

Title: Bayesian models describing microhabitat associations of infrequently captured small mammals sampled under a complex hierarchical design.

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1 Abstract

2 Knowledge about the relationship between habitat structure and abundance of a target species
3 facilitates biodiversity conservation in managed forests. However, modeling the relationship
4 for infrequent small mammal species in silvicultural experiments introduces the challenge of
5 excessive zero counts and complex hierarchical sampling. A common solution has been to
6 ignore infrequent species. The goal of this study was to model microhabitat associations of
7 infrequently captured forest floor small mammal species with Bayesian models that
8 accounted for subsampling and the blocking design of a large-scale variable-retention harvest
9 experiment. Poisson, negative binomial and overdispersed Poisson Generalized Linear Mixed
10 Models (GLMMs) were fitted to data for three small mammal species with different rates of
11 capture. Shrew-mole (*Neurotrichus gibbsii*) and Keen's deer mouse (*Peromyscus keeni*) were
12 the two infrequent species and southern red-backed vole (*Myodes gapperi*) was the frequent
13 species selected for modeling. Capture rate was predicted from variables representing
14 vegetation structure, and results were compared to corresponding Generalized Linear Models
15 (GLMs). GLMMs predicted stronger and sometimes contrary effects of vegetation structure
16 with wider confidence intervals compared to GLMs. The overdispersed Poisson GLMM
17 provided the most consistent and adequate fit to infrequent species. Capture rate of the
18 shrew-mole was found to be negatively associated with tall shrub cover and coarse woody
19 debris volume. Similarly, capture rate of Keen's deer mouse was negatively associated with
20 herb cover and coarse woody debris volume. Finally, captures of southern red-backed vole
21 was associated negatively with herb cover and coarse woody debris volume but positively
22 associated with vertical complexity of overstory vegetation. With correct GLMM
23 specification, statistical inferences of habitat predictors were more reliable as autocorrelation

24 between samples was properly accounted for and valid standard errors were estimated.
25 Furthermore, the GLMMs in this study fitted capture rates of infrequent species well and
26 produced admissible results on the association of these species to microhabitat features.
27 Infrequent species need not be excluded from analysis; in fact, inclusion of these species is
28 crucial to conservation of species diversity by designing silvicultural treatments that produce
29 or protect suitable habitat.

30 **Keywords:** Bayesian hierarchical model; forest floor small mammal; variable-retention
31 harvesting; mixed effects model; habitat suitability; biodiversity conservation.

32 **1. Introduction**

33 Modeling the relationship between habitat features and species presence or abundance
34 provides the fundamental ecological understanding required for maintaining the biodiversity
35 of managed forests. Beyond gaining ecological insights, the developed relationship can also
36 be used to predict distribution of species across a landscape (Elith and Leathwick, 2009).

37 However, this modeling effort faces two common challenges with data from large-scale
38 silvicultural experiments: (1) a majority of species are captured infrequently, and (2)
39 sampling is typically systematic and involves a hierarchical structure.

40 The first challenge comes naturally from low population abundance and corresponding low
41 detection probability of certain species (Cunningham and Lindenmayer, 2005). A common
42 approach to addressing low abundance and capture frequency has been to exclude
43 infrequently captured species from statistical analysis. Among 23 studies investigating forest
44 floor small mammal responses to silvicultural treatments in the Pacific Northwest, on
45 average only 62% of the captured species were analyzed (e.g., Klenner and Sullivan, 2003;
46 Suzuki and Hayes, 2003). Some species were ignored because they were non-target species
47 or transient species not normally associated with the sampled habitat (Carey and Johnson,
48 1995), but most were avoided because their low frequency rendered traditional statistical
49 models based on the normal distribution unsuitable. One solution has been to group
50 infrequently captured species during analysis (e.g., MacCracken, 2005). Nevertheless, rare
51 species are particularly deserving of conservation efforts because they are most prone to local
52 extirpation (Meffe and Carroll, 1997). For that reason, understanding their individual habitat
53 requirements is crucial to conservation of biodiversity.

54 The second challenge mentioned above is an unavoidable consequence of field experiments
55 that strive for operational and ecological relevance (Maguire et al., 2007). These experiments
56 generally contain large experimental units that necessitate nested and systematically arranged
57 sampling units, causing observations in an experimental unit to be autocorrelated. To handle
58 potential autocorrelation between subsamples within experiment units, count data from the
59 sampling units are often summarized by experimental unit as a mean or total before analysis
60 (e.g., Steventon et al., 1998). This approach is appropriate if the objective is to assess only
61 stand-level treatment effects. An analysis on the experimental unit level addresses one spatial
62 scale, but it may not be the most efficient use of information contained in individual
63 sampling units. With data aggregation, resolution is lost for detecting microhabitat attributes
64 that drive responses to treatments. For example, Miller and Getz (1973) found that
65 microclimatic conditions likely influenced the local distribution of southern red-backed vole.
66 Thus, greater ecological insight may be gained from statistical models that maintain
67 attributes of sampling units while accounting for dependencies between these units and
68 avoiding data aggregation at the level of entire experimental units.

69 Variable-retention regeneration harvesting systems are considered preferred options for
70 managing Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests on public lands in the
71 Pacific Northwest, USA, where management objectives call for a combination of timber
72 production and other ecosystem services. The resulting complex stand structures are viewed
73 as more amenable to conservation of biodiversity. The systems have specific goals of
74 providing refugia to closed-canopy organisms and promoting more rapid recolonization of
75 regenerated stands by these species (Franklin et al., 1997). To establish successful refugia,
76 knowledge about the habitat elements perceived by targeted taxa and the spatial scale at

77 which they respond are essential. This information can be gained from modeling
78 microhabitat association of targeted taxa.

79 Forest floor small mammals in the Pacific Northwest forests play an important role as
80 predators, consumers, and prey (Sullivan and Sullivan, 2001), so they contribute to both
81 species and functional diversity of forests (Carey and Johnson, 1995). Individual species are
82 variably associated with coarse woody debris, herbaceous vegetation and fungal fruiting
83 bodies (Ure and Maser, 1982). These habitat variables indicate quantity and quality of cover
84 and food provided by vegetation comprising a forest stand. By knowing the functional
85 associations, silviculturists can design treatments that produce or protect specific habitat
86 structures. Rigorous modeling of habitat associations becomes a key tool of forest
87 management to successfully balance timber harvest with maintenance of forest biodiversity.

88 The goal of this study was to model the association between microhabitat features and
89 captures of infrequent small mammal species by taking full account of the complex
90 hierarchical design in a large-scale silvicultural experiment in the Pacific Northwest, USA.

91 Three forest floor small mammal species were selected to compare the performance of
92 alternative statistical models for describing the relationship between microhabitat features
93 and capture frequency. Two species were infrequently captured, to the extent that many
94 observations were zero, and one species was very common, resulting in very few zero
95 observations. The statistical models were constructed as Generalized Linear Mixed Models
96 (GLMMs) to accommodate both the nature of count data and the complex hierarchical
97 sampling. Counterparts that ignored the hierarchical sampling structure were formulated as
98 Generalized Linear Models (GLMs) to provide a basis of comparison. The objectives were:
99 (1) to compare modeling results between statistical models that accounted for autocorrelation

100 among sampling units within an experimental unit to those that did not, and (2) to provide an
101 example of how these models can enhance knowledge about microhabitat relationships of
102 small mammal species infrequently captured on the forest floor.

