

14 Abstract. The combined effects of fire history, climate, and landscape features (e.g., edges) on
15 habitat specialists need greater focus in fire ecology studies, which usually only emphasize
16 characteristics of the most recent fire. Florida scrub-jays are an imperiled, territorial species that
17 prefer medium (1.2-1.7 m) shrub heights, which are dynamic because of frequent fires. We
18 measured short, medium, and tall habitat quality states annually within 10 ha grid cells (that
19 represented potential territories) because fires and vegetative recovery cause annual variation in
20 habitat quality. We used multistate models and model selection to test competing hypotheses
21 about how transition probabilities vary between states as functions of environmental covariates.
22 Covariates included vegetative type, edges (e.g., roads, forests), precipitation, openings (gaps
23 between shrubs), mechanical cutting, and fire characteristics. Fire characteristics not only
24 included an annual presence/absence of fire covariate, but also fire history covariates: time since
25 the previous fire, the longest fire-free interval, and the number of repeated fires. Statistical
26 models with support included many covariates for each transition probability, often including
27 fire history, interactions and nonlinear relationships. Tall territories resulted from 28 years of fire
28 suppression and habitat fragmentation that reduced the spread of fires across landscapes. Despite
29 35 years of habitat restoration and prescribed fires, half the territories remained tall suggesting a
30 regime shift to a less desirable habitat condition. Edges reduced the effectiveness of fires in
31 setting degraded scrub and flatwoods into earlier successional states making mechanical cutting
32 an important tool to compliment frequent prescribed fires.

33 Key words: adaptive management; edges; fire; fragmentation; Florida scrub-jays; mapping;
34 multistate; scrub; transition.

35

36 INTRODUCTION

37 Lightning-caused fire regimes have been major evolutionary drivers on nearly all continents
38 (Tucker and Cadotte 2013), but the significance and management needs of biodiversity hotspots
39 characterized by natural fire remain underestimated (Parr et al. 2014, Noss et al. 2015, Rundel et
40 al. 2016). The North American Coastal Plain (NACP) has been subject to 70% habitat loss and
41 has only been recently recognized as a global biodiversity hotspot that needs practical models to
42 guide science-based fire management to restore and maintain its unique plants and animals (Noss
43 et al. 2015). The Florida scrub-jay is an endemic bird confined to the Florida scrub and
44 flatwoods ecosystem of the NACP and is an declining indicator species for habitat management
45 (Noss et al. 1995, Coulon et al. 2010).

46 The natural fire regime of the scrub and flatwoods ecosystem has been greatly altered by
47 humans (Duncan et al. 2009), as has occurred among fire adapted communities within the NACP
48 and worldwide (Driscoll et al. 2010). The scrub and flatwoods ecosystem requires prescribed
49 fire management to sustain biodiversity and prevent catastrophic wildfires from impacting
50 human interests because anthropogenic landcover types (e.g., roads, cities) impede fire spread
51 (Duncan and Schmalzer 2004).

52 The interactions among factors that influence the transitory dynamics of fire-maintained
53 ecosystems are important to understand and manage to conserve biological diversity, but most
54 studies focus only on habitat responses relative to the last fire (Nimmo et al. 2013). New
55 approaches are needed to quantify spatial variation that results from repeated fires that do not
56 burn all areas equally (Bradstock et al. 2005, Driscoll et al. 2010). Fire history seems may be
57 particularly in scrub and flatwoods because repeated fires influence above-ground fuels
58 characteristics (e.g., dead fuels above ground) and dominant plants depend on accumulated

59 below-ground biomass (roots, buds, starches) for sprouting after fire (Menges and Hawkes
60 1998).

61 Mechanical cutting is often needed to restore long unburned oak scrub because the habitat
62 becomes difficult to ignite and support fire spread (Schmalzer and Boyle 1998). Evaluating
63 ecosystem restoration usually involves comparing restoration sites to historical references, but
64 one or a few reference sites often don't capture spatial and temporal variability (Kirkman et al.
65 2013). Restoration trajectories are often not linear or smooth; failure to understand alternative
66 endpoints or exceptions to a deterministic trajectory can limit success (Matthews et al. 2009).
67 Interactions between environmental variables (e.g., rainfall) and fire history have many effects
68 on the direction and stochasticity of restoration trajectories (Zedler et al. 1983, Artman et al.
69 2001, Drewa et al. 2002, Clarke et al. 2014).

70 Variations in the intervals between fires can produce nonlinear relationships that are often
71 described as memory or legacy effects (e.g., cavities, snags, stored underground biomass)
72 (Ripplinger et al. 2015, Johnstone et al. 2016). Nonlinear relationships cause management
73 thresholds in ecosystem state changes described by resilience theory (Ghermandi et al. 2010,
74 Mori 2011, Johnson et al. 2013). Resilience theory commonly uses state-and-transition models
75 that summarize ideas about how complex systems work through feedback loops, thresholds, and
76 triggers (Bagchi et al. 2012, Ratajczak et al. 2014).

77 Multistate models are new approaches to empirically quantify ecosystem dynamics by
78 measuring states and using generalized linear models to estimate how environmental covariates
79 influence transition probabilities between states (Breininger et al. 2010, Veran et al. 2012, Zweig
80 and Kitchens 2014). We previously used multistate models and multimodel inference to quantify
81 scrub and flatwoods habitat transition probabilities of potential Florida scrub-jay territories at 5-

82 year intervals (1994-2004) using combinations of environmental factors that focused on
83 vegetation type, edges, and management actions as covariates (Breininger et al. 2010). We used
84 landscape units that defined potential Florida scrub-jay territories because transition probabilities
85 within potential territories provide the parameters to predict how alternative management actions
86 can be used to better manage and restore the scrub and flatwoods ecosystem (Williams et al.
87 2011).

