

# A Habitat Suitability Model for Six Rare Pacific Northwest Fungi Using Ecological Niche Factor Analysis

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Draft – 4 January 2007

## ABSTRACT

Habitat models can be useful tools for assessing risk and conservation needs of rare organisms. Habitat suitability maps were generated using Ecological Niche Factor Analysis within Oregon's Western Cascade ecoregion for six ectomycorrhizal fungi: *Ramaria amyloidea*, *Ramaria araiospora*, *Ramaria aurantiisiccescens*, *Ramaria celerivirescens*, *Ramaria largentii*, and *Turbinellus kauffmanii*. The three species with the fewest reported locations were combined to create an adequate number of presence occurrences for analysis. The models indicate that suitable habitat for these species are much narrower than they have been characterized in published reports. Minimum temperature, humidity, and to a lesser degree precipitation were the most important explanatory variables for all the models, except for *R. celerivirescens*. *Turbinellus kauffmanii* had the least amount of modeled suitable habitat within the study area although *R. araiospora* has the least amount of mapped suitable habitat within reserved land allocations. *Ramaria celerivirescens* had the most suitable habitat in the study area. Old-growth stand conditions were uncorrelated with all of the models except for *R. celerivirescens*, which was the weakest model.

## INTRODUCTION

Old-growth forests in the Pacific Northwest declined rapidly in the first several decades following the Second World War, primarily due to timber harvest. This led to concern over loss of species that appeared to be dependent upon the habitats that old-growth forests provide (USDA, Forest Service et al. 1993). As a result, a number of species that appeared to be associated with late-successional or old-growth forests were designated for special management under the Northwest Forest Plan (USDA, Forest Service and USDI, Bureau of Land Management 1994). These species were largely associated with taxonomic groups, including fungi, which had previously received relatively little attention from conservation biologists.

Management of rare fungi presents a special challenge because of the subterranean habit of their vegetative state (mycelium), their unpredictable production of sporocarps, and the generally poor understanding of their population biology and habitats. These circumstances make it difficult to develop efficient survey protocols, evaluate conservation needs, or determine whether a species is indeed at risk. When the distribution and abundance data for a species is suspect, it is difficult to adequately assess its conservation needs. Habitat models can be valuable tools in bridging this information gap.

Species that are difficult to detect or that occupy only a small percentage of their suitable habitat at any given time can be difficult to model. Most multivariate analyses used in ecological models such as generalized additive models (GAM) and generalized linear models (GLM)

depend on having both presence and absence data (Hirzel et al. 2002). Collection of accurate presence/absence data is nearly impossible with fungi. Richardson (1970) determined that sampling the same site every two weeks for an entire season would still fail to detect roughly half of the macrofungal species that had produced sporocarps.

When absence data is misleading, it can lead to a Type II error (missed change error). Ecological niche factor analysis (ENFA) is a recently developed multivariate analysis tool for generating habitat-suitability maps that does not require absence data (Hirzel et al. 2002). ENFA employs a Hutchinsonian (1957) concept of fundamental niche. The fundamental niche represents the multidimensional volume of space equal to the number of environmental variables that limit the survival and reproduction of the species. The realized niche is a subset of the fundamental niche where, due to competition and other processes, the species actually occurs.

ENFA has been packaged in a relatively user-friendly, free software program, developed by Alexandre Hirzel, known as BIOMAPPER (<http://www2.unil.ch/BIOMAPPER/>). BIOMAPPER utilizes ENFA and Geographic Information System (GIS) grid (raster) maps to analyze a set of ecological variables in multidimensional space to develop habitat-suitability maps. Hargrove and Hoffman (2000) found that niche hypervolume techniques, such as those employed by ENFA, are useful for mapping suitable habitat for species with limited geographic ranges or limited occurrence data (i.e., rare species).

The principle objective of this study was to model suitable habitat for six rare epigeous, ectomycorrhizal (EM) fungi that occur in the western Oregon Cascade Range: *Ramaria amyloidea*, *Ramaria araiospora*, *Ramaria aurantiisiccescens*, *Ramaria celerivirescens*, *Ramaria largentii*, and *Turbinellus kauffmanii* (*Gomphus kauffmanii*). These six species are all designated for special management under the Northwest Forest Plan and are also on the Regional Foresters sensitive species list (USDA, Forest Service 2004). These species are all basidiomycetes that belong to the taxonomically complex Gomphales group (Giachini 2004). All the *Ramaria* spp. are endemic to the Pacific Northwest with known occurrences in the Cascade and Coast ranges from northern California to Washington (Castellano et al. 2003, USDI, Bureau of Land Management 2006). The secondary objective of this study was to assess the conservation status of these species based on ENFA and habitat-suitability map (HSM) results and analyses.