103 **2. Materials and Methods**

104 **2.1 Materials**

105 The Demonstration of Ecosystem Management Options (DEMO) experiment was established
106 as a large-scale operational experiment to assess long-term effects of variable-retention
107 systems on plants, animals, ecological processes and public perceptions in Douglas-fir forests
108 of western Oregon and Washington, USA (Aubry et al., 1999). The silvicultural experiment
109 was implemented under a Randomized Complete Block Design (RCBD) with subsampling.
110 In each of six blocks, two in Oregon and four in Washington (Fig. 1), six 13-ha experimental
111 units were established and treatments were randomly assigned. The six harvest treatments
112 were defined by level (percentage of basal area) and spatial pattern (dispersed vs. aggregated)
113 of retained trees as follows (Fig. 1): (1) 100% retention (100%); (2) 75% aggregated
114 retention (75%A); (3) 40% dispersed retention (40%D); (4) 40% aggregated retention
115 (40%A); (5) 15% dispersed retention (15%D); (6) 15% aggregated retention (15%A).
116 Halpern et al. (2005) have provided further details on the study sites and vegetation sampling.

117 **[Insert Fig. 1 here]**

118 In each 13-ha unit, a permanent 8×8 or 7×9 sampling grid with 40-m spacing was installed
119 for vegetation and forest floor small mammal sampling. The grid was buffered by 40 m
120 between the outer grid points and the edge of the unit. At each sample point, small mammals
121 were trapped using a pitfall trap made from two stacked No. 10 cans and operated as a death

122 trap partially filled with water (Gitzen et al., 2007; Oregon Department of Fish and Wildlife
123 Scientific Taking Permits 306-93, 097-34, 075-95, 106-96, 022-99, and 083-00; Washington
124 Department of Fish and Wildlife Permits 99-281 and 00-148). Traps were continuously
125 opened for 28 days between late September and early November, and captured animals were
126 collected and identified weekly (Gitzen et al., 2007). Overstory and understory vegetation
127 were studied concurrently with small mammal trapping. At each sample point, percent cover
128 of herbaceous and small shrub species (<1 m tall) was recorded on a cluster of 24 microplots
129 (0.2 × 0.5 m). Percent cover of tall shrub species (>1 m tall) and of understory coniferous
130 trees (<5 cm dbh) was measured on four 6-m planar intercepts radiating out from the sample
131 point. Diameter of any downed wood (stems ≥10 cm) was measured at the point of
132 intersection with the vertical plane along these transects. Overstory trees were sampled with
133 nested circular plots that included a 0.01-ha plot for trees with dbh ≥5 and <15 cm and a
134 0.04-ha plot for trees with dbh ≥15 cm.

135 At each sample point, the response variable was the total number of captured individuals of a
136 small mammal species. The predictors included six attributes describing vegetation structure
137 at the level of each sample point: (1) mean percent herbaceous cover (HERB, %), (2) mean
138 percent understory conifer cover (CONIF, %), (3) mean percent tall shrub cover
139 (SHRUB, %), (4) mean coarse woody debris volume per hectare (CWDVOL, m³/ha), (5)
140 overstory crown structural heterogeneity (SHANNON), and (6) stand density (TPH,
141 trees/100-ha). Minima, means, maxima, and standard deviations were summarized in
142 Supporting Information (Table S1).

143 The coarse woody debris volume per hectare was estimated by the conventional technique of
144 planar intersect sampling (de Vries, 1986). Stand density in terms of overstory trees per

145 hectare ($\text{dbh} \geq 5$ cm) was estimated and rescaled by dividing by 100. SHANNON measured
146 the vertical distribution of live crown cross-sectional area, providing an index of vertical
147 complexity in overstory vegetation (Maguire et al., 2007). For each tree at each sample point,
148 crown cross-sectional areas were computed at 0.5-m height intervals and summed for each
149 height to construct a crown-area profile (Dubrasich et al., 1997). The Shannon diversity
150 index of this crown-area profile (SHANNON) represented relative variability in total crown
151 area among the 0.5-m height intervals. A higher SHANNON indicated greater vertical
152 diversity.

153 The habitat association modeling was based on data collected in 1999 immediately after
154 implementation of silvicultural treatments. In that year, vegetation sampling was
155 implemented on only a subset of sampling points, i.e., 32–37 sample points per unit
156 depending on treatment. Only those sampling points with both vegetation and small mammal
157 information were used for modeling. Of the 32 captured small mammal species (Gitzen et al.,
158 2007), two infrequent species were selected for modeling, the shrew-mole (*Neurotrichus*
159 *gibbsii*; NEGI) and Keen's deer mouse (*Peromyscus keeni*; PEKE). These two species had a
160 total number of captures equal to 91 and 90 individuals, respectively. In addition to a large
161 number of zero observations, only a single individual was captured in a high proportion of
162 traps (Supporting Information, Fig. S1a & b). The selected abundant species, the southern
163 red-backed vole (*Myodes gapperi*; MYGA), had a total number of captures equal to 322
164 individuals (Fig. S1c). The three small mammal species were chosen because of their
165 potential as indicator species and conservation value. Sullivan et al. (2005) found that
166 MYGA was a good indicator of old-growth forest conditions. Raphael (1984) and Carey and
167 Johnson (1995) suggested that NEGI and PEKE were more closely associated with older

168 forests, but these species were seldom studied. PEKE and MYGA did not occur in Oregon;
169 therefore, their analyses were based only on the four blocks located in Washington (Fig. 1).
170 In short, 1181 sample points from six blocks were available for NEGI, whereas 787 sample
171 points from four blocks were available for MYGA and PEKE.

172 **2.2 Statistical Models**

173 The GLMMs were multilevel GLMs with random effects for blocks and for experimental
174 units within which subsamples were nested in the DEMO experiment. We formulated the
175 GLMMs in the context of Bayesian Hierarchical Models (BHMs), which have the ability to
176 accommodate a small number of higher level units and all sources of uncertainty in
177 estimating random effects (Congdon, 2006). The three models considered in the study were
178 the Poisson GLMM (POIS-GLMM), overdispersed Poisson GLMM (overPOIS-GLMM) and
179 negative binomial GLMM (NB-GLMM). We considered two random effects: (1) a random
180 effect for experimental units to account for the nested structure of sample points within units,
181 and (2) a random block effect consistent with the RCBD of the experiment. The layout of the
182 GLMM followed formulation of the RCBD in Littell et al. (2006) and BHM in Congdon
183 (2005).

184 The response and predictor variables for the models were defined as follows:

185 y_{ijk} = Observed count of individuals for a species at k -th trap in j -th unit of i -th
186 block

187 $HERB_{ijk}$ = Mean percent herb cover at k -th trap in j -th unit of i -th block

188 $CONIF_{ijk}$ = Mean percent understory conifer cover at k -th trap in j -th unit of i -th block

189 $SHRUB_{ijk}$ = Mean percent tall shrub cover at k -th trap in j -th unit of i -th block

190 $CWDVOL_{ijk}$ = Mean coarse woody debris volume per ha at k -th trap in j -th unit of i -th
 191 block

192 $SHANNON_{ijk}$ = Shannon index of vertical structural diversity of the overstory at k -th trap in
 193 j -th unit of i -th block

194 TPH_{ijk} = Tree density (hundreds of trees per ha) at k -th trap in j -th unit of i -th block

195 The POIS-GLMM on the trap level was formulated as follows:

$$196 \quad y_{ijk} \sim \text{Poisson}(\lambda_{ijk}) \quad (1)$$

197 where the expectation of captures at the k -th trap in the j -th unit of the i -th block (λ_{ijk}) was
 198 conditioned on a set of predictors in the GLM context and corrected for slight variation in
 199 number of trap nights:

$$200 \quad \log(\lambda_{ijk}) = b_{1ij} + b_{2ij}HERB_{ijk} + b_{3ij}CONIF_{ijk} + b_{4ij}SHRUB_{ijk} + \\ b_{5ij}CWDVOL_{ijk} + b_{6ij}SHANNON_{ijk} + b_{7ij}TPH_{ijk} + \log(tn_{ijk}) \quad (2)$$

