empirical estimation of the effects of zoning policies
108 on particular species or ecosystems. While not an exhaustive search of the literature, it is
109 emblematic of the lack of direct research on the conservation effects of zoning.

110 Zoning is a community effort to assign property rights concerning land-use (Mills 1990,
111 Jacobs 1998). As the U.S. Supreme Court famously asserted, zoning attempts to prevent “[the]
112 right thing from being in the wrong place, like a pig in the parlor instead of the barnyard
113 (Babcock 1969).” While zoning can prevent some land uses in some locations, it is important to
114 stress that zoning it is *not* a deterministic prescription for land use. Zoning deems some uses
115 permitted and others prohibited, however, there is likely a large range of landscape outcomes

116 possible within the realm of permitted uses. Zoning can influence many aspects of development,
117 including the size of a structure (height limits), the use of a structure (residential, commercial, or
118 industrial uses), and the placement of a structure (minimum set backs, clustering requirements)
119 to name just a few.

120 In our study the relevant zoning restriction is minimum shoreline frontage. Within the
121 minimum frontage requirement a land owner has a large range of development options. For
122 example, a minimum shoreline zoning requirement of 100 ft. (30.5m) lots does not prohibit
123 landowners from developing 200 ft. (61m) lots if they so choose. It is common in the recent
124 conservation literature to assume that land development occurs at the maximum density allowed
125 by zoning constraints that specify minimum lot size (e.g., Conway and Lathrop 2005, Pejchar et
126 al. 2007). This assumption confuses the private property owner's right to develop at a certain
127 density with a duty to do so. There is evidence that actual development does not always occur at
128 maximum density (although it may in some settings). For example, in exurban Maryland only
129 8% of newly created subdivisions develop to their full built-out state (McConnell et al. 2006).
130 Similarly, only 15% of subdivisions on northern Wisconsin lakeshores take place at the
131 maximum density allowed by zoning (Lewis et al. 2009). If subdivisions do not occur at their
132 maximum density, the policy effects of zoning cannot be deduced by a simple comparison of
133 deterministic landscapes.

134 Three effects of zoning on development are relevant in our setting. First, zoning may
135 have little effect on land markets and land conversion (Wallace 1988). In this case, zoning is
136 simply enacted in a way that reflects what would have taken place under a market scenario in the
137 absence of zoning. Zoning can also have little effect in cases where zoning is not enforced or
138 zoning laws change often (in our specific case, however, minimum frontage zoning is nearly

139 always enforced, and the zoning laws changed at most once over the 24 years of our study).
140 Second, zoning can act to constrain landowner's development decisions, and this is typically the
141 intended outcome of zoning policies. Third, zoning can also *increase* the probability that a lot
142 develops by increasing the open-space amenities in the neighborhood of the lot. There is
143 evidence that development rents are higher on landscapes with stricter zoning (Spalatro and
144 Provencher 2001), and any policy that increases the returns to residential development will
145 reduce the time to land-use conversion in formal economic models of land-use change (e.g.,
146 Capozza and Helsley 1989).

147 Development on lakeshores – the development process studied here – differs from the
148 commonly studied development of agricultural or forested land to residential uses (e.g.,
149 Bockstael 1996, Irwin and Bockstael 2004, Carrion-Flores and Irwin 2004). On lakeshores, the
150 typical decision is to subdivide an *existing* residential lot to increase its density. Therefore, if a
151 zoning policy that constrains lakeshore development generates open space amenities for
152 shoreline residents, then its effect on the probability of development is ambiguous because
153 zoning increases both the economic returns to the subdivision and the returns from keeping the
154 lot in its current state (Lewis et al. 2009). Thus, zoning's ultimate effect on landscape pattern is
155 an empirical question.

156 This study provides four main contributions. First, we quantified the ecological effects of
157 zoning by developing a coupled economic-ecological model focused on two ecological
158 indicators: coarse woody debris (CWD) in the littoral zone, and the growth rate of bluegills
159 (*Lepomis macrochirus*). Second, we analyzed the conditions under which zoning is likely to be
160 an effective policy for limiting the effects of shoreline development, thus offering a targeting
161 strategy for the application of zoning. Third, we applied a methodology developed by Lewis

162 (2009) that links econometric and ecological models to account for multiple sources of model
163 variation. There is significant uncertainty in both economic and ecological models, and our
164 methodology accounted for the estimated uncertainty in model parameters and sources of model
165 variation. Finally, we conducted a rigorous examination of empirically estimated distributions of
166 landscape change in response to policy scenarios.

167 **METHODS**

168 *Study Area*

169 We investigated the ecological effect of minimum shoreline zoning in Vilas County, WI.
170 Vilas County offered a unique opportunity to answer both policy and methodological questions
171 related to measuring and interpreting the effects of minimum shoreline zoning on littoral ecology
172 because: 1) residential development has increased in the county, 2) the ecological effects of
173 residential development have been well documented, 3) zoning is the main policy used to limit
174 residential growth, and 4) the goals of shoreline zoning contain explicit conservation goals.

175 Vilas County is located in Northern Wisconsin (Fig. 1). The county harbors 1320 lakes,
176 and water covers almost 15% of the surface area. The lakes of Vilas County are generally
177 nutrient poor, and many are connected by groundwater (Kratz et al.1997; Riera et al. 2000). Most
178 lakes are surrounded by second-growth forests (Curtis 1959). Old-growth of *Acer saccharum*
179 (sugar maple) and *Tsuga canadensis* (eastern hemlock) is limited to a few scattered reserves
180 (Mladenoff et al. 1993).

181 Abundant lakes make Vilas County a popular destination for vacations and second home
182 ownership. Over the course of our study, from 1974 to 1998, shoreline residential density
183 increased by 24% across the lakes in our sample, and over 50% of all homes in Vilas County are
184 located within 100m of a lake (Schnaiberg et al. 2002). In general, the lakes of Northern

185 Wisconsin face increasing disturbance due to residential development (Radeloff et al. 2001,
186 Scheuerell and Schindler 2004, Gonzalez-Abraham et al. 2007). Development has been linked to
187 a host of lake ecosystem changes (Carpenter et al. 2007) including the clearing of sunken logs
188 leading to decreased coarse woody debris (CWD) (Christensen et al. 1996, Marburg et al. 2006),
189 reduced growth rates for bluegills (Schindler et al. 2000), reduced populations of green frogs
190 (Woodford and Meyer 2003), and increased nutrient loading into lakes (Schindler 2006).