*Turbinellus kauffmanii* (A.H. Sm.) Giachini is typically referred to as *Gomphus kauffmanii* (A.H. Sm. & Morse) in regional floras. The genus *Turbinellus* Earle has recently been resurrected by Giachini (2004) to accommodate species of *Gomphus sensu lato* that are morphologically and genetically distinct from the rest of the group. *Turbinellus kauffmanii* is a large chanterelle-like species with pale brown to pale orange basidiocarps (Giachini 2004). Within the Pacific Northwest, this taxon occurs mostly west of the Cascade Range in Washington and Oregon and along the coast in California (Castellano et al. 2003). It is reported to be associated with rich, deep humus under *Pinus* and *Abies* species (Castellano et al. 2003).

*Ramaria amyloidea* is a coral fungus with white to orange-white basidiocarps (Castellano et al. 1999). It produces basidiocarps, during September and October, in humus or soil under *Abies* spp., *Pseudotsuga menziesii* (Mirbel) Franco and *Tsuga heterophylla* (Raf.) Sarg. (Castellano et al. 1999).

*Ramaria araiospora* is a coral fungus with red, fading to pale red, branches, and subacute to acute branch tips (Castellano et al. 1999). It produces basidiocarps, during October and November, in humus or soil under *Abies* spp., *Pseudotsuga menziesii* and *Tsuga heterophylla* (Castellano et al. 1999).

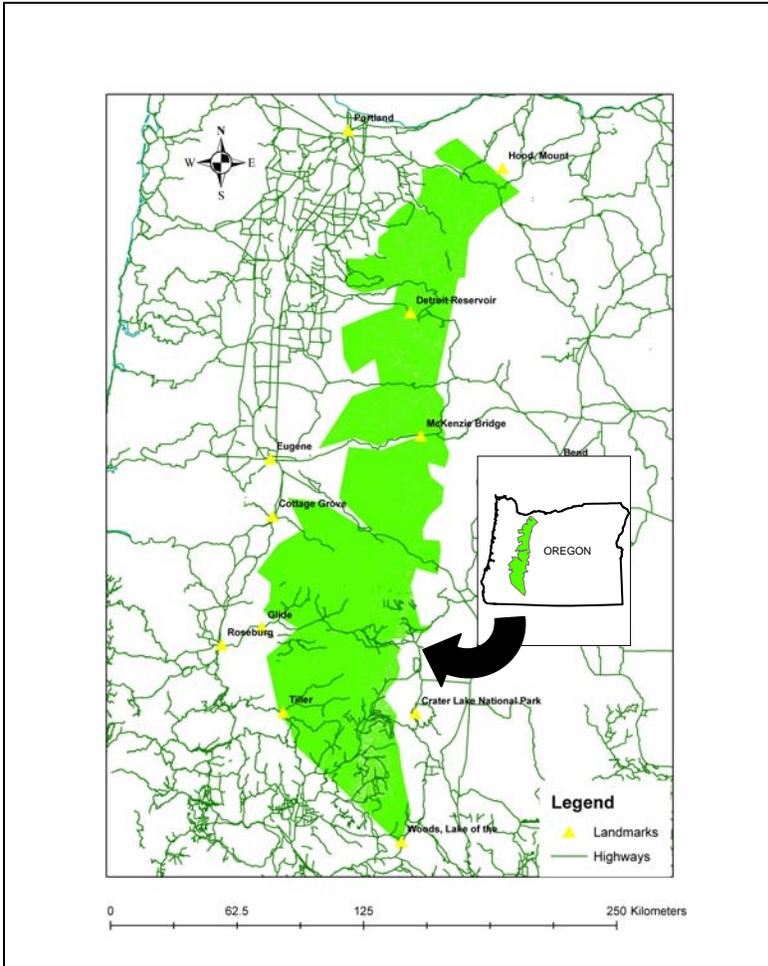
*Ramaria aurantiisiccescens* is a coral fungus with pale orange to orange-yellow upper branches and dark orange apices (Castellano et al. 1999). It produces basidiocarps, during October, in humus or soil under *Abies* spp., *Pseudotsuga menziesii* and *Tsuga heterophylla* (Castellano et al. 1999).

*Ramaria celerivirescens* is a coral fungus with pale to pale orange branches and pale to yellow apices (Castellano et al. 1999). It produces basidiocarps, during October and November, in humus or soil under *Abies* spp., *Pseudotsuga menziesii* and *Tsuga heterophylla* (Castellano et al. 1999).

*Ramaria largentii* is a coral fungus with pale orange branches and orange to pale apices (Castellano et al. 1999). It produces basidiocarps, during October, in humus or soil under *Abies* spp., *Pseudotsuga menziesii* and *Tsuga heterophylla* (Castellano et al. 1999).