88 Here we use multistate modeling and multimodel inference to predict how annual habitat
89 state transition probabilities (2004-2015) are influenced by environmental covariates important
90 in previous studies and new environmental covariates that incorporate information on fire
91 history, rainfall and open sandy areas. These new covariates were described as important in
92 many ecosystem studies and likely to be influential in early successional state transitions, which
93 dominated historical scrub and flatwoods landscapes (Duncan et al. 2004, Duncan et al. 2009).
94 Our approach for applying habitat states (short, medium, tall) for potential territories does not
95 consider all elements of Florida scrub-jay habitat quality (Burgman et al. 2001). However,
96 characterizing landscape units into these states is practical to conduct across broad geographic
97 areas annually and is useful for adaptive management (Johnson et al. 2011). Nearly 30 years of
98 data on demography and dispersal shows that short and tall states are population sinks where
99 mortality exceeds recruitment and the medium state is a source where recruitment exceeds
100 mortality (Breininger et al. 2014b). Although in other studies we have subdivided the medium
101 state into open and closed based on the amount of open sandy area between shrubs, here, we
102 focused on states defined entirely by height because we lacked enough samples to study how
103 many factors influence open state dynamics. However, we tested whether openings are an
104 important covariate influencing height state dynamics because openings can, for example,

105 influence fire spread as open sandy areas cause discontinuity in fuels (Schmalzer 2003, Menges
106 et al. 2008, Duncan et al. 2015). Fires in scrub can also spread poorly depending on
107 meteorological conditions such as soil and fuel moisture that can be influenced by rainfall
108 (Adrian 2006) and thus a rapidly changing climate is likely to further impact disturbance regimes
109 (Turner 2010, Foster et al. 2017).

110 Our primary objective was to test a competing model set to investigate whether a few simple
111 covariates or many covariates best describe transition probabilities in scrub and flatwoods,
112 including models with interactions and nonlinear effects. We also compare new state abundance
113 trends with predictions (Breininger et al. 2010) and use new transition probability estimates to
114 predict future trends of restoration success. Our final objectives include quantifying trends in
115 management effort based on the number of potential territories burned and cut each year.

116

117 METHODS

118 *Study system*

119 Our study was conducted on Kennedy Space Center/Merritt Island National Wildlife Refuge
120 (KSC/MINWR), a barrier island complex located along central Florida's Atlantic Coast. Oak
121 scrub and flatwoods are heterogeneous vegetative communities dominated by scrub oaks, saw
122 palmetto, grasses and ericaceous plants. Cover of scrub oaks is greatest on the most well-drained
123 soils ("oak") and declines on moderately drained soils ("flatwoods") where the more flammable
124 flatwoods species increase. Although considered distinct plant communities, oak and flatwoods
125 are often termed scrubby flatwoods when they are intermixed within fire management units

126 (Breininger et al. 2002). Plant composition changes little after fire because most plants are
127 clonal and re-sprout within weeks (Schmalzer and Hinkle 1992).

128 Scrub and flatwoods ecosystems on KSC/MINWR had many openings and little forest prior
129 to a fire suppression period (1950-1978), which caused a loss of openings and increases in tall
130 shrubs and forests (Duncan et al. 1999). Marshes are extensively intermingled within scrub and
131 flatwoods, but many of these became hardwood swamps during the fire suppression period. A
132 subsequent prescribed fire program focused on fuels management as part of a national program
133 to reduce threats of catastrophic fires on human interests. Getting the ecosystem back to short
134 and medium habitat states has been difficult, as tall shrubs and forests burn poorly and
135 mechanical cutting is generally needed to reintroduce fire into degraded areas (Schmalzer and
136 Boyle 1998). Currently, the fire return interval in a management unit can be as often as 3-5
137 years, but specific patches may burn only every 14 years or longer (Duncan et al. 2009).

138 *Data collection*

139 The study area was delineated by 695 10-ha square polygons that approximate all potential
140 Florida scrub-jay territories. Florida scrub-jay territories average 10 ha when habitat is fully
141 saturated by Florida scrub-jays; studying the dynamics of potential territories is useful because
142 most Florida scrub-jay populations have declined by >50% leaving much potential habitat
143 unoccupied (Breininger et al. 2006). These 695 potential territories represented all potential
144 habitat within areas managed using prescribed fires, while excluding habitat fragments that were
145 no longer managed or relatively isolated scrub patches that had minimal contribution to the
146 Florida scrub-jay population (Carter et al. 2006).

147 We measured habitat states (short, medium, tall) described below each year from 2004-2015
148 using 1.0 m resolution aerial photography. Field observations supplemented state estimation
149 because most potential territories were within long-term demographic study sites where we
150 uniquely mark and resight Florida scrub-jays (Breininger et al. 2009, Breininger et al. 2010).
151 Years were defined as April 1 to March 31 corresponding to Florida scrub-jay nesting season and
152 the timing of most aerial photographs. Short territories have many openings between shrubs,
153 medium has a uniform (flat) appearance and tall shows texture on images because tall shrubs
154 produce shade. Short lacks shrubs > 1.2 m tall and experienced a recent (< 5 years), extensive
155 burn. Medium and tall territories often had heterogeneous shrub heights because fires in oak and
156 flatwoods often burn in mosaic patterns so that potential territories include patches of vegetation
157 with different fire histories. Long-term demographic research that defined these criteria were
158 based on having enough medium shrubs to support recruitment that exceeded mortality, but not
159 too many tall shrubs that caused Florida scrub-jay territories to have mortality that exceeded
160 recruitment across a range of population densities. Medium includes at least 0.4 ha of shrubs
161 1.2-1.7 m tall (optimal height) and excludes large patches (>1.0 ha) of tall shrubs (>1.7 m tall).
162 Tall includes areas with > 1.0 ha of tall shrubs (Breininger et al. 2010). On average it takes 8
163 years without disturbance for oaks to reach medium height and 20 years for scrub to become tall
164 (Schmalzer and Hinkle 1992, Duncan et al. 1995).

165 We identified a suite of covariates predicted to influence the transition probabilities between
166 habitat states. The static (non-time varying) covariate “oak” identified potential territories
167 intersecting well-drained soils, and “flatwoods” identified potential territories that included
168 moderately drained soils with smaller patches of oaks than are found on well-drained soils. The
169 static covariate “edge” recorded whether a man-made or forest edge intersected a potential

170 territory. The dynamic (time-varying) covariate “open” was a categorical variable that
171 distinguished whether scrub in potential territories was open (>50% or area had open sandy gaps
172 between shrubs) or closed (few gaps). The dynamic covariate “cutting” distinguished territories
173 where at least ¼ of the territory was subject that year to mechanical cutting of trees and shrubs.

174 The fire history of territories differed across the KSC/MINWR landscape; in order to
175 encompass these differences we incorporated several dynamic covariates related to the fire
176 histories that we predicted had an influence on transition probabilities. The dynamic covariate
177 “fire” distinguished territories where at least ¼ of the territory burned that year based on remote
178 sensing and fire records (Shao and Duncan 2007). We chose 3 fire history variables that reflected
179 different hypotheses about how fire history would affect habitat transitions that we predicted to
180 be uncorrelated with fire and each other. The first fire history covariate time-since-fire, “TSF”,
181 represented the number of years without fire prior to the current interval and therefore
182 independent of “fire” during the current interval. We selected TSF because growth is more rapid
183 soon after fires and then slows (Schmalzer 2003). The second fire history covariate longest fire
184 interval, “LFI”, represented the longest period without fire during the previous 20 years,
185 recognizing that fire free intervals approaching 20 years result in states resilient to fire (Duncan
186 et al. 1999). The third fire covariate “NF” included the number of fires for the previous 10 years
187 because repeated, short-interval fires can deplete underground biomass (Saha et al. 2010).