191 In order to reduce the effects of development on lakes, some townships in Vilas County
192 have used zoning since the 1950s to limit rapid residential growth. In 1965, the State of
193 Wisconsin passed a statute (Wisconsin Administrative Code Chapter NR 115) mandating at least
194 100 ft (30.5 m) of frontage for all residential shoreline lots. Between 1974 and 1998, seven of the
195 14 townships in Vilas County further strengthened zoning ordinances and required at least 200 ft
196 (61 m) of frontage for new lakefront lots. Shoreline zoning is a particularly relevant example in
197 which to examine the conservation effects of zoning. The legal statute which establishes
198 statewide shoreline zoning specifies that shoreline zoning is needed to “prevent and control
199 water pollution; protect spawning grounds, fish and aquatic life; control building sites, placement
200 of structure and land uses and reserve shore cover and natural beauty (State of Wisconsin 2009).”
201 Therefore, the motivation for shoreline zoning matches well with general goals of conservation
202 as well as the specific ecological indicators used in this study.

203 *The Economic and Ecological Models*

204 *The economic model*

205 We used an existing economic model to predict the probability that subdivision will
206 occur, and how many new lots are created by each subdivision (Lewis et al. 2009). A panel
207 dataset representing subdividable lots on 140 lakes from 1974 to 1998 was used as input to the

208 econometric model. Parameter values were estimated using a jointly estimated Probit-Poisson
209 model, which accounted for unobserved spatial heterogeneity and sample selection bias. In
210 particular, a suite of lot specific characteristics (e.g. lot size, soil restrictions for development),
211 lake specific characteristics (e.g., lake size, water clarity, and development density), time specific
212 dummy variables, interactions between characteristics, and random effects were used to estimate
213 the Probit model based on observed lot subdivisions. The Probit portion of the model identified
214 the factors that affected the probability that landowners subdivide. If a subdivision occurred, a
215 Poisson count model was estimated using a similar set of variables to determine the expected
216 number of new lots created.

217 In prior studies, we showed that the effects of zoning on development were variable
218 (Lewis et al. 2009, Lewis 2009). Increased residential zoning did not significantly change the
219 probability of lot subdivision. However, zoning did reduce the expected number of new lots
220 created when a subdivision occurred. The overall effect of zoning, therefore, is to reduce
221 development density over time in our study area relative to a counter-factual scenario with less
222 restrictive zoning.

223 *Coarse Woody Debris Model*

224 CWD is an important link between lakes and forest ecosystems in Northern Wisconsin,
225 promoting production of benthic invertebrates, and offering refuge to prey fishes, which in turn
226 are consumed by piscivorous fishes (Roth et al. 2007). Christensen et al. (1996) modeled the
227 amount of CWD located along a given shoreline as a function of residential density for 16 lakes
228 located in Vilas County and the adjoining county to the north, Gogebic County, Michigan. The
229 lakes were selected to represent a gradient of residential densities. CWD abundance was sampled
230 on a total of 125 plots. When analyzing the mean CWD for each lake, the amount of CWD was

231 significantly and negatively correlated with residential density (Christensen et al. 1996). The
232 precision of the estimate was lowered somewhat due to the large variation in CWD on lakes with
233 no development. Overall, 71% of the variation in CWD was explained by residential density. We
234 directly integrate the estimates from this research; specifically we use the estimated equation:

235 $CWD = 628 - 500 * \log_{10} RD + e$ (page 1146 in original text), where RD is equal to the
236 residential density in cabins per kilometer, to estimate CWD in our land use simulation setting.

237 *Bluegill Growth Rate Model*

238 Schindler et al. (2000) modeled the growth rate of bluegills in northern forested lakes as a
239 function of residential density. Their study included samples from 14 lakes in Vilas County,
240 Wisconsin and Gogebic County, Michigan. Fish sampling was performed in June and July of
241 1996. Electroshocking took place 30 minutes after sunset along the 1 m depth contour. Collected
242 fish were identified to species, and their lengths were measured to the nearest 1 mm. Weight
243 measurements and scale samples were taken from most collected bluegills. Bluegill growth rates
244 were determined with the Fraser-Lee method (Schindler et al. 2000). Statistical models showed
245 that bluegill growth rates declined as housing density increased, but the relationship is non-
246 linear. When density increases from 0 to 1 residence/km, bluegill growth rates drop by nearly
247 4mm/yr. However, as residential density increases further, the effect of an additional residence
248 becomes less pronounced; the marginal change in bluegill growth is only 0.7 mm/yr when
249 density increases from 5 to 6 residences/km, and by the time density reaches 10 residences/km
250 the marginal change for an additional residence is only 0.36 mm/yr. The original estimates from
251 Schindler et al. (2000) are directly applied to the land use simulation in this paper:

252 $\log_{10} Growthrate = 1.50 + -.11 * \log_{10}(RD + 1) + e$ (page 234 in original text).

253 *Using the econometric model to simulate residential development*

254 The economic model provides an estimate of the probability that a parcel subdivides,
255 along with probabilistic estimates of the number of new lots upon subdivision. These transition
256 probabilities are functions of parcel-scale and lake-scale covariates, including the zoning status
257 of each lake. Spatial data on each covariate in the economic model is used to link the estimated
258 transition probabilities to specific parcels along each lakeshore. The transition probabilities are
259 then used as a set of rules determining the development path of each parcel in a series of Monte
260 Carlo simulations programmed with original Matlab code. The simulation model predicts the
261 time-path of development decisions for each parcel on the landscape over the time period of our
262 study – 1974 to 1998. These simulations provided estimates of development density used as input
263 to the ecological models. Since the economic model is a function of zoning, it provides the basis
264 for simulating the effects of different zoning scenarios– 100 ft., 200 ft., 300 ft., and 400 ft.
265 minimum frontage – on landscape and ecological change. This methodology allows us to
266 compare the effects of zoning on residential density, CWD, and bluegill growth over the four
267 zoning scenarios for the time period 1974-1998. Thus, the simulation model estimates *counter-*
268 *factual* paths that lakes zoned 100 ft. could have taken from 1974 to 1998, had they been zoned
269 differently. A more detailed description of this methodology follows.

270 In order to include all sources of variation from the economic model, and thereby
271 represent the stochastic nature of land use change, we followed Lewis (2009) and introduced
272 three stochastic elements to the landscape simulations. First, we draw a set of parameter values
273 for the economic model by implementing the Krinsky-Robb procedure (Krinsky and Robb 1986,
274 Lewis 2009). Using this procedure, the parameters are random variables drawn from the
275 asymptotic distribution of the parameter estimates of the econometric model. Second, following
276 Lewis and Plantinga (2007) and similar to Markov models, we interpreted the fitted subdivision

277 probabilities as a set of rules that govern land-use change. That is, if the subdivision probability
278 for a particular lot is 0.1, the owner of the lot will subdivide 10% of the time, given that the
279 choice is repeated enough times. Third, the number of new lots created was determined
280 stochastically by an iterative process using the estimated Poisson probabilities. For a given lot,
281 the Poisson probability that one new lot is created is compared to a random number on the unit
282 interval. If the Poisson probability is greater than the random number, one new lot is created. If
283 not, then the random number is compared to the Poisson probability that two new lots are
284 created. This process continues until either the random number is smaller than the Poisson
285 probability for a given number of lots – at which point that number of lots is assigned to the lot –
286 or the maximum number of new lots given the zoning regime is reached. Fourth, all lot and lake
287 level characteristics were updated in the model, and the simulation continued onto the next time
288 period - the simulation was run in four year intervals over the time period 1974 to 1998.