## **STUDY AREA**

The study area encompassed 17,043 km<sup>2</sup> in the Western Cascade Range of Oregon (Fig. 1). Because of data gaps, mostly associated with the vegetation data, the actual size of the study area was reduced to 16,377 km<sup>2</sup>. The study area was selected to reflect the range extent of the study EM fungi in Oregon's Western Cascade ecoregion. The southern edge of the Columbia River Gorge was the study area's northern terminus. The southern terminus corresponded roughly with the southern end of the Western Cascades in Oregon. It did not go farther south than Lake of the Woods in the Rogue River National Forest. Elevations ranged from approximately 700 to 2,800 m. The most prevalent forest community in the study area is dominated by Douglas-fir (*Pseudotsuga menziesii*) and/or western hemlock (*Tsuga heterophylla*). At the drier, southern end of the province forests of Douglas-fir and western hemlock are largely replaced by mixed-conifer forest of Douglas-fir, grand fir (*Abies grandis*) and incense cedar (*Calocedrus decurrens*) (USDA, Forest Service and USDI, Bureau of Land Management 1994). The less common forest communities in the study area are dominated by *Abies* spp., *Tsuga mertensiana*, and/or *Pinus* spp. The majority of the land in the study area is managed by the USDA Forest Service. The next largest portion is administered by the Bureau of Land Management. Private landowners and other agencies own a very small portion of land in the study area.



**Figure 1.** Study area (shaded in green) in the Western Cascade Mountains of Oregon.

## METHODS

Species presence GIS grids were created for each fungus in the study. *Ramaria amyloidea*, *R. aurantiiscescens*, and *R. largentii* were combined and treated as a single taxon to create an adequate number (44 total) of presence occurrences for the model. The assumptions and ramifications associated with this grouping are discussed further in the Discussion Section. Presence data were obtained from GeoBob (USDI, Bureau of Land Management 2006). These polygon occurrences were converted to cells; a single occurrence ranged from 1 to several cells in size. The specific number of occurrence cells used in the model is given by species in the BIOMAPPER results summary sheets given in the appendix.

Twenty-seven ecogeographic variables (EGVs) were used in the analysis. The majority of the EGVs were meteorological data derived from the DAYMET, U.S. Data Center for Daily Surface Weather Data and Climatological Summaries 1980-1997 (<http://www.daymet.org>). The EGVs involved different measurements of precipitation, temperature, and humidity across the landscape. Elevation, slope, and solar radiation were derived from a Oregon digital elevation model (DEM) while distance to major streams was generated from a river/stream layer developed for Oregon (<http://www.gis.state.or.us/data/alphalist.html>). Vegetation data were

limited to stand structure characteristics, specifically quadratic mean diameter (qmd) of tree boles in stands and canopy cover (cc) of conifers. These data were obtained from the Interagency Vegetation Mapping Project website (<http://www.or.blm.gov/gis/projects/ivmp.asp>). Table 1 includes the complete list of EGVs.

**TABLE 1.** Ecogeographic variables (EGV) used in the ecological niche factor analysis of six rare fungi.

EGV code	EGV name	EGV code	EGV name
cc	Canopy Cover	rivdis	Distance To Rivers Or Streams
elev	Elevation	slope	Slope
frost	Frost days	solar08	Solar Radiation (August)
human	Humidity (Annual)	solar12	Solar Radiation (December)
hum08	Humidity (August)	tmax01	Maximum Temperature (January)
hum12	Humidity (December)	tmax08	Maximum Temperature (August)
humv01	Humidity Variability (January)	tmaxan	Maximum Temperature (Annual)
humv11	Humidity Variability (November)	tmin01	Minimum Temperature (January)
pre08	Precipitation (August)	tmin08	Minimum Temperature (August)
pre12	Precipitation (December)	tmin11	Minimum Temperature (November)
prean	Precipitation (Annual)	tminan	Minimum Temperature (Annual)
pree	Precipitation Event Size	tminv01	Min. Temperature Variability (Jan.)
pref	Precipitation Frequency	tminv11	Min. Temperature Variability (Nov.)
qmd	Quadratic Mean Diameter (conifer)		

Maps were developed or converted, for each EGV, from raster format to ArcGIS grids with a cell size of 50 x 50 m (2,500 m<sup>2</sup>). The DAYMET climate data were the least precise grids, by a factor of 400, at a cell size of 1,000 x 1,000 m (1,000,000 m<sup>2</sup> or 1 km<sup>2</sup>). All the grids were clipped to the study area and masked to the qmd map (the grid map with the most data gaps). All EGVs were normalized using a Box-Cox transformation. Because the qmd map had missing data for some cells, the total grid area analyzed was slightly less than the total area bounded by the study area perimeter.