188 The dynamic covariate standardized precipitation index, “SPI”, was obtained from Florida
189 climate division 3 from the National Climatic Data Center, Asheville, NC
190 (www.ncdc.noaa.gov/). The SPI describes the observed precipitation over a time period as the
191 number of standard deviations above or below the long-term mean precipitation for that time
192 period (McKee et al. 1993) and has been useful in studying responses in scrub vegetation

193 (Foster et al. 2014, 2015). We used the 12-month SPI for April – March 31 as a measure of
194 drought. The 12 month SPI for March compares the cumulative precipitation from the previous
195 April to the current March to the historic pattern of precipitation for that time period.

196 *Data analyses*

197 We used multistate models to analyze annual transition probabilities between states (Fig. 1) as a
198 multinomial model of static and dynamic environmental covariates. Static variables were
199 oak/flatwoods and edge/no edge. One dynamic variable (SPI) was the same for all potential
200 territories, but unique to each interval. Other dynamic variables were specific to each interval
201 and potential territory: fire/no fire, mechanical cutting/no cutting, openings/no openings, 3 fire
202 history variables.

203 Each multistate model consisted of a likelihood combining 3 multinomials, 1 for each of the
204 3 states. We estimated transition probabilities for state changes (e.g., short-to-medium);
205 transition probability estimates of states remaining the same between years (e.g., short-to-short)
206 were estimated by subtracting the transition probability estimates of state changes from 1.0. The
207 transition of short-to-tall was constrained to zero because it didn't occur, which enhanced
208 numerical estimation. We developed 40 competing models representing hypotheses of how
209 combinations of different variables, two-way interactions, linear and quadratic relationships
210 would affect state transitions. Models were implemented in Program Mark (White et al. 2006),
211 which produced an AIC_c model-selection table, estimates of β s (regression parameters), and
212 transition probabilities along with and their precision (i.e., SE and CI). We made *a priori*
213 predictions about the direction for each β , similar to the previous modeling in order to represent
214 specific ecological hypotheses for each transition probability (Breininger et al. 2010).

215 We used a simple approach to present how state transitions (and measures of precision)
216 varied annually based only on plant composition (oak versus flatwoods), excluding
217 environmental covariates because oak and flatwoods are often considered distinct plant
218 communities. We also predicted future abundances of each state for the next 12 years by
219 Markov projections, beginning with the 2015 vector of state abundances, as we did previously
220 (Breininger et al. 2010). The Markov matrices for the future predictions were estimated with
221 time constant models, separately for oak and flatwoods without other environmental covariates
222 (Breininger et al. 2010). To determine if there were trends in management effort, we used linear
223 regression of the number of grid cells burned (1983-2015) and cut (2004-2015) for time periods
224 with data on these management efforts.

225 RESULTS

226 No simple models that included only vegetation type (oak/flatwoods) or habitat management
227 actions (fire/no fire, cutting/no cutting) had support, whereas 6 more complicated models had >
228 99% of the empirical support (Table 1). There was much similarity amongst the top models, but
229 differences among transition probabilities regarding which covariates were important. Models
230 with support included all covariates that were previously important (oak, edge, fire, and cutting)
231 and new covariates involving fire history (time-since-fire, longest fire free interval, number of
232 fires in previous 10 years, openings) and annual rainfall (standardized precipitation index).

233 Table 2 compares our *a priori* predictions with results for all covariates important in the best
234 supported model. We presented only the best model because other top models were similar and
235 β 's absent in the top model involved interactions that had standard errors many times greater
236 than mean estimates. The best model had mean β 's with CI's that overlapped zero, but excluding
237 these effects during *post hoc* analyses produced models without AIC_c support. The main effect

238 for β 's describing the oak versus flatwoods often had CI that overlapped zero, but we included
239 the oak versus flatwoods effect because all supported models included an oak versus flatwood
240 effect, and many covariates had different effects depending on whether the site was oak or
241 flatwoods (Table 2). All supported models had an effect for whether fire occurred in the current
242 interval, but the CI's overlapped zero for transitions from earlier to later successional states.

243 Every transition probability included an edge effect; β 's representing covariates in the best
244 model usually had the same direction of effects that we predicted, except for the number of fires
245 in the previous 10 years. The negative β 's for openings clarified the effect where authors
246 disagreed on *a priori* predictions. Supported models included many covariate effects for
247 transitions between short-to-medium, medium-to-short and for medium-to-tall, which were
248 transition probabilities that previously had low sample sizes and therefore limited our abilities to
249 test many covariate effects. In this study, transitions from short and medium to other states were
250 more common because the states had greater relative abundances, and we estimated transition
251 probabilities from 11 annual intervals versus 3 5-year intervals (Breininger et al. 2010).

252 The fire history TSF affected transitions from earlier to later successional states, with a
253 nonlinear effect for short-to-medium. Other fire history covariates (NF and LFI) often had weak
254 effects (small β 's) with uncertain directions (CI overlapped zero). Fire history covariates were
255 not highly correlated ($r^2 < 0.4$) and post hoc analyses to remove covariates from models with
256 multiple fire history covariates did not improve model support or change directions of the β
257 estimates of fire history covariates, as can occur when covariates are highly correlated (Zuur et
258 al. 2010). Each of the 3 covariates was chosen for a different *a priori* mechanism that might
259 affect transition probabilities (e.g., nonlinear growth, underground biomass depletion, developing
260 inflammable above ground fuels structure) and eliminating 1-2 fire history covariates in *post hoc*

261 analyses resulted in models that had no support compared to the top models indicating that the 3
262 fire history covariates provided different information, albeit with comparably weak effects and
263 poor precision.

264 Precipitation did not influence transitions to a later successional state (growth) but
265 influenced transitions to an earlier successional state and in oak. The quadratic relationship
266 occurred because transition probabilities peaked at low to medium drought conditions being
267 lowest during severe droughts (when prescribed fires are not allowed) or when rainfall was
268 average or greater.