201 where,

202 λ_{ijk} = expectation of captures at k -th trap in j -th unit of i -th block

203 b_{hij} = h -th random coefficient for j -th unit of i -th block

204 tn_{ijk} = Number of trap nights at k -th trap in j -th unit of i -th block

205 A Poisson model in general might be subject to overdispersion; that is, the variance may
 206 exceed the mean, because no variance parameter is included to capture any case of
 207 overdispersion (Gelman and Hill, 2007). The overPOIS-GLMM extended the POIS-GLMM
 208 by including a trap-level random error term ε_{ijk} to capture any possible additional variation

209 beyond what was already accounted for by the multilevel modeling (Congdon, 2005). The
 210 implied model was therefore:

$$211 \quad \log(\lambda_{ijk}) = b_{1ij} + b_{2ij}HERB_{ijk} + b_{3ij}CONIF_{ijk} + b_{4ij}SHRUB_{ijk} + \quad (3)$$

$$b_{5ij}CWDVOL_{ijk} + b_{6ij}SHANNON_{ijk} + b_{7ij}TPH_{ijk} + \log(tn_{ijk}) + \varepsilon_{ijk}$$

212 where ε_{ijk} was assumed normally distributed with mean of 0 and variance σ_ε^2 .

213 The negative binomial model is an alternative model accounting for overdispersion in count
 214 data. Following Ntzoufras (2009) and Zuur et al. (2009), we specified the NB-GLMM as:

$$215 \quad y_{ijk} \sim NegBin\left(\theta / (\theta + \lambda_{ijk}), \theta\right) \quad (4)$$

216 where, *NegBin()* denoted a negative binomial distribution. The parameter θ captured
 217 overdispersion in the data, with smaller values of θ implying greater overdispersion. The
 218 expected species count (λ_{ijk}) was conditioned on the same set of predictors shown in Eq. (2).

219 For the three GLMMs, let $\mathbf{B}_{ij} = [b_{1ij} \quad b_{2ij} \quad \dots \quad b_{7ij}]'$, $\mathbf{U} = [\mu_1 \quad \mu_2 \quad \dots \quad \mu_7]'$,
 220 $\mathbf{D}_i = [d_{1i} \quad d_{2i} \quad \dots \quad d_{7i}]'$ and $\mathbf{E}_{ij} = [e_{1ij} \quad e_{2ij} \quad \dots \quad e_{7ij}]'$, where μ_h was the overall mean for
 221 the h -th random coefficient for the corresponding covariate; d_{hi} was the random block effect
 222 on the h -th random coefficient of i -th block; e_{hij} was the random error on the h -th random
 223 coefficient for j -th unit of i -th block; $h = 1, \dots, 7$ (an intercept plus coefficients for six
 224 predictors); $i = 1, \dots, m$ blocks ($m = 6$ for NEGI and $m = 4$ for MYGA and PEKE); $j = 1, \dots, 6$
 225 units; $k = 1, \dots, n_{ij}$ traps (where n_{ij} was 32–37). On the unit-level, each coefficient was
 226 partitioned into an overall mean, a random block effect, and a random error following the
 227 construct of RCBD as $\mathbf{B}_{ij} = \mathbf{U} + \mathbf{D}_i + \mathbf{E}_{ij}$. Thus, the full model for coefficients on the
 228 experimental unit-level was,

$$\begin{matrix} 229 \\ \end{matrix}
\begin{bmatrix} \mathbf{B}_{11} \\ \vdots \\ \mathbf{B}_{16} \\ \mathbf{B}_{21} \\ \vdots \\ \mathbf{B}_{26} \\ \vdots \\ \mathbf{B}_{m6} \end{bmatrix} = \begin{bmatrix} \mathbf{U} \\ \vdots \\ \mathbf{U} \\ \vdots \\ \mathbf{U} \\ \vdots \\ \mathbf{U} \end{bmatrix} + \begin{bmatrix} 1 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 1 & 0 & \cdots & 0 \\ 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 1 & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots \\ 0 & 0 & \cdots & 1 \end{bmatrix} \begin{bmatrix} \mathbf{D}_1 \\ \mathbf{D}_2 \\ \vdots \\ \mathbf{D}_m \end{bmatrix} + \begin{bmatrix} \mathbf{E}_{11} \\ \vdots \\ \mathbf{E}_{16} \\ \mathbf{E}_{21} \\ \vdots \\ \mathbf{E}_{26} \\ \vdots \\ \mathbf{E}_{m6} \end{bmatrix} \quad (5)$$

230 The full vector \mathbf{B}_{ij} for all ij (Eq. 5) was assumed to follow a multivariate normal (MVN)
231 distribution, i.e., $[\mathbf{B}_{11} \ \cdots \ \mathbf{B}_{m6}]' \sim MVN([\mathbf{U} \ \cdots \ \mathbf{U}]', \mathbf{ZGZ}' + \mathbf{R})$, where \mathbf{Z} , \mathbf{G} and \mathbf{R} were
232 defined as follows. Let σ_h^2 and τ_h^2 be the variance of the random error and the random block
233 effect, respectively, associated with the h -th coefficient, and $\rho_{hh'}$ and $\varphi_{hh'}$ be the correlation of
234 random errors and random block effects, respectively, between h -th and h' -th coefficients,
235 where $h \neq h'$. Assuming that the random error vector \mathbf{E}_{ij} and random block effect vector \mathbf{D}_i
236 followed a MVN distribution, i.e., $\mathbf{E}_{ij} \sim MVN(\mathbf{0}, \Sigma_R)$ and $\mathbf{D}_i \sim MVN(\mathbf{0}, \Sigma_D)$, where $\mathbf{0}$ was a
237 7×1 vector of zeros, the variance-covariance matrix of the random error vector \mathbf{E}_{ij} , Σ_R , was,

$$\begin{matrix} 238 \\ \end{matrix}
\Sigma_R = \begin{bmatrix} \sigma_1^2 & \rho_{12}\sigma_1\sigma_2 & \cdots & \rho_{17}\sigma_1\sigma_7 \\ \rho_{12}\sigma_1\sigma_2 & \sigma_2^2 & \cdots & \rho_{27}\sigma_2\sigma_7 \\ \vdots & \vdots & \ddots & \vdots \\ \rho_{17}\sigma_1\sigma_7 & \rho_{27}\sigma_2\sigma_7 & \cdots & \sigma_7^2 \end{bmatrix} \quad (6)$$

239 Similarly, the variance-covariance matrix of the random block effect vector \mathbf{D}_i , Σ_D , was,

$$\begin{matrix} 240 \\ \end{matrix}
\Sigma_D = \begin{bmatrix} \tau_1^2 & \varphi_{12}\tau_1\tau_2 & \cdots & \varphi_{17}\tau_1\tau_7 \\ \varphi_{12}\tau_1\tau_2 & \tau_2^2 & \cdots & \varphi_{27}\tau_2\tau_7 \\ \vdots & \vdots & \ddots & \vdots \\ \varphi_{17}\tau_1\tau_7 & \varphi_{27}\tau_2\tau_7 & \cdots & \tau_7^2 \end{bmatrix} \quad (7)$$