289 The four steps above generated a unique simulated landscape that reflected the estimated
290 economic parameters and the stochastic nature of development. From this simulated landscape,
291 we calculated the residential density under the assumption that each lot had one residence. To
292 bolster our assumption, we used aerial photos from 1996 and 2001 to digitize all residence on
293 our sample lakes. We found, on average, 1.1 buildings per lot. Given that some of these
294 buildings are likely not residences, we assumed that the one residence per lot was reasonable. In
295 order to obtain robust results, the simulation was run 1000 times, a process that generates 1000
296 landscape configurations consistent with the underlying economic model of landowner behavior.

297 A few important assumptions stemming from the economic model and landscape
298 simulation deserve additional attention. First, the land use conversation model is a partial-
299 equilibrium model; therefore as zoning regulations change, demand for shoreline lots remains the

300 same. That is, in this model, increased regulation in Vilas County will not shift the demand curve
301 for new shoreline lots. Second, the effect of zoning was econometrically estimated on lakes that
302 were zoned either 100 ft. or 200 ft. minimum frontage - Lewis et al. (2009) estimate the model
303 with a binary zoning indicator (1=200 ft.; 0=100 ft.). Simulations for 300 ft. and 400 ft. zoning
304 provide a richer set of scenarios, but require us to use the model with minimum frontages beyond
305 the range of the data used in estimation. We re-scale the zoning indicator as a function of the
306 minimum frontage: $(Zone - 100)/100$, where $Zone = 100, 200, 300, \text{ or } 400\text{ft}$; thereby allowing us
307 to simulate zoning scenarios of 300 and 400 ft. minimum frontage. Due to the non-linear
308 Poisson model, we find diminishing effects of stricter zoning on the expected number of new lots
309 upon subdivision.

310

311 *Estimating the effect of policy changes on residential development and lake ecology*

312 We estimated the effect of changing zoning regulations on residential density, the amount
313 of CWD, and bluegill growth rates across a set of 89 lakes that were zoned 100 ft. minimum
314 frontage from 1974 to 1998. We examine three counter-factual zoning scenarios where the
315 minimum frontage was increased to 200, 300 and 400 ft (61, 91, and 122 m) respectively. The
316 effect of each zoning scenario is evaluated relative to a baseline simulation with 100 ft. minimum
317 frontage. In each zoning scenario, lots which could no longer subdivide under the minimum
318 frontage were dropped from the simulation – for example, a lot with 400 ft. frontage cannot
319 subdivide under the 300 and 400 ft zoning regimes, but can subdivide under the 200 ft scheme.
320 Also, the maximum number of new lots that could be created was updated for each lot under the
321 alternative zoning scenarios.

322 After the three hypothetical scenarios depicting the new zoning rules were run 1000 times
323 each, residential density, CWD counts and bluegill growth were estimated for each simulation.
324 This was done by applying each simulated residential density pattern to the CWD and bluegill
325 growth models. Rather than applying the estimated coefficients of the ecological models at the
326 mean parameter values (which would ignore the unexplained variance in the ecological models),
327 we modeled the stochastic nature of the parameters by drawing 1000 different parameter values
328 from a normal distribution with the mean and variance given from the estimates (Fig 2).

329 The combination of land use simulations and drawn parameter values from the
330 ecological models resulted in 1000 simulated values of residential density, CWD and bluegill
331 growth for each lake, and for the landscape as a whole, at *each* of the four zoning scenarios (100,
332 200, 300, and 400 ft minimum frontage). We compared these distributions to quantify the effects
333 of zoning. Each distribution (89 lakes + the landscape level = 90 observations x 4 zoning

334 scenarios x 3 indicators = 1080 total distributions) was tested for normality using the
335 Kolmogorov-Smirnoff test. All distributions failed this test. Therefore, non-parametric methods
336 were used to analyze the changes in the distribution, median, variance, and skewness for varying
337 policies and indicators.

338 Distributions were compared using a two sample Kolmogorov-Smirnoff test which
339 indicated if the distributions of indicators on the same lakes differed among policies. In addition,
340 a Wilcoxon rank-sum test was conducted on paired distributions to test for changes in the
341 median. To test for changes in the distribution's variance and skewness, 10,000 variance and
342 skewness estimates were bootstrapped for each distribution. These bootstrapped distributions of
343 variance and skewness were then compared using a two sample Kolmogorov-Smirnoff test to
344 test for changes in the distributions of the variance and skewness across distributions. Finally,
345 Wilcoxon rank-sum tests were run to test for changes in the median of variance and skewness of
346 each lake and of the landscape as a whole.

347 We hypothesized that initial lake conditions strongly influence the ability of zoning to
348 decrease residential density, increase CWD, and increase bluegill growth rates on a given lake. If
349 this is the case, a helpful policy exercise is to group lakes with similar initial conditions, and then
350 compare the effects of zoning across lakes with different initial conditions. We use the following
351 methodology to group lakes together. Each of the 1000 simulated residential densities, CWD
352 counts, and bluegill growth rates for the 100 ft. zoning policy were randomly matched with a
353 simulated outcome from the 400 ft. zoning simulation. Differences between matched pairs were
354 taken to create a distribution of policy effects that arise due to a zoning increase from 100 to 400
355 ft. We use a stepwise weighted least squares procedure to estimate the effects of various initial
356 lake conditions on the simulated policy effects. From 18 possible variables, the percent of

357 shoreline that is subdividable, and the average size of subdividable lots, prove to be the most
358 important variables in explaining the effect of initial conditions on the effect of zoning –
359 regression results are available from the authors upon request. Lakes were then sorted into
360 groups based on these variables and differences between outcomes were compared.