269 All habitat states were widely distributed throughout the landscape (Figure 2), and tall
270 territories remained the most abundant habitat state (Figure 3). Tall territories declined and
271 medium (optimal) territories increased confirming predictions made from the earlier model
272 (Breininger et al. 2010). Our use of Markov processes to generate a vector of state abundances
273 predicted almost no change in state abundances across the next 12 years versus a continued tall
274 state decrease and medium state increase as predicted from the earlier data (Breininger et al.
275 2010). There was a slight increase in the number of grid cells burned each year and no trends in
276 cutting. Cutting only occurred in <25 grid cells each year, except for 2006 and 2011 (Figure 4).

277 Transitions probabilities from tall to earlier successional states were usually among the
278 smallest and annual transition probabilities varied greatly, especially for short-to-medium which
279 generally had the greatest transition probabilities between states (Table 4). Transition
280 probabilities to earlier successional states were greatest during the greatest droughts (2007-2008,
281 2011-2012).

282 DISCUSSION

283 Multistate models provided a unifying modeling framework to empirically quantify the effects of
284 many environmental variables on habitat dynamics, by breaking a large landscape into potential
285 territories and developing a longitudinal history of states and environmental covariates. No
286 simple model explained habitat dynamics, as all models with empirical support included many
287 environmental factors for each transition probability; these effects included interactions and
288 nonlinear relationships, which are common in fire ecology studies (Driscoll et al. 2010). Results
289 expanded previous work (Breininger et al. 2010) identifying complex interactions between
290 covariates, and many new covariate effects (fire history, precipitation, openings) for many
291 transitions (e.g., short-to-medium, medium-to-short, medium-to-tall).

292 Restoration and management actions (e.g., fire, cutting) had important effects, but
293 environmental factors often had greater effects on transition probabilities (e.g., edge effects on
294 tall-to-medium: Table 2). Edges (roads and forests), primarily resulting from anthropogenic
295 factors, were among the most influential factor across transition probabilities; these strong
296 effects made sense because edges disrupt fire spread (Duncan and Schmalzer 2004). Forests
297 were relatively rare in the historical landscapes and resulted from reductions in fire frequency
298 from natural fire regimes causing low flammability (Duncan et al. 1999, Duncan et al. 2004).
299 Habitat fragmentation typically increases ignitions and fire spread in other ecosystems, but still
300 has detrimental impacts (Kraaij et al. 2013).

301 Cutting was an important management action influencing transitions because tall scrub had
302 become resistant to fire, and cutting along edges and frequent fire appear to be the only solution
303 to Florida scrub-jay population recovery on KSC/MINWR (Johnson et al. 2011). We agree with
304 colleagues that mechanical cutting is not a replacement for fire, and care is needed to avoid the

305 spread of exotics and reducing the cover of species important for spreading fires (Schmalzer and
306 Boyle 1998, Menges and Gordon 2010).

307 Fire history effects were practical to study in our system because fires occurred every few
308 years instead of decades, or longer. The presence/absence of fire during an annual interval
309 usually had a larger effect than fire history variables, except that time since fire (TSF) had a great
310 effect for the short-to-medium transition in oak. The presence/absence of fire might have had a
311 lesser impact than TSF because short scrub generally lacks enough fuels to burn extensively.
312 The TSF nonlinear effect could be explained by growth being most rapid a few years after fire
313 (Schmalzer and Hinkle 1992).

314 We predicted stronger effects from other fire history covariates, especially for the length
315 of the fire free interval (LFI) because scrub is difficult to restore once it is unburned for ≥ 20
316 years. We expected that LFI would be important because increasing underground biomass
317 allows for more rapid regrowth after fire (Maliakal et al. 2000, Boughton et al. 2006). One
318 explanation for only small fire history effects might be that the effects of fire history on
319 vegetation might have occurred at a smaller geographic scale than potential territories, which
320 would have had heterogeneous fire histories. The number of fires (NF) decreased tall-to-short
321 and tall-to medium transitions contradicting our *a priori* hypothesis, but the effect was poorly
322 estimated (CI overlapped zero). One explanation might be that it takes at least 3-5 years for
323 enough fuels to accumulate to carry fire and greater fuel levels might be needed for fires to burn
324 severely enough to spread into tall scrub patches. Another explanation is that fires did not burn
325 often enough to deplete underground biomass because there were not enough grasses to carry
326 frequent fire (see below).

327 Fire severity can be an important habitat covariate (Lindenmayer et al. 2013, Fang et al.
328 2015), but can be challenging to measure and is often related to fire size (Miller et al. 2009,
329 Cansler and McKenzie 2014). We are investigating methods to develop longitudinal fire severity
330 histories across our study sites and acknowledge that lack of fire severity data is an important
331 limitation. However, management objectives in our study sites often do not include severe fires
332 because of the proximity to cities and space program facilities and the negative impacts of
333 extensive fires to Florida scrub-jay survival (Breininger et al. 2009).

334 Historical benchmarks or reference conditions are often used to evaluate progress towards
335 habitat recovery, however, these should include spatial and temporal variability (Kirkman et al.
336 2013). In addition to edge effects, we suspect that fire spread today often differs from historical
337 conditions because prescribed fires vary in seasonality and meteorology with natural, lightning
338 ignited fires (Duncan et al. 2009). There are many vegetative differences in the flammability
339 within landscapes, and grasses are especially important for spreading fire (Breininger et al.
340 2002). The growth and flowering of many important grass species (e.g., *Aristida stricta*
341 *var. beyrichiana*) is dependent on fires that occur at the transition between the dry and
342 thunderstorm seasons when most lightning fires occurred (Platt et al. 1988, Noss 2013).

343 The Pre-European landscape might have been resilient to change because frequent lightning
344 fires could spread easily through grasses among short and medium territories that lacked roads
345 and forests to impede fire spread (Duncan et al. 1999). Early landscapes had many open sandy
346 areas, which usually disappear within 1-2 years after fire in recent times (Schmalzer and Hinkle
347 1992). The negative relationship we observed between in open scrub and the transition from
348 medium-to-tall might have occurred because open scrub was an indicator of slower growth.
349 Slower growth might have resulted from site differences (e.g., topography) or fire severity.

350 Anthropogenic effects often produce alternative states that are resistant to change or states
351 that are unstable (Scheffer and Carpenter 2003, Larson et al. 2013, Johnstone et al. 2016).
352 Following 28 years of fire suppression, 35 years of prescribed fires only reduced slightly the
353 extent of tall territories that had become resistant to restoration. Other complications included
354 restrictions on prescribed fires that must be ignited under particular wind directions to avoid
355 smoke impacts to smoke sensitive areas. These restoration challenges occur across the
356 geographic region making many small Florida scrub-jay populations vulnerable to extinction
357 (Duncan et al. 2004, Breininger et al. 2006).