241 Hence, the full random error vector \mathbf{E}_{ij} for all ij (Eq. 5) had a MVN distribution,

242 $[\mathbf{E}_{11} \ \dots \ \mathbf{E}_{m6}]' \sim MVN\left([\mathbf{0} \ \dots \ \mathbf{0}]', \mathbf{R}\right)$, where $\mathbf{R} = \mathbf{I}_{(m \times 6)} \otimes \boldsymbol{\Sigma}_R$, and $\mathbf{I}_{(m \times 6)}$ was $m \times 6$

243 identity matrix. The full vector of random block effects \mathbf{D}_i for all ij (Eq. 5) was also assumed

244 a MVN distribution, $[\mathbf{D}_1 \ \dots \ \mathbf{D}_m]' \sim MVN\left([\mathbf{0} \ \dots \ \mathbf{0}]', \mathbf{G}\right)$, where $\mathbf{G} = \mathbf{I}_{(m \times m)} \otimes \boldsymbol{\Sigma}_D$, and

245 $\mathbf{I}_{(m \times m)}$ was the $m \times m$ identity matrix. Matrix \mathbf{Z} was the design matrix of the full vector \mathbf{D}_i for

246 all ij with 0s and 1s (Eq. 5). As a result, the variance-covariance matrix for the full vector \mathbf{B}_{ij}

247 (Eq. 3) was $\mathbf{ZGZ}' + \mathbf{R}$ and could be constructed from \mathbf{Z} , $\boldsymbol{\Sigma}_R$, $\boldsymbol{\Sigma}_D$ and corresponding identity

248 matrices. Further details can be found in Lam (2010).

249 The hyperparameters of the variance-covariance matrices and the general mean were given

250 non-informative prior distributions reflecting prior ignorance about the nature of the

251 parameters (Congdon, 2006). For the general mean, a non-informative MVN distribution was

252 assigned, i.e., $\mathbf{U} \sim MVN(\mathbf{0}, 1000000 \cdot \mathbf{I}_7)$, where $\mathbf{0}$ was a 7×1 vector of zeros and \mathbf{I}_7 was a 7×7

253 identity matrix. An inverse-Wishart distribution was assumed for $\boldsymbol{\Sigma}_R$ (Eq. 6) and $\boldsymbol{\Sigma}_D$ (Eq. 7);

254 i.e., $\boldsymbol{\Sigma}_R \sim inv\text{-Wishart}(\boldsymbol{\Omega}, \nu)$ and $\boldsymbol{\Sigma}_D \sim inv\text{-Wishart}(\boldsymbol{\Omega}, \nu)$, where $\boldsymbol{\Omega}$ was a 7×7 identity

255 matrix and $\nu = 7$. For overPOIS-GLMM, a non-informative uniform prior distribution was

256 assigned to σ_ε^2 , i.e., $\sigma_\varepsilon^2 \sim U(0, 1000000)$. For NB-GLMM, a non-informative gamma prior

257 distribution was assumed for θ , i.e., $\theta \sim gamma(0.001, 0.001)$.

258 The GLMMs were specified and fitted using WinBUGS (Lunn et al., 2000). Three disparate

259 sets of initial values (chains) were used. The MCMC algorithm was run with 250,000

260 iterations and the initial 20,000 iterations were dropped. The convergence of the algorithm

261 was judged from trace and history plots of the MCMC samples, the Brooks-Gelman-Rubin

262 (BGR) statistic (Brooks and Gelman, 1998), and the Monte Carlo (MC) errors of estimated
 263 parameters. The trace and history plots and BGR statistics showed convergence for all three
 264 models and for all three small mammal species. The MC errors on average were less than 2%
 265 of the corresponding posterior standard deviations of the estimated parameters. Thinning of
 266 the MCMC samples was necessary for some parameters to reduce autocorrelation between
 267 samples.

268 We based model comparison for each species on the Deviance Information Criterion (DIC)
 269 (Spiegelhalter et al., 2002) with smaller values indicating better model fit. Posterior estimates
 270 of a given h -th coefficient, \tilde{b}_{hij} , were averaged over all units,

$$271 \quad \bar{b}_h = \frac{\sum_{i=1}^m \sum_{j=1}^6 \tilde{b}_{hij}}{m \times 6} \quad (8)$$

272 , and their 95% credible intervals were reported.

273 For comparison, we formulated Poisson GLM (POIS-GLM) and negative binomial GLMs
 274 (NB-GLM) ignoring the RCBD and subsampling structures by pooling all sample points and
 275 treating the coefficients in Eq. (2) as fixed effects. We reported the estimated coefficients and
 276 their 95% confidence intervals, and used the corrected Akaike Information Criteria (AICc,
 277 Burnham and Anderson, 2004) as a measure of relative model performance. The POIS-GLM
 278 and NB-GLM were fitted with the glm and MASS packages available from the open source
 279 statistical software R (R Development Core Team, 2010).

280 We evaluated the performances between the GLMMs and GLMs by comparing their DIC,
 281 AICc, consistency in parameter estimates, and patterns in credibility and confidence intervals.
 282 Then, we selected the GLMM model having the minimum DIC as the best model. We

283 subsequently applied backward elimination and forward selection based on 95% credible
284 intervals to this model for variable selection, and a final model was fitted to the number of
285 captures of the three small mammal species in response to variables representing habitat
286 structure.

287 **3. Results**

288 **3.1 *Neurotrichus gibbsii* (NEGI)**

289 Results between GLMMs and GLMs were noticeably different for NEGI (Table 1). The 95%
290 credible intervals for the estimated coefficients from GLMMs were consistently wider than
291 the corresponding 95% confidence intervals from GLMs (Table 1). Under GLMs TPH was
292 inferred to be statistically significant, but under GLMMs it became non-significant. On the
293 other hand, significant negative effects of CWDVOL predicted by GLMMs became non-
294 significant under GLMs. Almost half of the posterior coefficient estimates of CWDVOL in
295 individual units were negative, and the rest were generally neutral, reflecting the relatively
296 wide 95% credible intervals (Fig. 2a). Thus, GLMMs predicted an average negative effect of
297 CWDVOL on number of captures, whereas the effect might go undetected when data were
298 pooled under GLMs. One of the most noticeable differences was the strongly negative effect
299 of HERB in the GLMM versus a positive and weaker effect in the GLM (Table 1).

300 **[Insert Table 1 here]**

301 **[Insert Fig. 2 here]**

302 Among the three small mammal species, captures of NEGI showed the largest overdispersion
303 by having the smallest $\tilde{\theta}$ under NB-GLMM and the largest $\tilde{\sigma}_\epsilon^2$ under overPOIS-GLMM (0.08
304 and 4.945, respectively; Tables 1–3). The overPOIS-GLMM indicated the best fit among the

305 GLMMs by having the lowest DIC, achieving a 41–46% reduction in DIC relative to POIS-
306 and NB-GLMM (Table 1). Hence, overPOIS-GLMM was selected as the final microhabitat
307 association model for NEGI, with backward elimination and forward selection of predictors
308 to retain only those that were statistically significant. As a result, the final model for NEGI
309 indicated that capture rate responded negatively to SHRUB and CWDVOL (Table 4). The
310 mean number of NEGI captures declined by 27% and 19% with each 1% increase in SHRUB
311 and each 1 m³/ha increase in CWDVOL, respectively.