361 **RESULTS**

362 Comparing the simulated landscape change with the actual landscape over the period
363 1974 through 1998 provided an accuracy assessment of our model. Overall, the simulated
364 landscapes were similar to the actual landscape at the end of the study period. On average, the
365 model predicted the number of subdivisions across the study area within 3%, and the number of
366 new lots created within 2%. At the lake scale, the average absolute deviation between the actual
367 number of new lots created and the results of the simulation was approximately 6 lots. Using the
368 1000 simulations for each lake as the empirical distribution, the actual number of new lots
369 created on each lake was within one standard deviation of the average number of predicted new
370 lots on 86% of the 140 lakes in our sample. Further, our results shed light on the importance of
371 modeling development *density* with the Poisson model, as opposed to simply assuming that all
372 subdivided lots are developed at their maximum allowable density. Results indicate that a
373 maximum density assumption overestimates the number of new lots created by 257% - see Lewis
374 (2009) for further discussion.

375 At the landscape scale, our results suggest that zoning likely changed development
376 density and CWD, but did not have much effect on bluegill growth rates according to the two-
377 sided Kolmogorov-Smirnov tests. Looking at the medians, we found statistically significant
378 changes in density and CWD for changes between 100 vs. 200 ft., 100 vs. 300 ft., 100 vs. 400 ft.,
379 and 200 vs. 400 ft. zoning, but not for the 200 vs. 300 ft. or 300 vs. 400 ft zoning (Table 1).

380 Median bluegill growth rates did not differ significantly between any policies. Looking at the
381 bootstrapped variances and skewness values, at the landscape scale the two-sided Kolmogorov-
382 Smirnov test rejected the null hypothesis of equal distributions for density and CWD across all
383 policy changes, but could not reject the null hypothesis that bluegill growth rate distributions
384 remained the same (Fig. 3).

385 We found similar results when examining the effect of zoning on individual lakes (Table
386 2). In general, for density and CWD distributions, medians, variances, and skewness changed
387 between policies for most lakes. However, significant changes in bluegill growth only occurred
388 on a few lakes. The two-sided Kolmogorov-Smirnov test suggested different distributions among
389 policies for every lake for density and CWD, but no significantly different distributions for any
390 lakes for bluegill growth.

391 Following the stepwise regression results, lakes were divided by initial conditions
392 according to two variables representing the development density of lakes: percent of shoreline
393 that is subdividable (PPS), and average size of subdividable lots (ASP). Graphical analysis does
394 not reveal any breaks in the data where the policy effect of zoning changes sharply. Hence, we
395 use heuristic breaks to separate the lakes into three groups: High Development ($PPS \leq 33\%$ $n=27$;
396 $ASP \leq 500ft$ $n=20$), Medium Development ($66\% \leq PPS < 33\%$ $n=40$; $1000ft \leq ASP < 500$ $n=40$), and
397 Low Development ($PPS > 66\%$ $n=20$; $ASP > 1000ft$ $n=27$). Statistically significant changes in the
398 medians were found between each group for both variables (Figures 4 and 5), although the
399 magnitude of the change for bluegill growth was quite small. Geographically, the lakes in
400 different categories are dispersed rather randomly across the landscape (Figures 6 and 7).

401

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DISCUSSION

403 Our results showed that minimum frontage zoning policies on lake shorelines
404 significantly reduced residential density and increased CWD counts. However, bluegill growth
405 rates were, in general, not changed by zoning. Across the larger landscape, our results suggest
406 that zoning policies have heterogeneous effects on different indicators of ecosystem function.

407 Results for individual lakes were similar to the results obtained for the entire landscape.
408 Changes in the median, variance, and skewness occurred on a large number of lakes for
409 development density and CWD, but not for bluegill growth. As the level of zoning increased,
410 results indicated that more lakes exhibit lower density and higher CWD counts, although bluegill
411 growth rates changed little. Furthermore, our results showed diminishing ecological “returns” to
412 zoning. That is, zoning had the greatest effect when raising the minimum shoreline frontage from
413 100 to 200 ft. Additional zoning did further change the distributions of the ecological metrics,
414 but by less than a change of 100 to 200 ft. These results are undoubtedly influenced by the non-
415 linearity of the economic model of development density as a function of zoning, and the non-
416 linearity of the ecological model as a function of development density.

417 The variation in the observed effects among different lakes also suggested that zoning is
418 not uniformly effective. Initial development conditions on a lake were a good predictor of
419 zoning’s effectiveness. In general, zoning worked best on relatively undeveloped lakes, where
420 lots are relatively large, and where no one land owner’s decision has a disproportionate effect on
421 shoreline density. Prudent policy may focus zoning on such lakes.

422 The coupled economic-biological model allowed the variance present in the econometric
423 and ecological models to be fully propagated throughout the simulations. The Krinsky-Robb
424 method (Krinsky and Rob 1986) was used to draw the parameters of the econometric model. The
425 Markov type landscape simulation model captured the stochastic nature of landscape

426 development and provided a distribution of possible landscape outcomes. Finally, the parameters
427 of the biological models were modeled as random parameters drawn from a normal distribution
428 with the mean and standard deviation of each parameter. Taken together, these techniques
429 provided simulation outputs that accounted for model variation in the estimated parameters and
430 in the error components.

431 Propagating errors caused, of course, confidence intervals to become larger. Reducing
432 variance is rarely a major goal in ecological modeling and model selection focuses on model
433 accuracy (i.e., a predicted mean without any bias) rather than model precision (i.e., smaller
434 confidence limits). However, reducing the variance is essential if the ultimate goal is to build
435 integrated models of coupled human-natural systems, and lower variance may even justify minor
436 bias in the predicted means. Alternative model selection tools such as Lasso (Tibshirani 1996)
437 that minimize variance may be particularly valuable for integrated economic-ecological models.

438 Our findings with regards to variance and skewness of the estimated distributions have
439 important policy implications that have been mostly ignored in previous coupled landscape
440 simulation models (Lewis and Plantinga 2007; Nelson et al. 2008). With our econometric
441 estimates, stricter minimum frontage zoning decreased development. Therefore, variance
442 necessarily decreased with increased zoning, and the distributions became generally more
443 skewed to the left of the mean. From a policy perspective, this means that the likelihood of a bad
444 ecological outcome decreased with an increase in zoning. Hence, even though zoning cannot
445 assure an outcome on a lake, it can have the policy-relevant effect of reducing the likelihood of
446 extreme outcomes that may be undesirable.

447 From a modeling perspective, our results highlighted the importance of the functional
448 form of the underlying models. In this application, the non-linearity of the bluegill growth rate

449 model meant that even large changes in residential density caused only small changes in the
450 bluegill growth rate once residential density reached a threshold of approximately 5 residences
451 per km. Since 83% of the lakes in our sample had a density higher than this threshold at the
452 beginning of our study, it was not surprising that zoning had little effect on bluegill growth rates
453 for most lakes. This finding is an empirical demonstration of the importance of ecological
454 thresholds for conservation targeting (Wu and Boggess 1999), and the management implication
455 is that efficient bluegill conservation efforts should be targeted towards lakes that are relatively
456 undeveloped, as even small changes to density on these lakes can have large ecological effects.
457 In addition, the ecological models we used suggested that CWD goes to zero at 18 residences per
458 km, which is within the simulated range of densities we estimate. Hence, our model suggests that
459 highly developed lakes with no CWD are possible.