358 Restoration programs often focus on conducting enough management to get past a threshold
359 that alters system behavior, removing feedback loops that lead to a degraded state, and enhancing
360 feedback loops that produce a desired stable state (Suding 2011). Burning during the best season
361 to stimulate grasses and promote fire spread might be advantageous, but fire managers in our
362 study sites had extreme limitations regarding meteorological and operational constraints that
363 made burning only during the dry-to-wet transitional season (e.g., May) difficult. Cutting was an
364 expensive tool, and it may be unreasonable to remove most forest edges and edges associated
365 with human landscape features so that prioritization of management efforts becomes necessary.
366 We have observed many habitat and population management restoration successes in particular
367 landscapes, but most conservation areas are at less than half Florida scrub-jay carrying capacity
368 (Breininger et al. 2006). Population modeling and Florida scrub-jay sociobiology suggest that
369 habitat management prioritization might focus on maintaining the largest populations because
370 population recovery can be slow, especially when there are not large numbers of nonbreeding
371 individuals (Breininger et al. 1999, Breininger et al. 2014b).

372 Funding for prescribed fires often focuses on maximizing fuels reduction allowing fuels to
373 accumulate until fires can burn them extensively, causing potential Florida scrub-jay territories
374 to have a large sink (short, tall) to source (medium) habitat ratio, as occurred herein. We believe
375 “optimal habitat management” might be better at reducing catastrophic fire risk than fuels
376 management in priority areas (Breininger et al. 2014a). In an optimal habitat management
377 strategy, prescribed fires would be initiated sooner than a fuels reduction strategy by attempting
378 prescribed fires before all fuels are likely to ignite thus creating transitory openings and
379 heterogeneity among shrub patches at the territory scale. In habitat occupied by Florida scrub-
380 jays near carrying capacity, optimal habitat management would attempt mosaic fires to provide
381 some unburned patches to serve as nest sites, provide acorns, and areas to escape predators. Such
382 fire mosaics would require greater post-fire monitoring because unburned patches might reignite.
383 Fire modeling suggests this strategy would reduce fuels continuity decreasing the risk of
384 spreading potentially catastrophic fires (e.g., wildfires) that are expensive to control (Duncan et
385 al. 2015). In our view, waiting until fuels accumulate to levels that support complete fires
386 increases the risks of catastrophic wildfires between controlled fires. Frequent and severe fires
387 could be conducted in unoccupied Florida scrub-jay habitat in an attempt to set the system back
388 into an earlier successional state associated with historical conditions promoting population
389 recovery in those areas at a later date.

390 Our study does not take into account the effects of a changing climate; however, it is likely
391 that the areal extent of oak and flatwoods will be reduced with rising sea levels putting pressure
392 on managing biodiversity in increasingly smaller areas (Foster et al. 2017). Changes in
393 precipitation might include heavier precipitation events and longer periods between precipitation
394 events; droughts may become more frequent (Karl et al. 2009). We observed the effects of SPI

395 on oak transitions to earlier successional states were not linear because drought promotes fire
396 spread, but extreme droughts force a shutdown of prescribed fire because of increased
397 catastrophic fire risk. Droughts might not have effected flatwoods because the vegetation is
398 more flammable and the water table closer to the root zone (Schmalzer and Hinkle 1992).

399 Scientists need to broaden study implications, but generalizations also lead to debates as to
400 whether Florida scrub-jays, for example, should be a scrub management indicator for all scrub
401 (Menges and Gordon 2010). A nuanced approach could consider regional biodiversity where
402 opportunities for conservation vary among species and conservation areas. In our study region,
403 conservation opportunities are limited by urbanization and species geographic differences
404 (Duncan et al. 2004). Most species of conservation concern in our study site benefited by
405 conditions best for Florida scrub-jays, and we know of no species of conservation concern that
406 would decline from Florida scrub-jay management directed at one of the species last remaining
407 extant large populations.

408 Plant ecologists recommend pyrodiversity to account for the requirements of lesser known
409 species while animal ecologists have increasingly questioned whether pyrodiversity creates
410 faunal biodiversity (Parr and Andersen 2006, Menges 2007, Clarke 2008, Farnsworth et al.
411 2014). Our study site had great pyrodiversity was of poor habitat quality for Florida scrub-jays
412 because of too much tall scrub. Rather than simple statistical distributions, fire frequency should
413 be based on species biology (Gill and McCarthy 1998, Kelly et al. 2015), such as habitat and
414 population state (Johnson et al. 2011, Williams et al. 2011). Optimal Florida scrub-jay territories
415 in our study area includes a specific fire mosaic because openings disappear a few years after fire
416 and medium height scrub on average is 8-20 years post fire (Breininger et al. 2014b).

417 Long-term studies have shown geographic differences in vegetative response to fire and fire
418 return rates (Menges et al. 2008). Depth to water table, nutrient availability, and the geological
419 age of soils help explain these geographic differences (Schmalzer and Hinkle 1992). Focusing
420 on broad scale approaches does not always consider spatial and temporal complexities and fine
421 scale habitat features important to endemic species (Bond and Parr 2010, Watson et al. 2011,
422 Noss et al. 2015). A strength of our study is demonstrating that a monitoring approach can
423 evaluate how management and environmental factors interact to effect habitat quality while
424 being site-specific.

425 Monitoring is often most effective when it informs decision making (Williams et al. 2002,
426 Nichols and Williams 2006). The transition probabilities estimated herein can be updated
427 through monitoring to drive management decision models (Johnson et al. 2011, Williams et al.
428 2011) and link habitat quality to population predictions (McCarthy and Thompson 2001,
429 Akcakaya et al. 2004, Burgman et al. 2005, Duarte et al. 2016). Multistate modeling enhanced
430 the ability to examine relationships among environmental factors and fire history, as such
431 relationships have been understudied (Haslem et al. 2012, Levick et al. 2015). Quantification of
432 progress towards desired conditions that incorporates the ability to account for spatial and
433 temporal variability might be more useful than simple comparisons with historical benchmarks
434 or reference sites (Kirkman et al. 2013).

435

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675

Table 1. Model selection table for top 6 models (AICc weight > 0.01) of the 40 *a priori* models.