312 **3.2 *Peromyscus keeni* (PEKE)**

313 As was the case for NEGI, significant microhabitat predictors from GLMMs for PEKE
314 differed from those of GLMs (Table 2). Despite the consistently wider 95% credible intervals
315 of GLMMs, the number of PEKE captures was negatively correlated with HERB and
316 CWDVOL but not significantly correlated with CONIF. This was contrary to the trends
317 found under GLMs, where HERB and CWDVOL were positively correlated with the number
318 of PEKE captures and correlation with CONIF was significant (Table 2). With respect to
319 CWDVOL, one-third of the units exhibited a strongly negative effect, as was the case for
320 NEGI, despite relatively wide 95% credible intervals (Fig. 2b). Thus, the average CWDVOL
321 effect was significantly negative under GLMMs. On the contrary, the effect of CWDVOL
322 predicted by GLMs was either positive or non-significant (Table 2). Captures of PEKE were
323 less overdispersed than those of NEGI but more than those of MYGA with intermediate $\tilde{\theta}$
324 under NB-GLMM and $\tilde{\sigma}_\epsilon^2$ under overPOIS-GLMM (0.199 and 2.484, respectively; Tables 1–
325 3). The overPOIS-GLMM was the best fitting model for PEKE among the three GLMMs, as
326 indicated by a DIC that was 18–20% lower than the DIC of POIS- and NB-GLMM (Table 2).
327 The final result of variable selection in the overPOIS-GLMM indicated that number of

328 captures was negatively associated with HERB and CWDVOL (Table 4). The mean number
329 of PEKE captures decreased by 13.6% and 7.6% with each 1% increase in HERB and each 1
330 m³/ha increase in CWDVOL, respectively.

331 **[Insert Table 2 here]**

332 **[Insert Table 4 here]**

333 **3.3 *Myodes gapperi* (MYGA)**

334 Except for CWDVOL, average posterior coefficient estimates of the other two significant
335 habitat predictors in the GLMMs were similar to the parameter estimates from the
336 corresponding GLMs (Table 3). The variables CONIF, SHRUB, and TPH were significant in
337 at least some of the GLMs but not in the GLMMs due to the wider 95% credible intervals
338 under GLMMs. The correlation between CWDVOL and MYGA captures was similar to that
339 for both NEGI and PEKE captures in that some units showed strongly negative effects
340 despite relatively wide 95% credible intervals, and other units exhibited close to neutral
341 effects (Fig. 2c). On the other hand, the posterior coefficient estimates for HERB by
342 individual unit showed high variability (Fig. 3). The individual unit effect ranged from a
343 marginally significant positive effect to a strongly negative effect, but with a majority close
344 to a neutral effect. Interestingly, the posterior estimates for the 40%A treatment (units 34, 44,
345 54, 64) varied from neutral to significantly positive or significantly negative depending on
346 the block that the corresponding units were in (Fig. 3). Nevertheless, the average posterior
347 coefficient estimates of HERB under GLMMs and the coefficient estimates under GLMs
348 were all negative.

349 **[Insert Table 3 here]**

350 **[Insert Fig. 3 here]**

351 Overdispersion was the least for MYGA captures with the highest $\tilde{\theta}$ under NB-GLMM and
352 the lowest $\tilde{\sigma}_\epsilon^2$ under overPOIS-GLMM (1.328 and 0.895, respectively; Table 3). Consistent
353 with the two infrequent species, overPOIS-GLMM had the best fit (DIC = 1105.3; Table 3).
354 However, the fits of POIS- and NB-GLMM were arguably similar since their DICs were only
355 7-9% higher than that of overPOIS-GLMM. To simplify comparisons among species,
356 overPOIS-GLMM was selected as the best final model form. After variable selection, the
357 number of MYGA captures was negatively associated with HERB and CWDVOL but
358 positively associated with SHANNON (Table 4). The mean number of MYGA captures
359 increased by 4.4% and 2.8% with each 1% increase in HERB and each 1 m³/ha increase in
360 CWDVOL, respectively. On the other hand, a one-unit increase in SHANNON was inferred
361 to increase MYGA captures by an average of 90.6%.

362 **4. Discussion**

363 Knowledge about the relationship between the abundance of a target species and habitat
364 structure is built by trapping small mammals and measuring associated habitat variables,
365 followed by application of appropriate statistical models to infer biologically significant
366 relationships. Differences in capture frequencies among different species for a given
367 sampling design are caused by differences in population size, activity patterns, and many
368 other factors. Statistical models selected for analysis should be appropriate for the sampling
369 design to ensure valid statistical inferences. This study compared GLMMs and GLMs for
370 inferring habitat associations of three small mammal species with a wide range in capture
371 frequency. The resulted differences between GLMMs and GLMs were surprisingly large. For

372 example, inferences for some predictors changed from being significant in the GLMs to
373 becoming non-significance under GLMMs. Furthermore, some predictors had opposite
374 effects between GLMMs and GLMs. Perhaps of greatest importance, this study demonstrated
375 that infrequently captured species need not be excluded from analysis because their habitat
376 requirements can be assessed with proper selection and specification of statistical models.

377 **4.1 Modeling Issues**

378 One basic assumption of most statistical models is that observations are independent.
379 Blocked and nested sampling points in this study would tend to be more similar due to
380 proximity and similarities in physical environment, biological community, and other factors
381 that are influenced by proximity. Hence, the assumption of independent observations is likely
382 to have been violated. The multilevel models in this analysis could reasonably assume
383 observations to be independent, particularly after conditioning on random effects of both
384 blocks and experimental units in the DEMO experiment. Accounting for autocorrelation is
385 required for valid standard error estimates of coefficients; otherwise, inferences may be
386 incorrect due to potential inflation or deflation of estimated variances (Congdon, 2005). This
387 effect is corroborated by the fact that 95% credible intervals under GLMMs were
388 consistently wider than the corresponding 95% confidence intervals under GLMs that did not
389 account for autocorrelation. Of practical significance is the observation that inferences about
390 parameter estimates changed substantially for some microhabitat descriptors in all three
391 small mammal species.

392 These changes included changes in the significance of parameter estimates as well as shifts in
393 the direction of predictor variables effects. Management strategies developed for the three
394 small mammal species would clearly differ depending on which of these alternative statistical

395 models were accepted as appropriate. For example with PEKE, the association of CWDVOL
396 is positive under GLMs but negative under GLMMs. As a result, a management strategy
397 based on the former would propose increasing amount of coarse wood while a strategy based
398 on the latter would suggest the opposite. Ecological responses have been shown to differ
399 across several spatial scales (e.g., Maguire, 1985), so accounting for these potential
400 differences in statistical models can be important for enhancing our understanding of
401 ecological mechanisms and ultimate factors. In this analysis, GLMs were stand-level analysis
402 whereas GLMMs provided insight into within-stand responses. In the case of PEKE, greater
403 amounts of coarse wood at the stand-level may provide higher quality habitat and thus,
404 greater abundance. At this spatial scale, the presence and amount of coarse wood may
405 indicate the availability of cover habitat or travel corridors between open patches. Within an
406 experimental unit, the species was trapped more frequently in open microhabitat
407 characterized by lower amounts of coarse wood, perhaps because their activity is higher in
408 these areas as they forage for food. In short, coarse wood is an essential habitat structure, and
409 the spatial scale at which it is distributed can be important, keeping in mind that other habitat
410 features also play a role. An appropriate management strategy for PEKE is implied to
411 provide coarse wood within a stand but distributed in a manner that creates aggregates and
412 edge habitat between aggregates of coarse wood and open patches. Similar interpretations
413 can be extended to other changes in inferences drawn between models and between small
414 mammal species.