460 We found that lakes could be classified into groups based on various measures of their
461 initial development level. Relatively undeveloped lakes had a higher percentage of shoreline that
462 is subdividable and larger subdividable lots on average. Our results indicated that stricter
463 minimum frontage zoning standards had a larger ecological effect on relatively undeveloped
464 lakes. Classifying lakes into categories based on their initial development levels provides a
465 simple measure that enables zoning to be targeted towards lakes where it can have the largest
466 ecological effect.

467 One notable exception to these results takes place on lakes where nearly all of the
468 shoreline is owned by one landowner; two such lakes exist in our dataset. On these lakes, the
469 average effect of zoning is negligible even though most of the shoreline is subdividable and the
470 size of the subdividable lot is large. In this case, the important question is not at what density the
471 landowner will develop, but rather will the lot be developed at all? Indeed, the two lakes where

472 one individual owns most of the shoreline face large potential changes in ecosystem indicators in
473 the event of development (density increases from less than 1 lot per km to on average over 20),
474 regardless of zoning regime. In such cases, alternative conservation methods, such as direct
475 purchase of the large lot or its development rights, may be useful.

476 In general, our results suggest that zoning can be an effective conservation tool only
477 under certain conditions. These findings are important in light of the various economic costs and
478 benefits associated with zoning. A stricter minimum frontage zoning policy generates costs to
479 landowners by constraining them from subdividing and selling off lots (Spalatro and Provencher
480 2001). Further, if strict zoning significantly reduces the supply of developable land, then lower-
481 income individuals may become priced out of strictly zoned neighborhoods (Glaeser and Ward
482 2008). In contrast, stricter zoning can yield economic benefits by 1) increasing the market value
483 of land due to a greater amount of open-space (Spalatro and Provencher 2001), and 2) producing
484 a non-market public good in the form of enhanced ecosystem services. Importantly for the
485 purpose of this paper, a zoning policy will yield *fewer* benefits to the public at large when zoning
486 results in minimal effects on ecosystem services. The modern property rights movement (also
487 known as the “wise-use” movement or anti-environmental movement) has gained momentum
488 from cases where community appropriation of property rights disadvantages a landowner with
489 little clear benefit to the public (Jacobs 1998). Strict zoning on lakes that are already nearly
490 “built up” may be another case of this. An efficient application of zoning must carefully target
491 zoning constraints towards landscapes where it will have significant environmental effects –
492 relatively undeveloped lakes in our application – and avoid placing constraints on landscapes
493 where it will yield minimal gains.

494 In extending our analysis to different landscapes where zoning is used, we suggest that
495 future research investigate the following hypothesized generalizations: 1) the most common
496 zoning controls (lot size minimums), are unlikely to provide certain ecological benefits at the
497 individual lot scale, but may have strong landscape scale effects; 2) at the intermediate scale
498 (such as lake level effects in our research), stricter zoning has larger ecological effects on
499 relatively undeveloped landscapes; and 3) conservation at the lot scale can only be certain when
500 all development rights are fully captured by the community; either through zoning or outright
501 purchase.

502

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508

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646

647 Table 1. Changes in landscape scale medians. The diagonal of the matrix (bolded) is the
 648 landscape scale median. The upper right hand side of the matrix (italicized) is the absolute
 649 change between medians for varying policies. The lower left corner (underlined) is the
 650 percentage change in medians for varying policies. * denotes significance at p<0.05

		<i>Change in median residential density (%)</i>			
Zoning scenario	100 ft	200 ft	300 ft	400 ft	
100 ft	10.0772	-0.7672*	-1.0472*	-1.1972*	
200 ft	<u>-0.07613</u>	9.31	-0.28	-0.43*	
300 ft	<u>-0.10392</u>	<u>-0.03008</u>	9.03	-0.15	
400 ft	<u>-0.1188</u>	<u>-0.04619</u>	<u>-0.01661</u>	8.88	
		<i>Change in median CWD (%)</i>			
Zoning scenario	100 ft	200 ft	300 ft	400 ft	
100 ft	180.6614	20.5834*	29.7545*	35.5277*	
200 ft	<u>0.113934</u>	201.2448	9.1711	14.9443*	
300 ft	<u>0.164698</u>	<u>0.045572</u>	210.4159	5.7732	
400 ft	<u>0.196654</u>	<u>0.074259</u>	<u>0.027437</u>	216.1891	
		<i>Change in median bluegill growth (%)</i>			
Zoning scenario	100 ft	200 ft	300 ft	400 ft	
100 ft	32.1995	0.0032	0.0053	0.0073	
200 ft	<u>9.94E-05</u>	32.2027	0.0021	0.0041	
300 ft	<u>0.000165</u>	<u>6.52E-05</u>	32.2048	0.002	
400 ft	<u>0.000227</u>	<u>0.000127</u>	<u>6.21E-05</u>	32.2068	

651

652 Table 2. Number of lakes (out of a total of 89) with a significant change ($p < 0.05$) in median,
 653 variance, and skewness for residential density, CWD, and bluegill growth.

654

	Median Change				Variance Change				Skewness Change						
		100 ft	200 ft	300 ft	400 ft		100 ft	200 ft	300 ft	400 ft		100 ft	200 ft	300 ft	400 ft
Residential density	100 ft		83	87	89	100 ft		89	89	89	100 ft		88	89	88
	200 ft			67	78	200 ft			84	84	200 ft			84	84
	300 ft				57	300 ft				78	300 ft				78
	400 ft					400 ft					400 ft				
CWD	100 ft		73	67	69	100 ft		87	87	89	100 ft		87	86	87
	200 ft			23	42	200 ft			83	83	200 ft			87	79
	300 ft				10	300 ft				73	300 ft				76
	400 ft					400 ft					400 ft				
Bluegill growth	100 ft		0	0	0	100 ft		7	6	12	100 ft		5	9	13
	200 ft			0	0	200 ft			5	7	200 ft			7	13
	300 ft				0	300 ft				2	300 ft				9
	400 ft					400 ft					400 ft				