Because organisms have niches that correspond to specific environmental conditions, their distribution over the landscape is expected to be nonrandom for each EGV. For example, a species with known occurrences averaging above 2,000 m in elevation is 1,000 m greater than an overall study area mean that might only be 1,000 m. ENFA refers to this difference in means as marginality (Hirzel et al. 2002). ENFA calculates marginality for each individual EGV and then computes an overall score in a multi-dimensional space (Hirzel et al. 2002). A second calculation called specialization represents the ratio of the standard deviation of the study area values for an EGV to that of the species (Hirzel et al. 2002). A random set of cells should have a specialization of one, anything greater indicates specialization (Hirzel et al. 2002). Like marginality, an overall specialization score was calculated for the EGVs.

Using eigenvectors in a multi-dimensional EGV space (Hirzel et al. 2002), factors were generated accounting for all the marginality and a decreasing amount of specialization with each factor generated. Most of the explained information is contained in the first few factors. Factors that were not considered significant were eliminated using MacArthur's broken-stick analysis. Factor maps were generated from the retained factors. BIOMAPPER synthesized the factor maps into habitat-suitability maps with cell values ranging from 0 (least suitable) to 100 (most suitable). BIOMAPPER provides four HSM algorithms for analysis. These algorithms include

minimum distance, median, harmonic mean, and geometric mean. All four algorithms were utilized for comparison purposes. K-fold cross-validation was applied to the resultant HSMs. This validation routine incorporates a boot-strapping-like algorithm to develop frequency curves. A random frequency line, represented by an area-adjusted frequency of 1, was included on the graph with the validation curves. The random frequency line is the point that separates model predictions into a group of validation points where there is more than expected by chance (above the line) and a group where there is less than expected (below the line) (Davis and Lint 2005). The variance, Spearman rank correlation scores (Rs), and frequency-curve shapes were important factors used to determine model robustness and algorithm selection. The HSMs for each algorithm were converted into suitable habitat presence/absence (0 or 1) maps. Suitable habitat was determined by the score where the frequency curves consistently stayed above the random frequency line. In other words, the resultant maps represent suitable habitat as developed by the factors in the model and not by random chance.

## RESULTS

*Turbinellus kauffmanii* had the largest overall marginality (2.481) and specialization (28.274) scores (Table 2). Although *R. celerivirescens* had the highest number of occurrence cells (75) used for the ENFA, it had the lowest overall marginality (0.499) and specialization (6.892) scores. *Ramaria araiospora* demonstrated strong overall marginality indicating that its habitat is distinct from the global mean of the study area although its habitat preferences are not as narrow as *T. kauffmanii*, as indicated by the lower overall specialization score. This is also reflected in the high percent of the variance explained by the marginality factor (58%). The three *Ramaria* spp. were just the opposite; lower marginality but high specialization.

The EGVs involving temperature and humidity, which is very dependent on temperature, were generally the most important explanatory variables, although less so for *R. celerivirescens* (Tables 3 and 4). The principle EGVs influencing marginality were nearly identical for *T. kauffmanii* and *R. araiospora* but with opposite values (Table 3). Specialization variables were slightly less constant between these taxa although humidity and temperature continued to be significant (Table 4). Both species, but especially *R. araiospora*, exhibit specialization for precipitation. The model for the three *Ramaria* spp. was influenced by the same general climatic categories of temperature, humidity and precipitation, although the specific EGVs that were most important were slightly different. For instance, minimum temperature in August was a more important EGV for marginality than minimum temperature in January for the three *Ramaria* spp. The opposite is the case for both *T. kauffmanii* and *R. araiospora*. However minimum temperature in January is a key specialization variable for the three *Ramaria* spp. while it had little affect on the other two models.

*Ramaria celerivirescens* was the most unique among the models. Temperature and humidity were largely uncorrelated with regards to marginality. Slope, solar radiation and quadratic mean diameter of conifers were the principle EGVs influencing marginality. The later EGV represents old-growth conditions for which *R. celerivirescens* exhibited a positive correlation. Precipitation, humidity and temperature were the important EGVs affecting specialization for this species. Conifer canopy closure and distance to a major stream or river were not important factors in the model for any of the fungi included in this study.

Habitat-suitability maps for *T. kauffmanii*, three *Ramaria* spp., *R. araiospora*, and *R. celerivirescens* are presented in Figures 2-5. With the exception of the three *Ramaria* spp., the cells with habitat suitability scores below 50 were determined to be statistically insignificant and consequently discarded in the HSMs. Habitat suitability scores below 70 were discarded for the three *Ramaria* spp. model.