415 The structure of GLMMs essentially caused individual regression models to be fitted for each
416 experimental unit, capturing the relationship between number of captures and microhabitat
417 structure for each species. This structure further allowed evaluation of the variation in

418 microhabitat relationships among units. Data pooling in the GLMs masked these unit-specific
419 relationships; e.g., the number of MYGA captures was positively correlated with coarse
420 wood in the GLMs, but the relationship could be seen to vary among units in the GLMMs. In
421 other words, GLMMs showed that the trend was positive across units but negative within
422 units. Conversely, a benefit of explicitly modeling the within-unit relationship is the
423 confidence gained by observing consistency in the relationship among units. Coefficient
424 estimates are expected to be generally consistent in direction but different in value among
425 units because the latter reflects unit-level differences attributable to treatment effects and
426 inherent levels of other habitat variables. Consistency in coefficient estimates among units
427 can provide strong evidence for general response of capture rate to a wider range in the
428 corresponding habitat variable. In contrast, inconsistencies such as those exemplified by the
429 effect of herbaceous cover on MYGA captures may imply interactions between this
430 microhabitat variable and unobserved characteristics of the units, or may represent nonlinear
431 responses if the variable covers a different part of the range in the corresponding habitat
432 conditions among different units. In this case, conclusions about general effects of the habitat
433 descriptor should be treated with caution.

434 The overPOIS-GLMM was selected as a suitable model for the two infrequent species due to
435 its ability to capture overdispersion, to identify tentatively important habitat variables, and to
436 produce the lowest DIC. Overdispersion was defined as the case in which the variance of
437 count data exceeded the mean, and the trap-level random error ε_{ijk} effectively captured this in
438 the data of the two infrequent species. For abundant species like MYGA, overPOIS-GLMM
439 only resulted in marginally better fits than POIS-GLMM. For infrequent species,
440 overdispersion becomes an issue because of the large number of zero counts, so the

441 overPOIS-GLMM could account for excessive zero counts without detailed structural
442 information about the random error ε_{ijk} .

443 Accurate estimation of population size, species richness, and species diversity require known
444 detection probability for the species of interest. The issue of detection probability has
445 received considerable attention, with three main factors identified as observer bias,
446 environmental conditions, and species features (Anderson, 2001). The traps in the DEMO
447 experiment lead to death of the trapped individual and, hence, their elimination from the
448 population. Detection probability of small mammal species is challenging at best without
449 mark-and-recapture techniques. A major objective of this silvicultural field trial was simply
450 to test for treatment effects on captures, realizing that detected treatment effects can be
451 attributed to one or more contributing mechanisms such as true changes in abundance,
452 modification of behavior, alteration of age class structure, shift in sex ratio, and many others.

453 More detailed study of individuals and more manipulative experimentation would be
454 required to establish with greater certainty the factors that drive capture rate under a given
455 trap design and the relationship of this capture rate to population abundance.

456 This analysis demonstrated that appropriate statistical models were very effective for
457 addressing the challenge of modeling habitat associations of infrequent species without
458 having to exclude them due to the high frequency of zero captures. One immediate question
459 is the threshold of rarity at which these models will fail to perform, a question that
460 conceivably could be investigated using a wider range of other small mammal species
461 captured in the DEMO experiment. Furthermore, these models need be tested with other
462 forest taxa, and be verified with capture and recapture data that allow estimation of detection
463 probability. For the latter, an alternative approach is estimating detection probability from

464 models that estimate site occupancy rates (e.g., MacKenzie et al., 2002), and using the
465 estimates to adjust the capture frequency. However, this requires careful consideration of
466 error propagation in the modeling. Alternative models for count data characterized by
467 excessive zero counts are zero-inflated (Lambert, 1992) and hurdle (Mullahy, 1986) models.
468 Specification of a zero-inflated or hurdle mixed effects model in a Bayesian framework is
469 considerably more complex. Boone et al. (2012) successfully specified a zero-inflated
470 Poisson regression model with multilevel hierarchical structure and spatial correlation to
471 model stream fish distribution and abundance. We attempted to incorporate the complex
472 design of DEMO experiment into both zero-inflated and hurdle regression models, but the
473 models failed to converge even with a small number of predictors. This may be caused by an
474 insufficient number of observations on the unit-level, but requires further examination. At
475 present, we think that priority must be placed on model structures that correctly and fully
476 account for the complexity of an experimental design and sampling, in turn ensuring that
477 inferences on microhabitat association are not misleading.

478 **4.2 Small Mammal Responses to Habitat Structures**

479 The final model in this study described a negative response of NEGI captures to volume of
480 coarse wood (CWDVOL). In contrast, Carey and Johnson (1995) predicted a positive stand-
481 level relationship between NEGI population size and CWDVOL. However, their regression
482 was carried out with stand-level mean habitat variables. Discrepancies are possible when
483 analyses are performed at different spatial scales because within-stand relationships can be
484 negative even while between-stand relationships are positive. Wilson and Carey (2000)
485 suggested that NEGI keyed more directly into the soil-litter interface than to understory
486 vegetation; however, the final model suggested a significant negative relationship between

487 NEGI captures and shrub cover (SHRUB). Suzuki and Hayes (2003) found that thinning
488 treatments did not affect abundance of NEGI. Our analysis supported their finding in that
489 stand density was not a significant predictor of NEGI captures. This small mammal species
490 also exhibited the largest overdispersion among the three analyzed species. This might have
491 been attributable to the high number of zero counts or variability imposed by omitted
492 covariates such as litter depth or soil conditions. In short, both coarse wood and shrub cover
493 were important habitat structures associated with NEGI. A suggested management strategy
494 for NEGI population could be maintaining a specified level of aggregated coarse wood
495 within a stand, and maintaining or creating relatively shrub-free openings that may be used
496 by the species for foraging or other activities.

497 The final model for PEKE suggested that captures responded negatively to herb cover
498 (HERB) and coarse wood (CWDVOL). Again in contrast, West (1991) found that PEKE
499 captures on the stand-level were positively correlated with the number of large coniferous
500 trees and percent cover of well-decayed logs. The trap design implemented by West (1991)
501 differed somewhat by imposing a 6×6 grid with 15-m spacing in each of 45 sites on the
502 western slopes of the southern Washington Cascade Range (West 1991). Because
503 comparative studies were few for this species, Wilson and Carey (2000) recognized that the
504 habitat determinants of PEKE abundance remained largely unknown. The statistical models
505 applied in this analysis of the DEMO data suggested that HERB and CWDVOL are
506 important habitat structures for PEKE. Thus, a possible approach for managing the stand-
507 level PEKE population is to retain a specific amount of aggregated coarse wood and creating
508 or maintaining conditions adverse to herb cover. However, directed manipulative studies are
509 needed to support this preliminary inference.

510 MYGA has been described as a good indicator of old-growth forest conditions (Sullivan et
511 al., 2005), but has not responded negatively to light regeneration harvests such as single-tree
512 selection treatments in boreal forests (Von Trebra et al., 1998). The final model for the
513 DEMO data suggested that the number of MYGA captures was positively correlated with
514 vertical complexity in the overstory (SHANNON). Because overstory vertical complexity
515 tended to diminish with decreasing retention (Maguire et al. 2007), the positive response of
516 MYGA to this habitat variable seemed consistent with its apparent preference for relatively
517 closed and undisturbed forest. Sullivan et al. (2005) suggested that stumps, rotting logs and
518 exposed roots could help provide a moist micro-climate that was preferable to MYGA. On
519 the other hand, our analysis suggested that a similar effect may not necessarily be imposed by
520 having greater amounts of coarse wood or greater herbaceous cover on the DEMO units.

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635 **Tables**

636 Table 1. Comparison of Generalized Linear Mixed Models (GLMMs) and Generalized
 637 Linear Models (GLMs) for the infrequent species *Neurotrichus gibbsii* (NEGI) during 1999
 638 in the DEMO study.