655

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657

658 **Figure Captions**

659 Figure 1. The study area, Vilas County, Wisconsin, and the sample of lakes used in the
660 simulations.

661 Figure 2. Schematic of the simulation methodology.

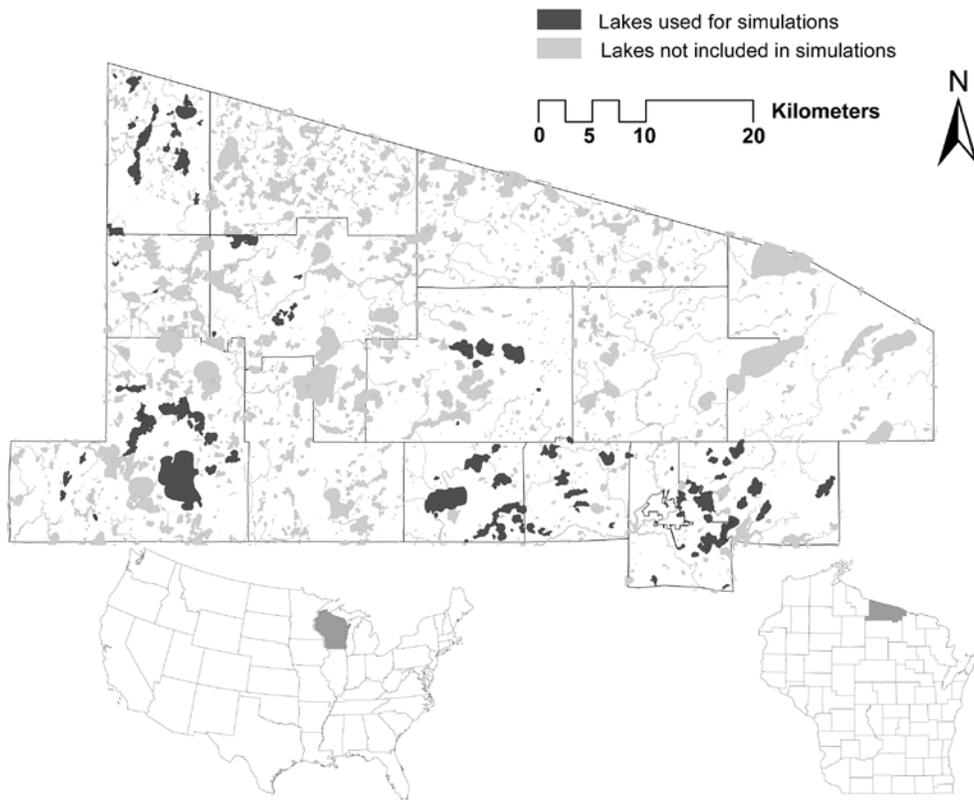
662 Figure 3. Landscape averages for 1000 simulations of residential density, CWD, and bluegill
663 growth rates under different zoning scenarios. Densities are estimated using Epanechnikov
664 kernel estimation. Bandwidths are: residential density = 0.065, CWD = 0.18, and bluegill growth
665 = 0.624.

666 Figure 4. Distributions of estimated policy change for lake types based on percent of shoreline
667 that is subdividable. Lakes with $\leq 33\%$ of shoreline subdividable are categorized as high
668 development. Lakes with 34%-66% of shoreline subdividable are categorized as medium
669 development. Lakes with $>66\%$ of shoreline subdividable are categorized as low development.

670 Figure 5. Distributions of estimated policy change for lake types based on the average size of
671 subdividable lots. Lakes with ≤ 500 ft average subdividable lot size are categorized as high
672 development. Lakes with average subdividable lot sizes from 501ft to 1000ft are categorized as
673 medium development lakes. Lakes with average subdividable lot sizes of >1000 ft are
674 categorized as low development lakes.

675 Figure 6. Geographic distribution of low, medium, and high development lakes as categorized by
676 the percent of subdividable shoreline.

677 Figure 7. Geographic distribution of low, medium, and high development lakes as categorized
678 by the average size of subdividable lots.



679

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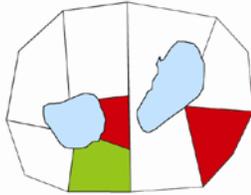
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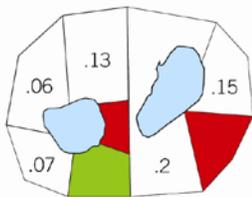
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LANDSCAPE SIMULATION AND THE EFFECT OF ZONING

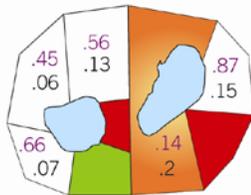
1. Initial landscape.



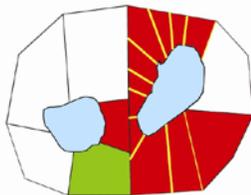
2. Each parcel is assigned a transition probability based on the estimated coefficients and variance of the land conversion model



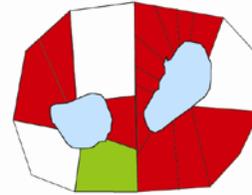
3. For each parcel a random number from the unit interval is drawn and compared to the transition probability. If the estimated transition probability is greater than the random draw the parcel subdivides.



4. The number of new lots created on the subdivided parcel is decided based on the estimated coefficients and variance of Poisson count model, the zoning restrictions that govern minimum allowable frontage, and a stochastic process which compares the number of new lots created to a random draw.



5. The landscape simulation continues through end of study with more lots subdividing.



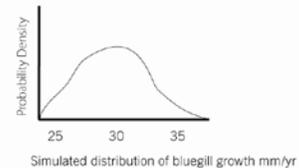
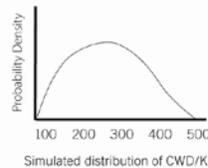
6. Residential density (RD) is calculated for each lake using the assumption of one home per parcel. RD is then input into the biological models for CWD and bluegill growth (Christensen et al. 1996, Schindler et al. 2000).

$$\log_{10} \text{Growthrate} = 1.50 - (.11 * \log_{10}(\text{RD}+1)) + e$$

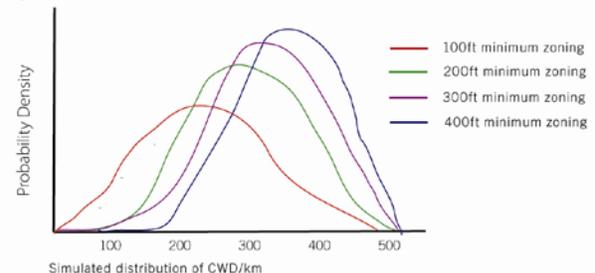
$$\text{CWD} = 628 - 500 * \log_{10} \text{RD} + e$$

Where e is approximated by drawing the model coefficients from a normal distribution with the estimated mean and variance.

7. The landscape simulation is run 1000 times providing the input to 1000 estimates of CWD and bluegill growth. These estimates form a simulated distribution of possible conservation outcomes for each lake and the landscape as a whole.