Model	Transition probabilities (ψ) affected by different covariates under top-supported models						Model selection results			
	Longest fire interval	SPI \times Fire	Openings	Openings \times Oak	Number fires	Number fires \times Oak	Delta AICc	AICc Weight	No. parameters	Deviance
1	$\psi^{SM} \psi^{TS} \psi^{TM}$		ψ^{MT}		$\psi^{TS} \psi^{TM}$		0.00	0.44	45	4420
2	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		ψ^{SM}	ψ^{MS}		$\psi^{TS} \psi^{TM}$	1.39	0.22	50	4411
3	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		ψ^{MT}				1.67	0.19	42	4427
4	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		$\psi^{SM} \psi^{MT}$	ψ^{MS}			3.72	0.07	48	4417
5	$\psi^{SM} \psi^{TS} \psi^{TM}$	$\psi^{MS} \psi^{TS} \psi^{TM}$	ψ^{MT}		$\psi^{TS} \psi^{TM}$		5.19	0.03	55	4405
6	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		$\psi^{SM} \psi^{MT}$		$\psi^{TS} \psi^{TM}$		5.25	0.03	52	4411

Superscripts refer to particular transition probabilities between states ^S = short, ^M = medium, ^T = tall. All top models included the effects of edge and oak \times fire for all ψ . All top models included a quadratic relationship for time since fire (TSF) in oak for ψ^{SM} ; the covariate TSF was not supported in flatwoods when predicting ψ^{SM} . All top models included a linear TSF effect for ψ^{MT} . The effect

of SPI (standardized precipitation index) applied only to oak for ψ^{MS} , ψ^{TS} , ψ^{TM} among the top models. The effect of cutting applied only to ψ^{MT} , ψ^{TS} , and ψ^{TM} for top models.

Table 2. Comparing estimated regression slopes (β 's) with *a priori* predictions for the best habitat transition model.

Transitions (ψ)	β description	β	Lower CL	Upper CL	<i>A priori</i> prediction	Explanation
ψ^{SM}	Flatwoods vs oak	-1.12	-1.93	-0.32	-	Agreement, flatwoods more likely to burn extensively
ψ^{SM}	Edge	0.41	0.12	0.70	+	Agreement, edges reduce fire spread
$\psi^{SM \text{ oak}}$	Fire vs no fire	-0.11	-0.77	0.56	-	Agreement (but CI overlapped 0.0), fires reduce height
ψ^{SM} flatwoods	Fire vs no fire	-1.56	-2.36	-0.76	-	Agreement, fires reduce height
$\psi^{SM \text{ oak}}$	TSF	0.48	0.26	0.70	+	Agreement, growth after fire
$\psi^{SM \text{ oak}}$	TSF squared	-0.02	-0.03	-0.01	-	Agreement, growth rapid immediately after fire than slows
ψ^{SM} flatwoods	TSF	1.01	0.66	1.36	+	Agreement, growth after fire
ψ^{SM} flatwoods	TSF squared	-0.08	-0.12	-0.05	-	Agreement, growth rapid immediately after fire than slows

ψ^{SM}	LFI	0.04	0.01	0.07	+	Agreement, longer fire intervals allow faster regrowth
ψ^{MS}	Flatwoods vs oak	0.05	-1.04	1.14	+	Agreement (but CI overlapped 0.0), we predicted flatwoods more likely to burn extensively
ψ^{MSoak}	Edge	-0.78	-1.22	-0.35	-	Agreement, edges reduce fire spread
ψ^{MSoak}	Fire vs no fire	3.38	2.51	4.24	+	Agreement, fires reduce height
$\psi^{MSflatwood}$ s	Fire vs no fire	3.72	2.96	4.49	+	Agreement, fires reduce height
ψ^{MSoak}	SPI	-1.17	-1.79	-0.54	-	Agreement, fire spread increases in drought for oak
ψ^{MSoak}	SPI squared	-1.49	-2.04	-0.95	-	Agreement, no prescribed fire in extreme drought
ψ^{MT}	Flatwoods vs oak	0.06	-0.27	0.39	+	Agreement (but CI overlapped 0.0), we predicted flatwoods recovers faster than oak
ψ^{MT}	Edge	1.07	0.74	1.39	+	Agreement, edges reduce fire spread
$\psi^{MT\ oak}$	Fire vs no fire	-0.58	-1.11	-0.05	-	Agreement, fires reduce height
ψ^{MT} flatwoods	Fire vs no fire	-0.24	-0.80	0.31	-	Agreement (but CI overlapped 0.0), fires reduce height
ψ^{MT}	TSF	0.06	0.01	0.11	+	Agreement, growth after fire
ψ^{MT}	Cutting	-2.09	-4.07	-0.11	-	Agreement, mechanical cutting decreases height

$\psi^{MT\ oak}$	Openings	-1.46	-1.94	-0.97	+ and -	Clarification, open areas suggest slow shrub recovery
ψ^{TS}	Flatwoods vs oak	0.91	-0.49	2.30	+	Agreement (but CI overlapped 0.0), we predicted flatwoods more likely to burn extensively
$\psi^{TS\ oak}$	Edge	-1.36	-1.83	-0.90	-	Agreement, edges reduce fire spread
$\psi^{TS\ oak}$	Fire vs no fire	3.94	2.67	5.22	+	Agreement, fires reduce height
$\psi^{TS\ flatwoods}$	Fire vs no fire	3.42	2.73	4.11	+	Agreement, fires reduce height
$\psi^{TS\ oak}$	Cutting	2.19	1.63	2.75	+	Agreement, mechanical cutting decreases height
$\psi^{TS\ oak}$	SPI	-1.07	-1.89	-0.25	-	Agreement, fire spread increases in drought
$\psi^{TS\ oak}$	SPI squared	-1.12	-1.72	-0.51	-	Agreement, no prescribed fire in extreme drought
ψ^{TS}	Number fires	-0.17	-0.43	0.09	-	Disagreement (but CI overlapped 0.0) , we predicted more fires increase recovery
ψ^{TS}	LFI	-0.03	-0.07	0.01	-	Agreement (but CI overlapped 0.0) , longer fire intervals slow restoration to earlier states
ψ^{TM}	Flatwoods vs oak	1.50	-0.21	3.21	+	Agreement (but CI overlapped 0.0), we predicted flatwoods more likely to burn extensively
$\psi^{TM\ oak}$	Edge	-0.71	-1.21	-0.21	-	Agreement, edges reduce fire spread
$\psi^{TM\ oak}$	Fire vs no fire	4.50	3.08	5.92	+	Agreement, fires reduce height