Covariates	POIS		NB		overPOIS
	GLMM ^a	GLM ^b	GLMM	GLM	GLMM
Intercept	-6.142 (-7.940, -4.805)	-6.514 (-7.097, -5.931)	-6.221 (-8.411, -3.959)	-6.452 (-7.239, -5.665)	-13.49 (-19.52, -8.991)
HERB	-0.242 (-0.477, -0.078)	0.028 (0.017, 0.039)	-0.177 (-0.471, 0.049)	0.029 (0.010, 0.048)	-0.184 (-0.461, 0.038)
CONIF	-0.136 (-0.568, 0.220)	0.005 (-0.015, 0.024)	-0.050 (-0.555, 0.416)	0.012 (-0.024, 0.048)	-0.116 (-0.662, 0.356)
SHRUB	-0.201 (-0.530, 0.063)	-0.009 (-0.019, 0.002)	-0.247 (-0.624, 0.069)	-0.010 (-0.025, 0.005)	-0.240 (-0.637, 0.087)
CWDVOL	-0.204 (-0.334, -0.114)	0.0001 (-0.001, 0.001)	-0.212 (-0.351, -0.115)	0.00003 (-0.002, 0.002)	-0.212 (-0.347, -0.119)
SHANNON	-0.005 (-0.568, 0.627)	-0.110 (-0.283, 0.063)	-0.216 (-1.129, 0.672)	-0.176 (-0.417, 0.065)	0.174 (-0.918, 1.319)
TPH	-0.105 (-0.604, 0.389)	0.076 (0.034, 0.118)	0.113 (-0.639, 0.894)	0.107 (0.032, 0.182)	-0.011 (-0.780, 0.740)
θ^c	–	–	0.082	0.080	–
σ_ε^{2d}	–	–	–	–	4.945
AICc	–	694.9	–	570.3	–
DIC	523.7	–	569.2	–	309.7

639 ^aAverage posterior coefficient estimates (\bar{b}_h ; Eq. 8) and their 95% credible intervals in parenthesis.

640 Statistically significant estimates are shown in bold.

641 ^bCoefficient estimates and their 95% confidence intervals in parenthesis. Statistically significant
642 estimates are shown in bold.

643 ^cEstimated and posterior overdispersion parameters.

644 ^dVariance of the random error ε_{ijk} .

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661 Table 2. Comparison of Generalized Linear Mixed Models (GLMMs) and Generalized
 662 Linear Models (GLMs) for the infrequent species *Peromyscus keeni* (PEKE) during 1999 in
 663 the DEMO study.

Covariates	POIS		NB		overPOIS
	GLMM	GLM	GLMM	GLM	GLMM
Intercept	-5.158 (-6.374, -4.165)	-6.310 (-6.911, -5.705)	-4.725 (-6.120, -3.295)	-6.151 (-6.832, -5.470)	-7.038 (-9.326, -5.291)
HERB	-0.144 (-0.282, -0.28)	0.029 (0.018, 0.040)	-0.162 (-0.319, -0.022)	0.025 (0.010, 0.039)	-0.166 (-0.332, -0.028)
CONIF	-0.140 (-0.449, 0.130)	0.053 (0.015, 0.090)	-0.058 (-0.415, 0.269)	0.050 (0.001, 0.098)	-0.092 (-0.456, 0.219)
SHRUB	-0.130 (-0.297, 0.006)	0.001 (-0.007, 0.009)	-0.141 (-0.342, 0.026)	0.003 (-0.007, 0.013)	-0.142 (-0.337, 0.022)
CWDVOL	-0.081 (-0.144, -0.048)	0.0009 (0.0001, 0.002)	-0.084 (-0.147, -0.039)	0.0008 (-0.0002, 0.002)	-0.084 (-0.148, -0.039)
SHANNON	-0.077 (-0.475, 0.315)	-0.053 (-0.231, 0.126)	-0.035 (-0.588, 0.511)	-0.077 (-0.282, 0.128)	0.029 (-0.562, 0.621)
TPH	0.006 (-0.301, 0.305)	-0.061 (-0.134, 0.012)	0.048 (-0.391, 0.491)	-0.057 (-0.141, 0.027)	0.029 (-0.398, 0.457)
θ	–	–	0.199	0.320	–
σ^2_ϵ	–	–	–	–	2.484
AICc	–	586.7	–	559.8	–
DIC	529.7	–	597.2	–	421.2

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667 Table 3. Comparison of Generalized Linear Mixed Models (GLMMs) and Generalized
 668 Linear Models (GLMs) for the common species *Myodes gapperi* (MYGA) during 1999 in the
 669 DEMO study.

Covariates	POIS		NB		overPOIS
	GLMM	GLM	GLMM	GLM	GLMM
Intercept	-5.891 (-6.809, -5.502)	-5.394 (-5.874, -4.914)	-5.769 (-6.815, -4.824)	-5.320 (-5.866, -4.775)	-6.233 (-7.273, -5.295)
HERB	-0.071 (-0.122, -0.026)	-0.014 (-0.022, -0.006)	-0.079 (-0.134, -0.032)	-0.022 (-0.033, -0.011)	-0.075 (-0.130, -0.028)
CONIF	-0.036 (-0.210, 0.116)	0.022 (0.009, 0.034)	-0.021 (-0.202, 0.140)	0.044 (0.021, 0.067)	-0.024 (-0.203, 0.141)
SHRUB	-0.019 (-0.073, 0.027)	-0.014 (-0.020, -0.008)	-0.015 (-0.070, 0.034)	-0.013 (-0.020, -0.005)	-0.018 (-0.073, 0.030)
CWDVOL	-0.031 (-0.061, -0.011)	0.0005 (0.0001, 0.0008)	-0.032 (-0.061, -0.012)	0.0004 (-0.0002, 0.001)	-0.032 (-0.060, -0.012)
SHANNON	0.445 (0.132, 0.762)	0.440 (0.308, 0.572)	0.434 (0.105, 0.795)	0.419 (0.263, 0.574)	0.452 (0.124, 0.806)
TPH	0.160 (-0.049, 0.376)	0.036 (0.016, 0.056)	0.189 (-0.043, 0.429)	0.046 (0.014, 0.079)	0.180 (-0.051, 0.410)
θ^c	–	–	1.328	0.687	–
σ_ε^2	–	–	–	–	0.895
AICc	–	1406.9	–	1288.2	–
DIC	1194.8	–	1215.6	–	1105.3

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673 Table 4. Relationship between habitat structure and *Neurotrichus gibbsii* (NEGI),
 674 *Peromyscus keeni* (PEKE) and *Myodes gapperi* (MYGA) captures during 1999 in the DEMO
 675 study, based on an overdispersed Poisson Generalized Linear Mixed Model (overPOIS-
 676 GLMM).

Covariates	NEGI ^a	PEKE	MYGA
Intercept	-7.545 (-9.231, -6.241)	-5.821 (-6.909, -4.844)	-6.435 (-7.600, -5.440)
HERB	–	-0.146 (-0.261, -0.053)	-0.045 (-0.083, -0.011)
CONIF	–	–	–
SHRUB	-0.313 (-0.633, -0.086)	–	–
CWDVOL	-0.204 (-0.329, -0.117)	-0.079 (-0.140, -0.037)	-0.028 (-0.054, -0.010)
SHANNON	–	–	0.645 (0.375, 0.991)
TPH	–	–	–
$\sigma_{\varepsilon}^{2^b}$	2.448	1.429	0.821
DIC	379.3	470.8	1114.6

677 ^aAverage posterior coefficient estimates (\bar{b}_h ; Eq. 8) and their 95% credible intervals in parenthesis.

678 ^bVariance of the random error ε_{ijk} .