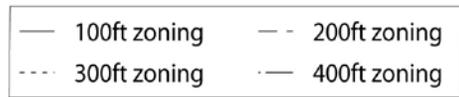
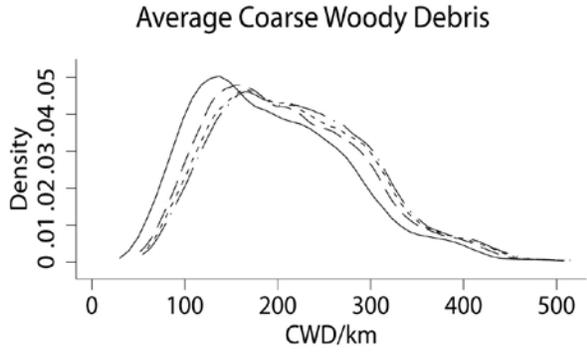
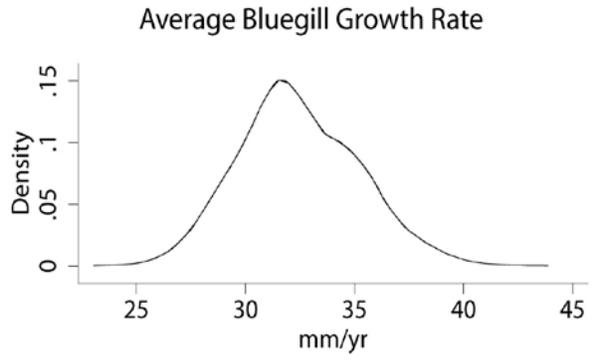
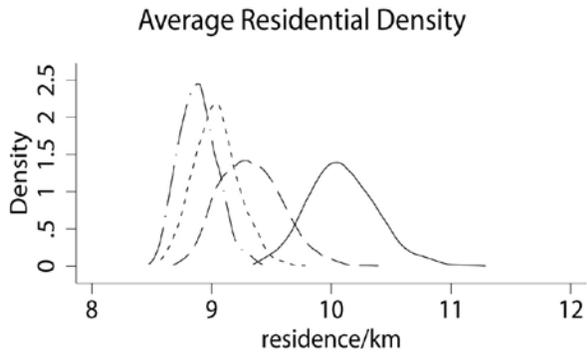


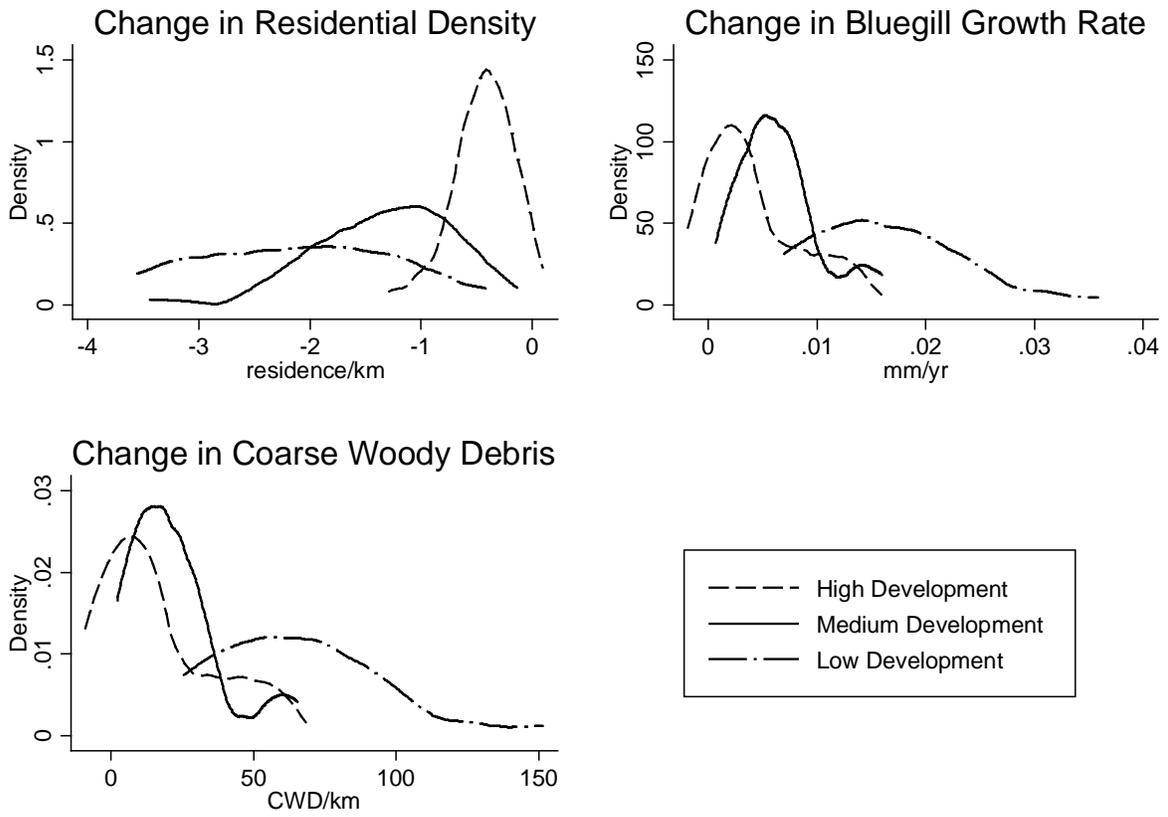
8. Changes in zoning were simulated by changing transition probabilities, the number of new lots created, and the number of new lots allowed. Distributions of ecological indicators were compared across zoning policies.