Habitat-suitability maps based on the median algorithm (Hirzel and Arlettaz 2003) were chosen for this study. With the exception of *R. celerivirescens*, the Spearman Rank scores for the median algorithm were greater than the other three algorithms provided with the model. For the median algorithm, distance between occurrences and groupings is not as important as is the median of two established classes (Hirzel and Arlettaz 2003). The minimum distance algorithm validated slightly better for *R. celerivirescens*, presumably because this species had more clustered locations than the other taxa. However, since the clustering of locations appears to be an artifact of unequal survey effort, this algorithm was rejected. In any event, the HSMs produced by either algorithm are similar in exhibiting a diffuse distribution of suitable habitat scattered throughout the study area.

ENFA and cross-validation results for each of the models are included in the appendix. Only the six most important factors and five EGVs are included for the sake of clarity.

**TABLE 2.** Overall ENFA marginality and specialization results.

	<i>Turbinellus kauffmanii</i>	<i>Ramaria araiospora</i>	Three <i>Ramaria</i> spp.	<i>Ramaria celerivirescens</i>
<b>Marginality</b>	2.481	1.925	1.006	0.499
<b>Specialization</b>	28.274	10.445	27.007	6.892

**TABLE 3.** Marginality coefficient values for the most important EGVs and percent variance (specialization) explained by the marginality factor (ENFA results Factor 1). Shading indicates the relative explanatory value of the coefficients. Negative coefficients represent an inverse relationship.

EGV	<i>Turbinellus kauffmanii</i>	<i>Ramaria araiospora</i>	Three <i>Ramaria</i> spp.	<i>Ramaria celerivirescens</i>
<b>Variance Explained</b>	<b>17%</b>	<b>58%</b>	<b>49%</b>	<b>49%</b>
Humidity (Dec.)	-0.28	0.29	-0.24	-0.06
Frost Days	0.27	-0.30	0.26	0.07
Min. Temp. (Jan.)	-0.27	0.30	-0.23	-0.07
Min. Temp. (Annual)	-0.26	0.28	-0.26	-0.13
Max. Temp. (Jan.)	-0.26	0.17	-0.11	0.05
Min. Temp. (Nov.)	-0.26	0.29	-0.24	-0.07
Humidity (Annual)	-0.25	0.31	-0.26	-0.05
Humidity Variability (Nov.)	-0.25	0.22	-0.14	-0.02
Elevation	0.22	-0.26	0.20	0.07
Ppt. Frequency	-0.07	0.26	-0.12	-0.01
Humidity (Aug.)	-0.17	0.27	-0.21	0.02
Min. Temp. (Aug.)	-0.24	0.24	-0.37	-0.26
Temp. Variability (Jan.)	0.22	-0.16	0.35	0.23
Temp. Variability (Nov.)	0.20	-0.12	0.31	0.13
Slope (Steepness)	-0.20	0.04	-0.27	-0.46
Solar Radiation (Aug.)	0.06	0.04	0.04	0.45
Solar Radiation (Dec.)	0.07	0.07	0.00	0.41
Quadratic Mean Diameter (Conifer)	0.05	0.06	-0.07	0.39