679 **Figures**

680 Fig. 1. Locations of the six DEMO blocks in western Oregon and Washington; DP: Dog
681 Prairie, WF: Watson Falls, LW: Little White Salmon, PH: Paradise Hills, BU: Butte, and CF:
682 Capitol Forest. The six harvest treatment designs are shown above the map. Solid gray
683 represents uncut forest (100% and 75% treatments) and uncut 1-ha forest aggregates (15%A
684 and 40%A treatments); black dots represented dispersed residual trees (15%D and 40%D
685 treatments).

686

687 Fig. 2. Posterior coefficient estimates (\tilde{b}_{sij}) and their corresponding 95% credible intervals
688 for CWDVOL under the POIS-GLMM on the j -th experimental unit in the i -th block for each
689 of the following small mammal species: (a) *Neurotrichus gibbsii* (NEGI); (b) *Peromyscus*
690 *keenii* (PEKE); and (c) *Myodes gapperi* (MYGA). Number of experimental units was 36 for
691 NEGI and 24 for MYGA and PEKE. Different blocks of units are depicted with distinct
692 symbols for easy identification.

693

694 Fig. 3. Posterior coefficient estimates (\tilde{b}_{2ij}) and their corresponding 95% credible intervals
695 for HERB under the POIS-GLMM on the j -th experimental unit in the i -th block for the small
696 mammal species *Myodes gapperi* (MYGA). Different blocks of units are depicted with
697 distinct symbols for easy identification.

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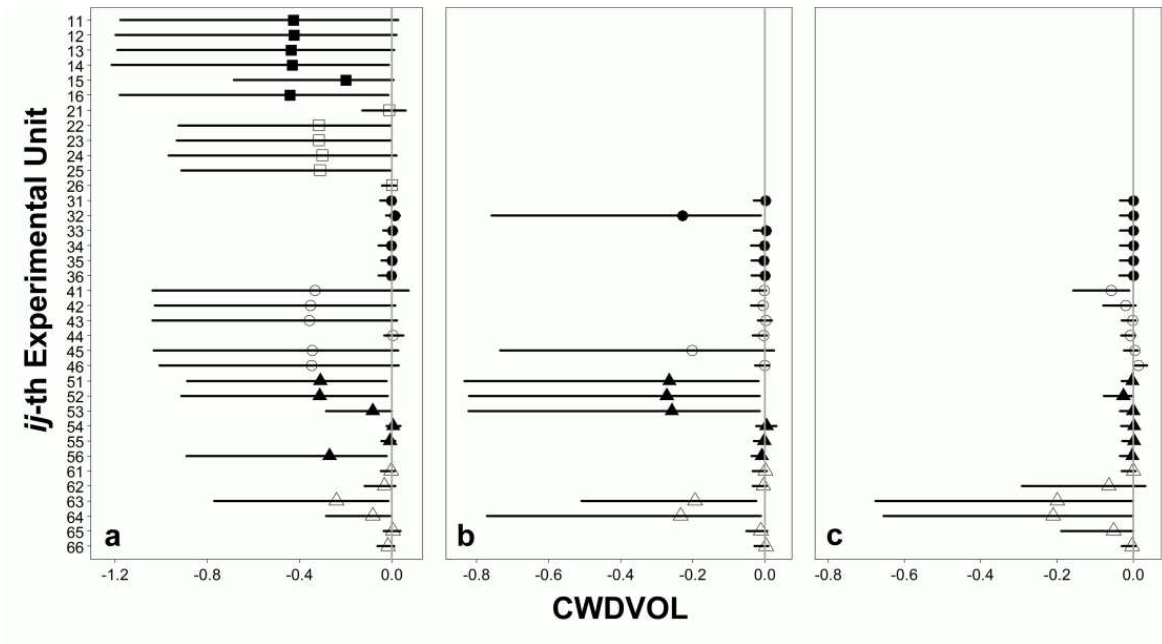
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701 **Figure 1**



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703 **Figure 2**



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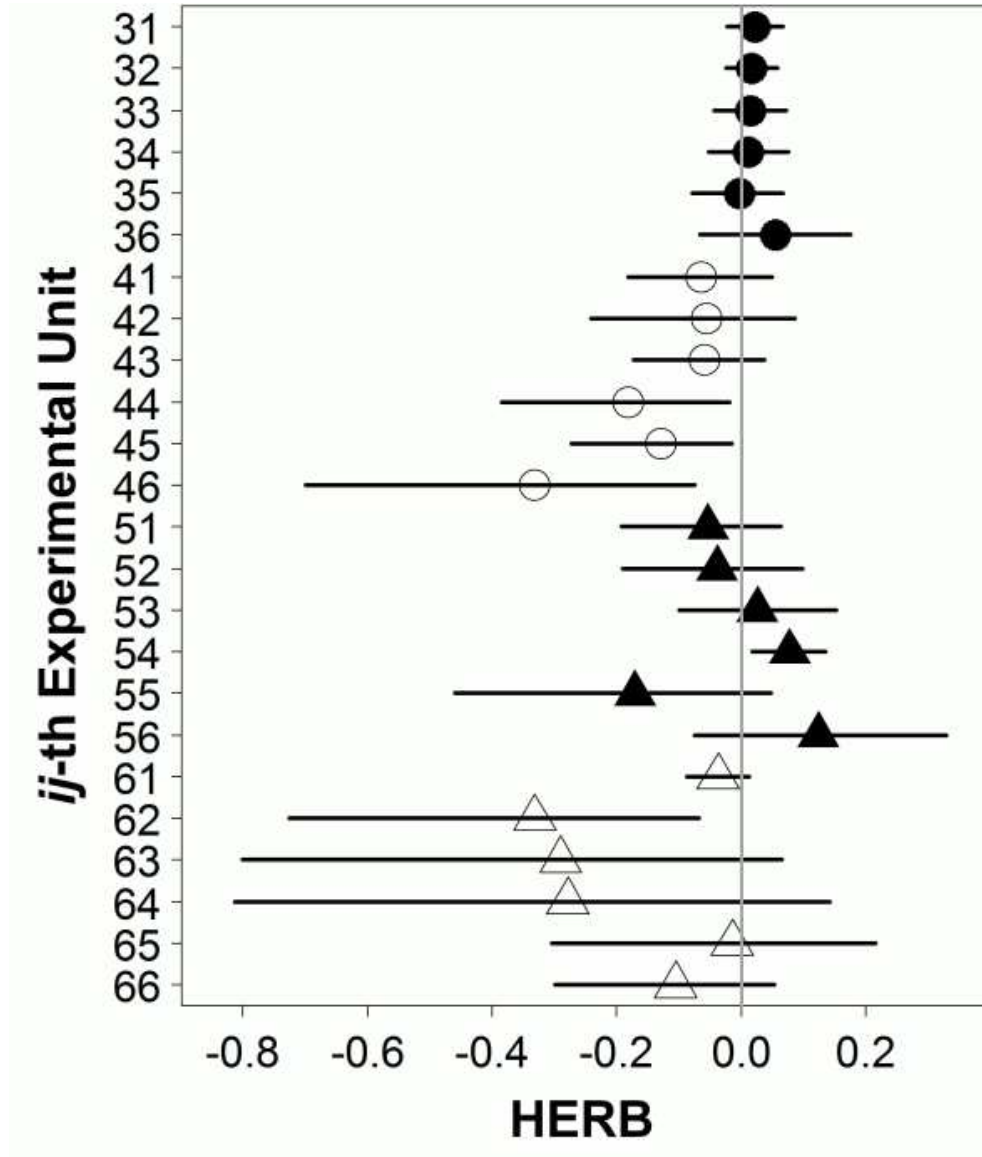
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717 **Figure 3**



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