Legend

- Developed
- Preserved
- Undeveloped
- Lake





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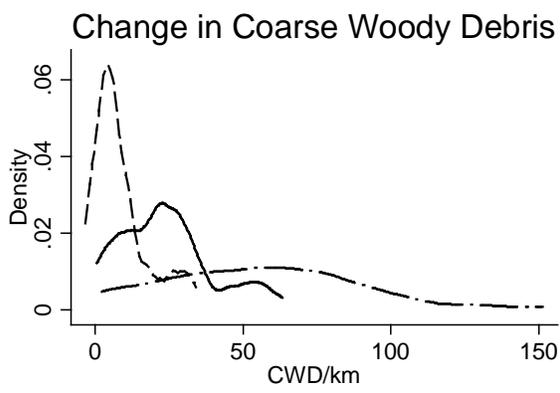
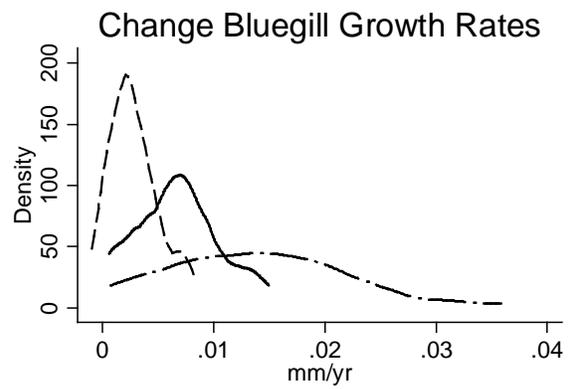
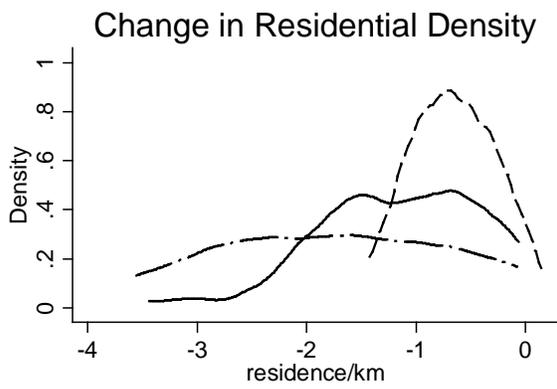
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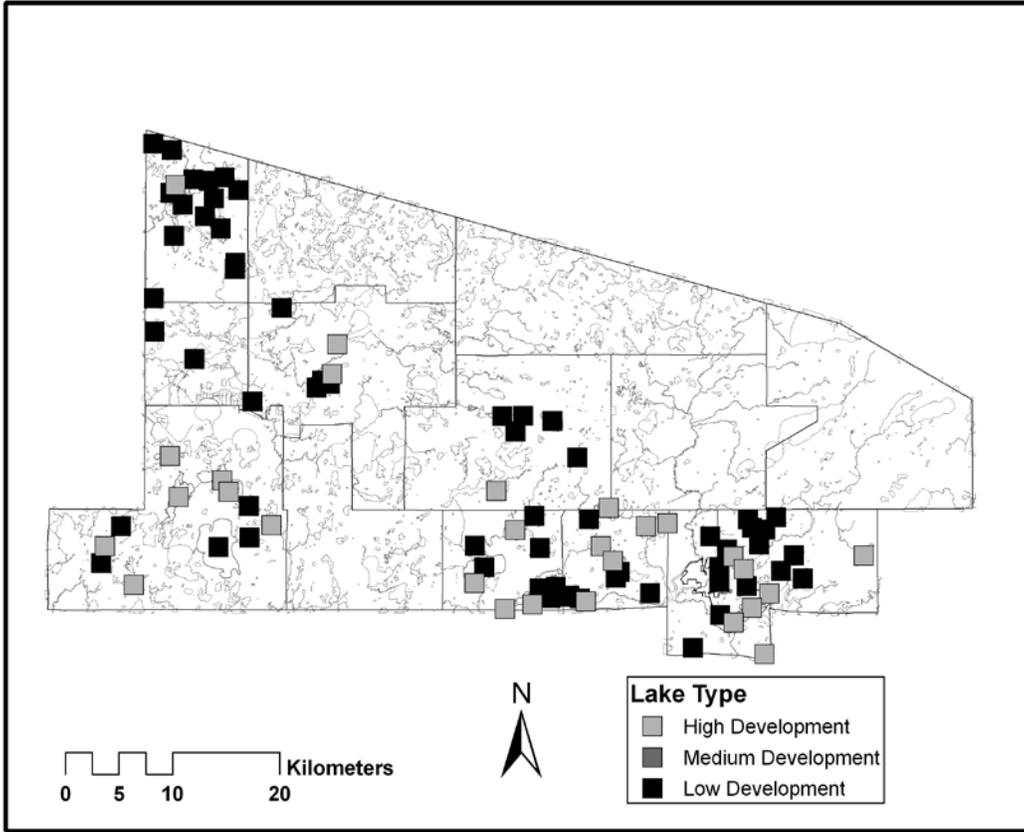
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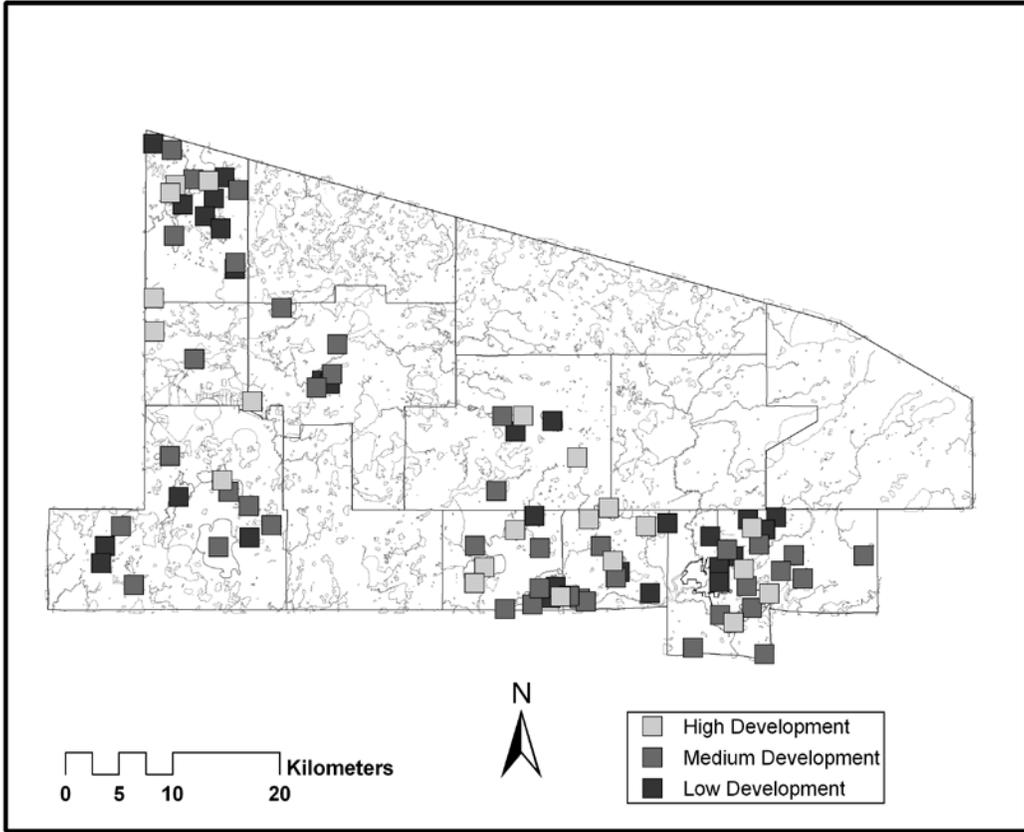
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