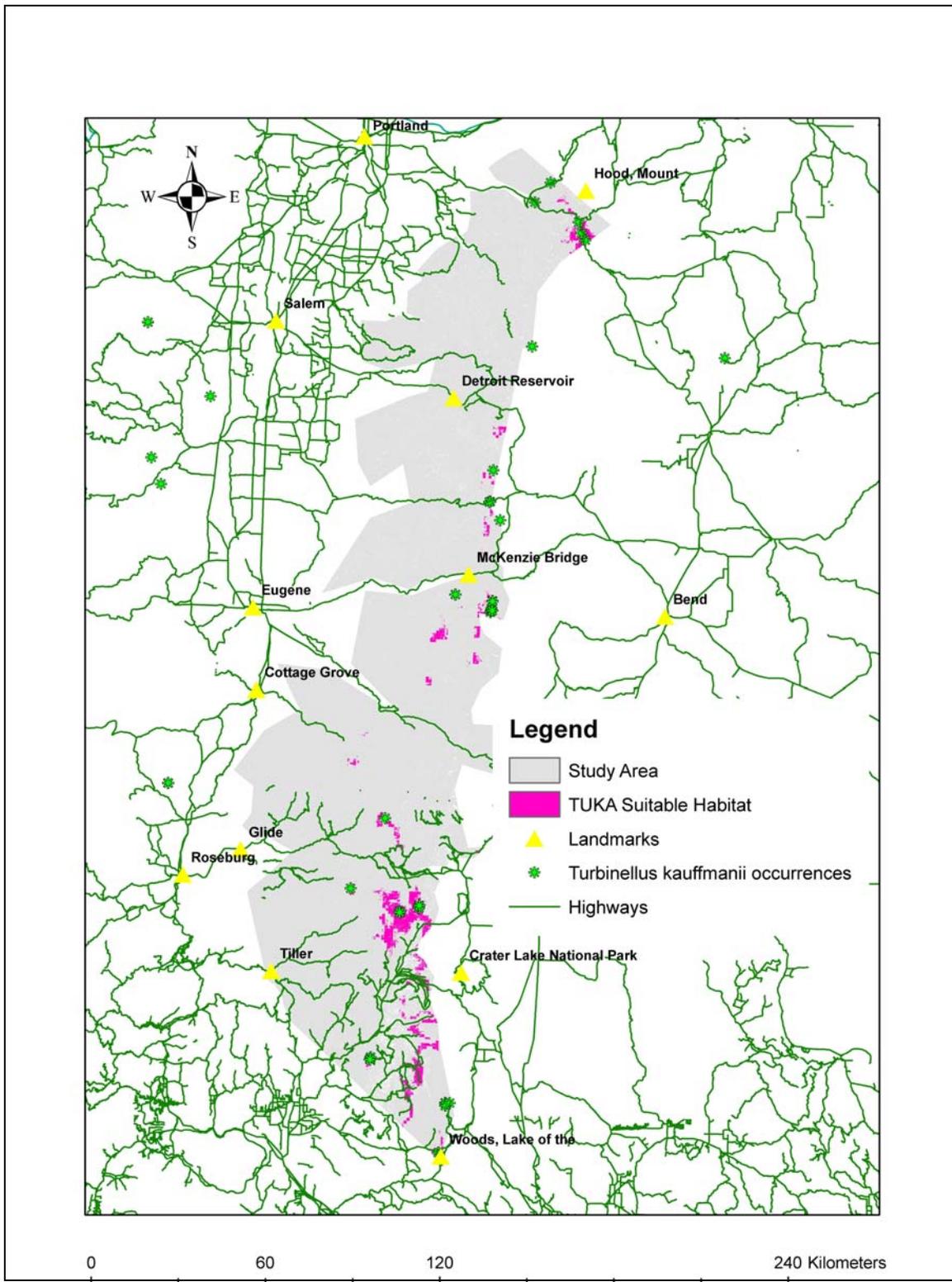
**TABLE 4.** EGVs with relatively high **specialization** coefficients in the first two ENFA specialization factors (ENFA results Factors 2 and 3). Overall variance (specialization) explained by the factors is presented under each factor. Shading indicates the relative explanatory value of coefficient

EGV	<i>Turbinellus kauffmanii</i>		<i>Ramaria araiospora</i>		Three <i>Ramaria</i> spp.		<i>Ramaria celerivirescens</i>	
	1	2	1	2	1	2	1	2
<b>Specialization Factor</b>	<b>1</b>	<b>2</b>	<b>1</b>	<b>2</b>	<b>1</b>	<b>2</b>	<b>1</b>	<b>2</b>
<b>Variance Explained</b>	<b>67%</b>	<b>9%</b>	<b>19%</b>	<b>9%</b>	<b>40%</b>	<b>7%</b>	<b>19%</b>	<b>12%</b>
Humidity (Annual)	0.52	0.57	0.58	0.12	0.54	0.32	0.13	0.35
Minimum Temp. (Nov.)	0.67	0.39	0.31	0.07	0.57	0.20	0.03	0.01
Frost Days	0.29	0.12	0.01	0.21	0.01	0.18	0.15	0.26
Humidity (Aug.)	0.28	0.30	0.25	0.16	0.15	0.08	0.07	0.29
Ppt. (Dec.)	0.18	0.34	0.06	0.12	0.03	0.02	0.23	0.20
Ppt. Event Size	0.09	0.31	0.06	0.63	0.25	0.38	0.33	0.44
Minimum Temp. (Annual)	0.21	0.05	0.65	0.09	0.17	0.31	0.31	0.05
Ppt. (Annual)	0.11	0.05	0.11	0.60	0.34	0.52	0.75	0.50
Ppt. Frequency	0.00	0.20	0.04	0.34	0.12	0.30	0.16	0.33
Minimum Temp. (Jan.)	0.00	0.21	0.09	0.09	0.31	0.43	0.10	0.22