ψ^{TM} flatwoods	Fire vs no fire	3.48	2.55	4.42	+	Agreement, fires reduce height
ψ^{TM}	Number fires	-0.25	-0.51	0.01	-	Disagreement (but CI overlapped 0.0), we predicted more fires increase transitions to earlier successional states
ψ^{TM}	LFI	-0.09	-0.13	-0.04	-	Agreement, longer fire intervals slow restoration to earlier states
ψ^{TM}	Cutting	0.62	-0.08	1.32	+	Agreement (but CI overlapped 0.0), mechanical cutting decreases height
$\psi^{\text{TM oak}}$	SPI	-0.87	-1.54	-0.20	-	Agreement, fire spread increases in drought
$\psi^{\text{TM oak}}$	SPI squared	-0.01	-0.52	0.50	-	Agreement, droughts have biggest effect

Transition probability superscripts were SM for short to medium, MS for medium to short, MT for medium to tall, TS for tall to short, TM for tall to medium. Superscripts that included oak had a β specific to oak, superscripts that included flatwoods had a β specific to flatwoods and superscripts without oak or flatwoods had a single β for both oak and flatwoods transitions. Abbreviations TSF = Time-since-fire, LFI = longest fire interval, SPI = standardized precipitation index. Nonlinear relationships were represented by a squared term (quadratic).

Table 3. Annual transition probability estimates (95% CI).

year	short-medium	medium-short	medium-tall	tall-short	tall-medium
scrub					
2004-2005	0.57(0.45-0.68)	n/a	0.18(0.12-0.26)	0.00(0.00-0.03)	0.01(0-0.04)
2005-2006	0.71(0.53-0.84)	0.04(0.02-0.09)	0.29(0.22-0.37)	0.01(0.00-0.04)	n/a
2006-2007	0.22(0.09-0.46)	n/a	0.09(0.05-0.16)	0.00(0.00-0.03)	0.01(0.01-0.04)
2007-2008	0.40(0.19-0.65)	0.28(0.21-0.37)	0.03(0.01-0.08)	0.08(0.05-0.11)	0.03(0.01-0.05)
2008-2009	0.19(0.11-0.31)	0.02(0.01-0.08)	0.05(0.02-0.12)	0.01(0-0.03)	0.03(0.01-0.06)
2009-2010	0.13(0.06-0.25)	0.01(0.00-0.07)	0.04(0.01-0.1)	n/a	n/a
2010-2011	0.48(0.34-0.62)	0.05(0.02-0.11)	0.15(0.09-0.23)	0.04(0.02-0.08)	0.03(0.02-0.06)
2011-2012	0.46(0.32-0.61)	0.06(0.03-0.12)	0.07(0.03-0.13)	0.03(0.02-0.06)	0.14(0.11-0.19)
2012-2013	0.24(0.13-0.41)	0.08(0.05-0.14)	0.02(0.01-0.06)	n/a	0.00(0.00-0.03)
2013-2014	0.12(0.05-0.26)	n/a	0.02(0.01-0.06)	n/a	n/a
2014-2015	0.17(0.08-0.32)	0.01(0.00-0.05)	0.07(0.04-0.12)	n/a	0.01(0-0.04)
flatwoods					
2004-2005	0.54(0.66-0.54)	0.09(0.04-0.20)	0.31(0.21-0.45)	0.08(0.05-0.13)	0.01(0-0.05)

2005-2006	0.38(0.26-0.52)	0.10(0.05-0.19)	0.31(0.21-0.42)	0.01(0.00-0.04)	n/a
2006-2007	0.23(0.12-0.39)	0.05(0.02-0.14)	0.21(0.13-0.33)	0.03(0.01-0.06)	n/a
2007-2008	0.16(0.07-0.31)	0.16(0.09-0.29)	0.11(0.05-0.22)	0.07(0.04-0.12)	0.01(0.00-0.04)
2008-2009	0.15(0.07-0.26)	0.15(0.07-0.28)	0.06(0.02-0.18)	0.03(0.01-0.06)	0.04(0.02-0.08)
2009-2010	0.12(0.06-0.23)	n/a	0.02(0.00-0.12)	n/a	n/a
2010-2011	0.44(0.31-0.58)	0.02(0.00-0.11)	0.12(0.06-0.23)	0.01(0.00-0.04)	0.01(0.00-0.04)
2011-2012	0.25(0.13-0.43)	0.17(0.10-0.28)	0.03(0.01-0.1)	0.12(0.08-0.18)	0.10(0.06-0.15)
2012-2013	0.10(0.05-0.21)	0.22(0.15-0.32)	0.01(0.00-0.08)	0.04(0.02-0.09)	0.07(0.04-0.12)
2013-2014	0.08(0.03-0.16)	n/a	0.07(0.03-0.15)	n/a	n/a
2014-2015	0.25(0.16-0.36)	0.11(0.06-0.2)	0.11(0.06-0.20)	0.08(0.05-0.14)	0.07(0.04-0.13)

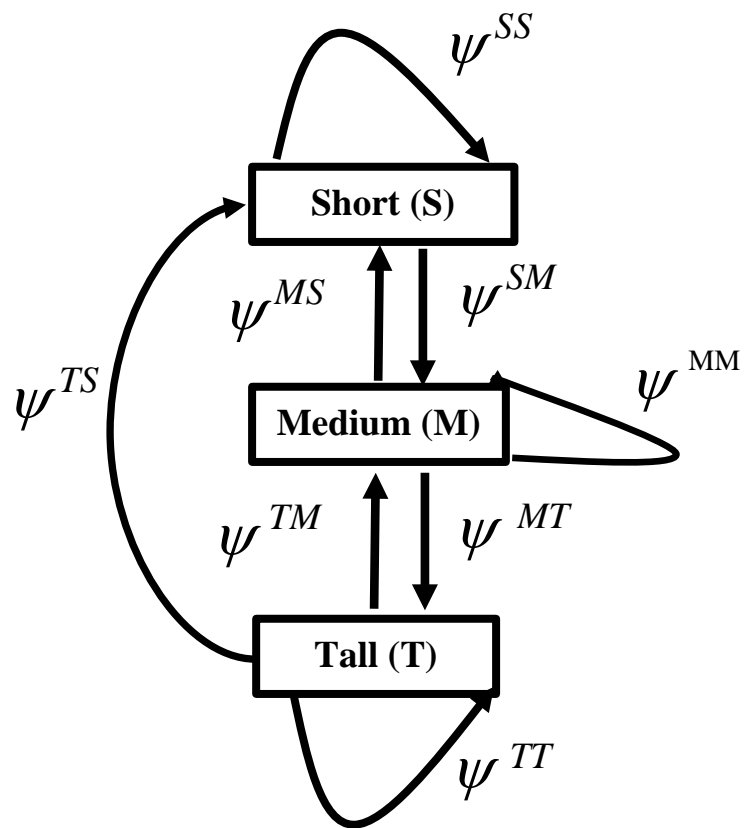
n/a = annual transitions that did not occur

Figure 1. Habitat quality states and transition probabilities (ψ) where superscripts sequentially indicate transitions between particular states.