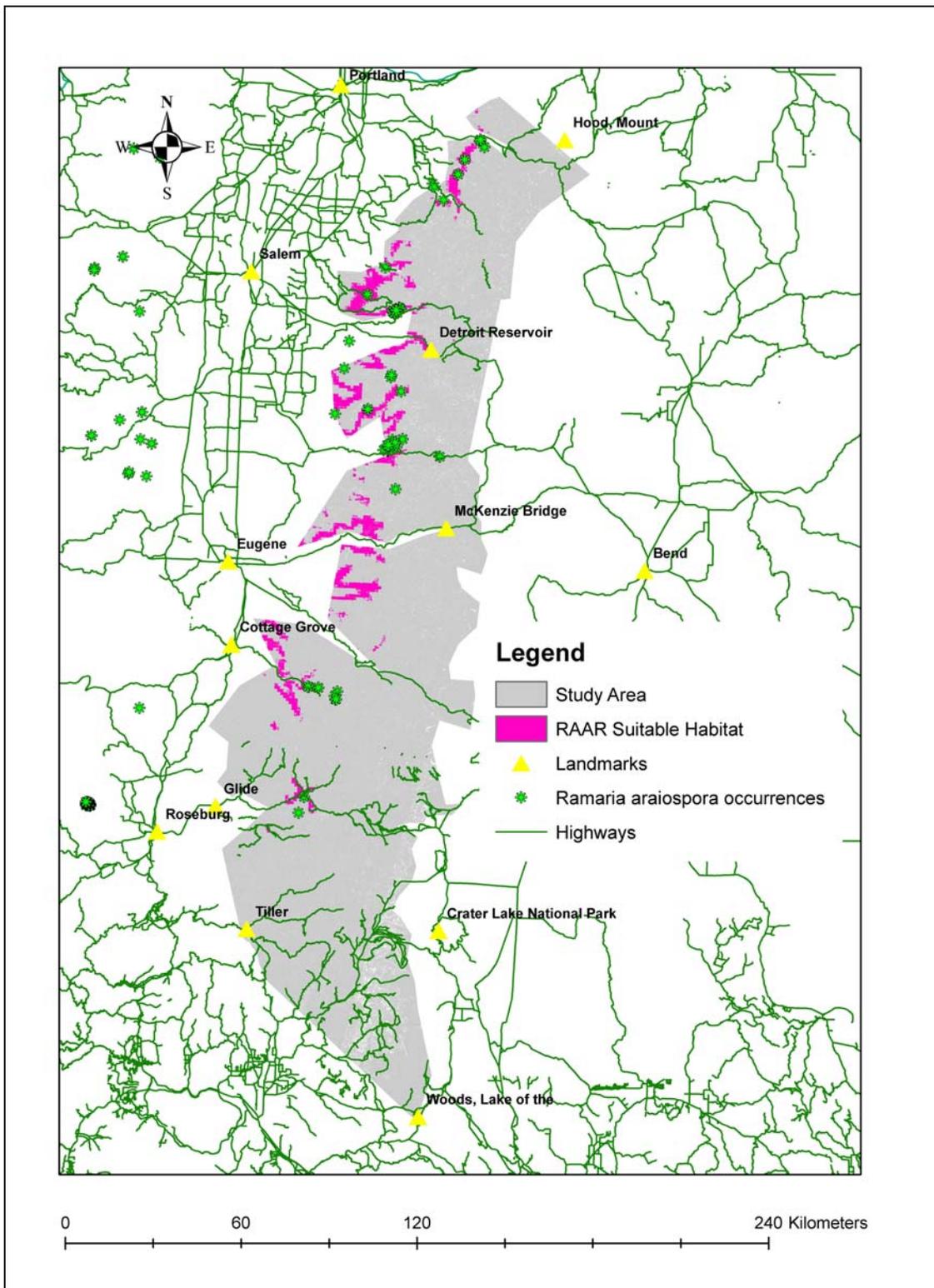
## DISCUSSION

Although the published habitat descriptions for each of these species are very similar (Castellano et al. 1999, Castellano et al. 2003, Exeter et al. 2006), the results of this study indicate that their actual habitat requirements are quite distinct. Available occurrence data for all 15 *Ramaria* spp. that occur in the study area, and are tracked by GeoBob (USDI, Bureau of Land Management 2006), were lumped for modeling with BIOMAPPER in order to test the similarity of habitat requirements within the genus. The resultant model scored very poorly. The overall marginality value was low (0.482) and all of the variance (specialization) was explained by the marginality. This indicates that the habitats at the known sites for the 15 species represent an essentially random subset of habitats within the study area. It is therefore striking that *Ramaria aurantiiscescens*, *R. amyloidea*, and *R. largentii* should model well as a group suggesting that there is some manner of concordance of their habitats. The ENFA for the three *Ramaria* spp. not only had a relatively high overall marginality score, but the HSM actually display far more discrete mapped habitat than *R. celerivirescens*. *Ramaria araiospora* and *T. kauffmanii* also produced strong models with clearly defined HSMs.