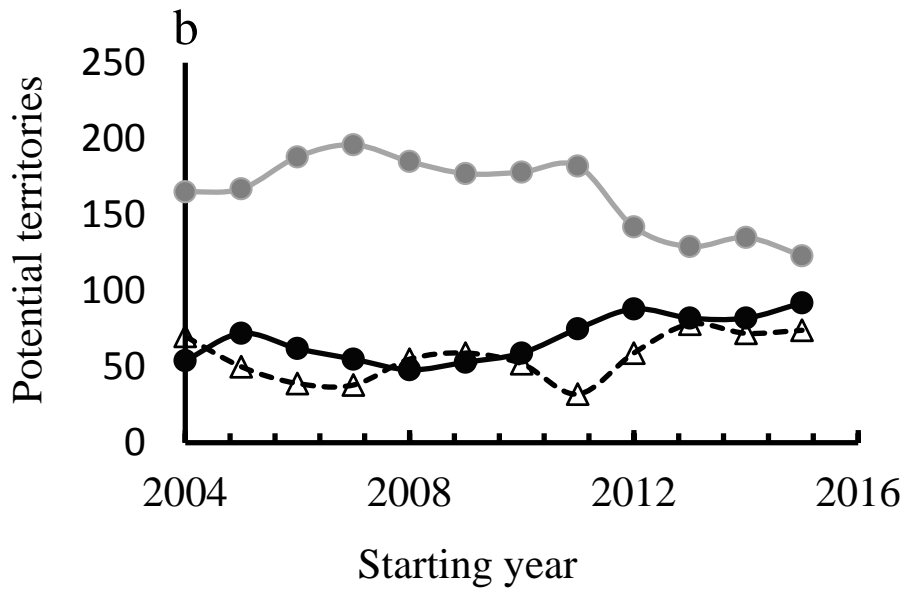
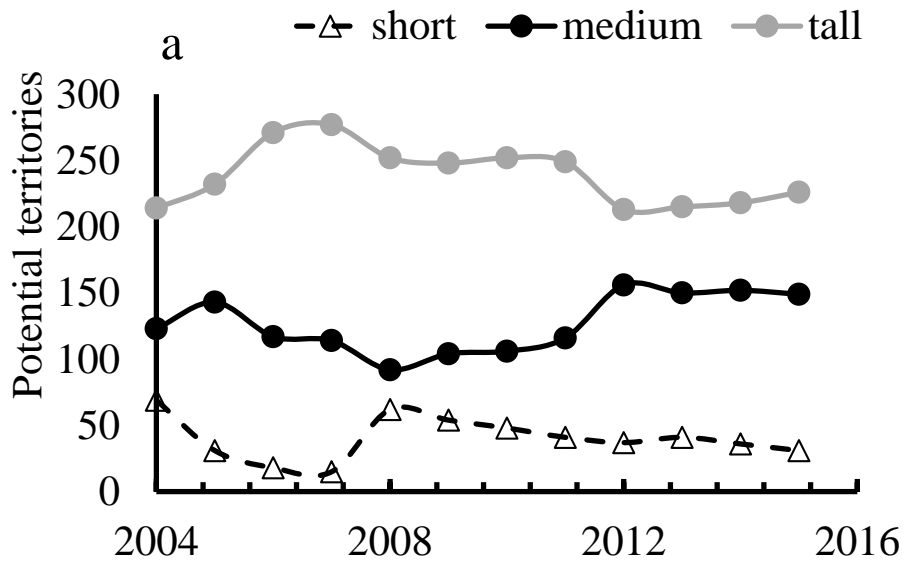
Figure 2. Map of habitat states for 2015. Background grey represents land and white represents water.

Figure 3. Annual habitat state abundances for (a) scrub, (b) flatwoods.

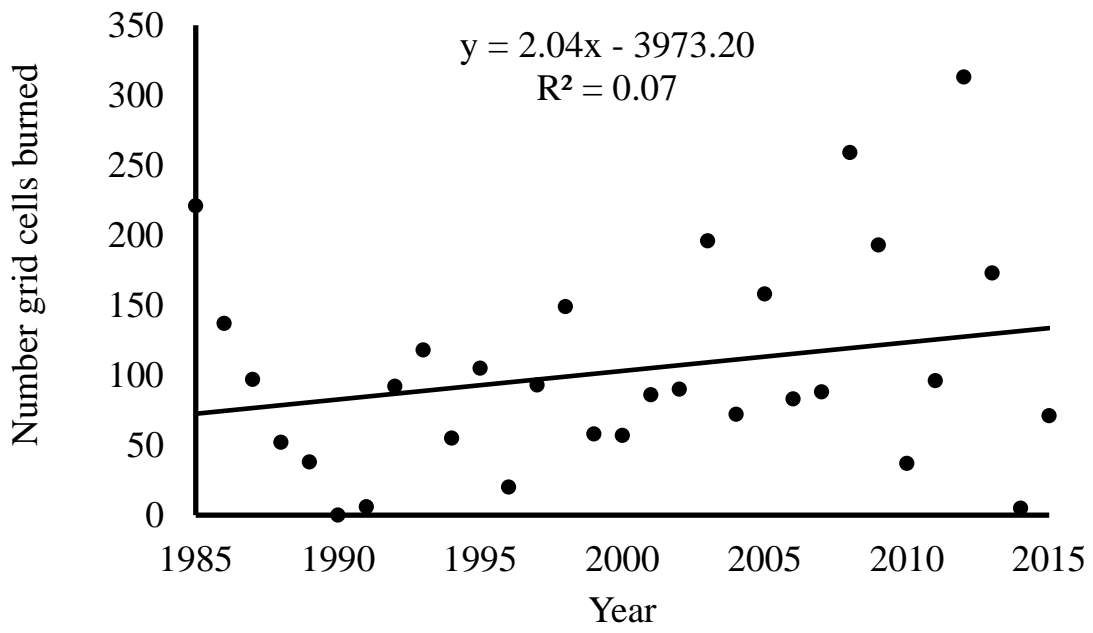
Figure 4. Trends in management effort during periods with available data (a) fire and (b) mechanical cutting.



Habitat state



a



b