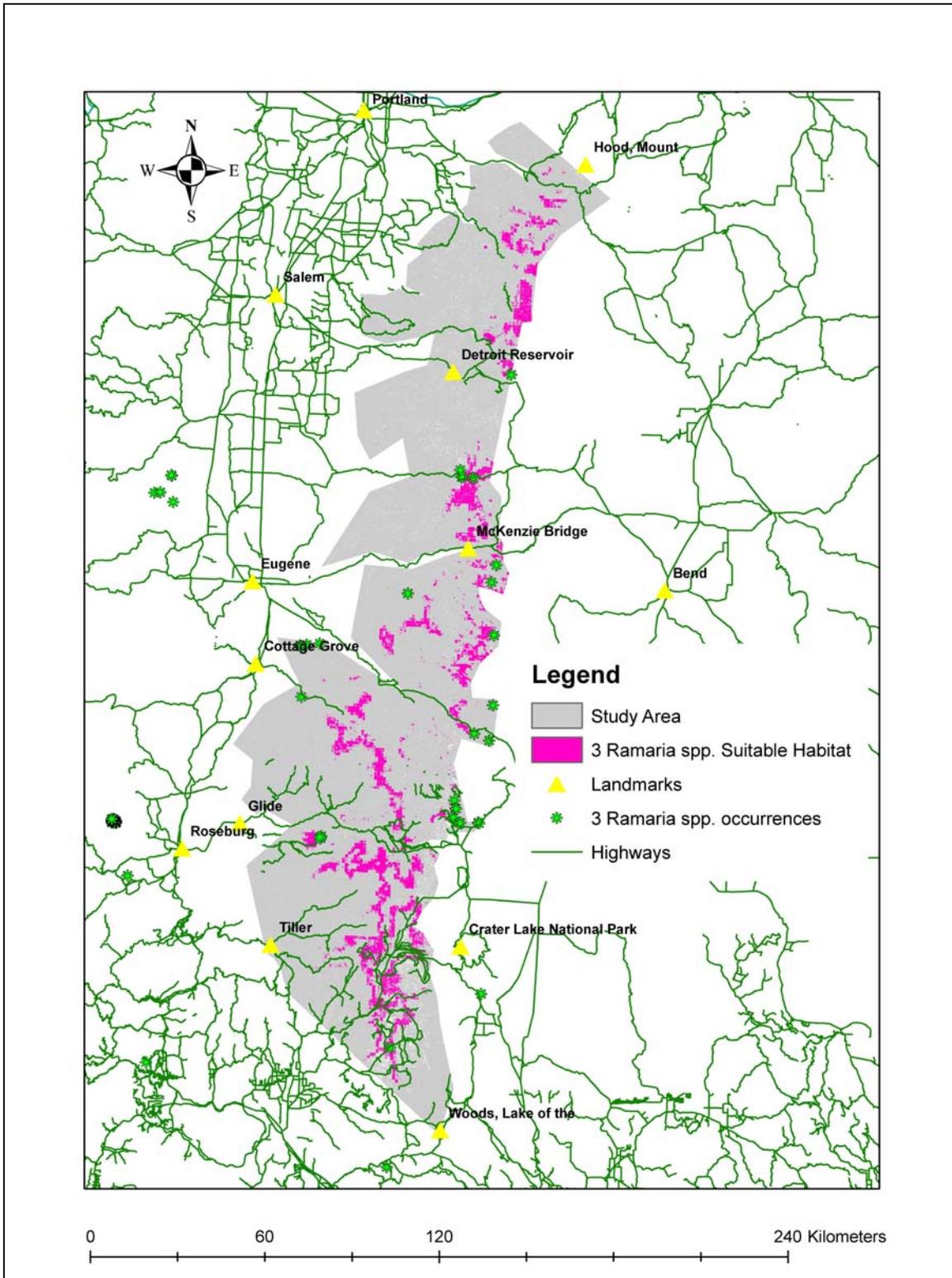
Humidity and minimum temperature EGVs were the most significant explanatory variables for the models overall, although much less so for *R. celerivirescens*. Annual humidity, humidity in December and humidity in August all exerted a similar influence upon the models, although humidity in December was only important in the marginality analysis. All the study species, except *R. araiospora*, prefer lower average humidity values than the overall study area average (Figures 6 & 7, Table 5). This is possibly attributed to elevation preference for the study species. Elevation marginality data, for each EM fungi, are inversely related to December's marginality values for humidity. That humidity in August should influence the model was a surprise since there is no obvious causal relationship between this variable and sporocarp production. It is possible that humidity at the site may be significant for summer survival of the mycelium but it equally plausible that this correlation has no direct causal link. Minimum temperature annually, in January, and in November also behaved similarly within the models.



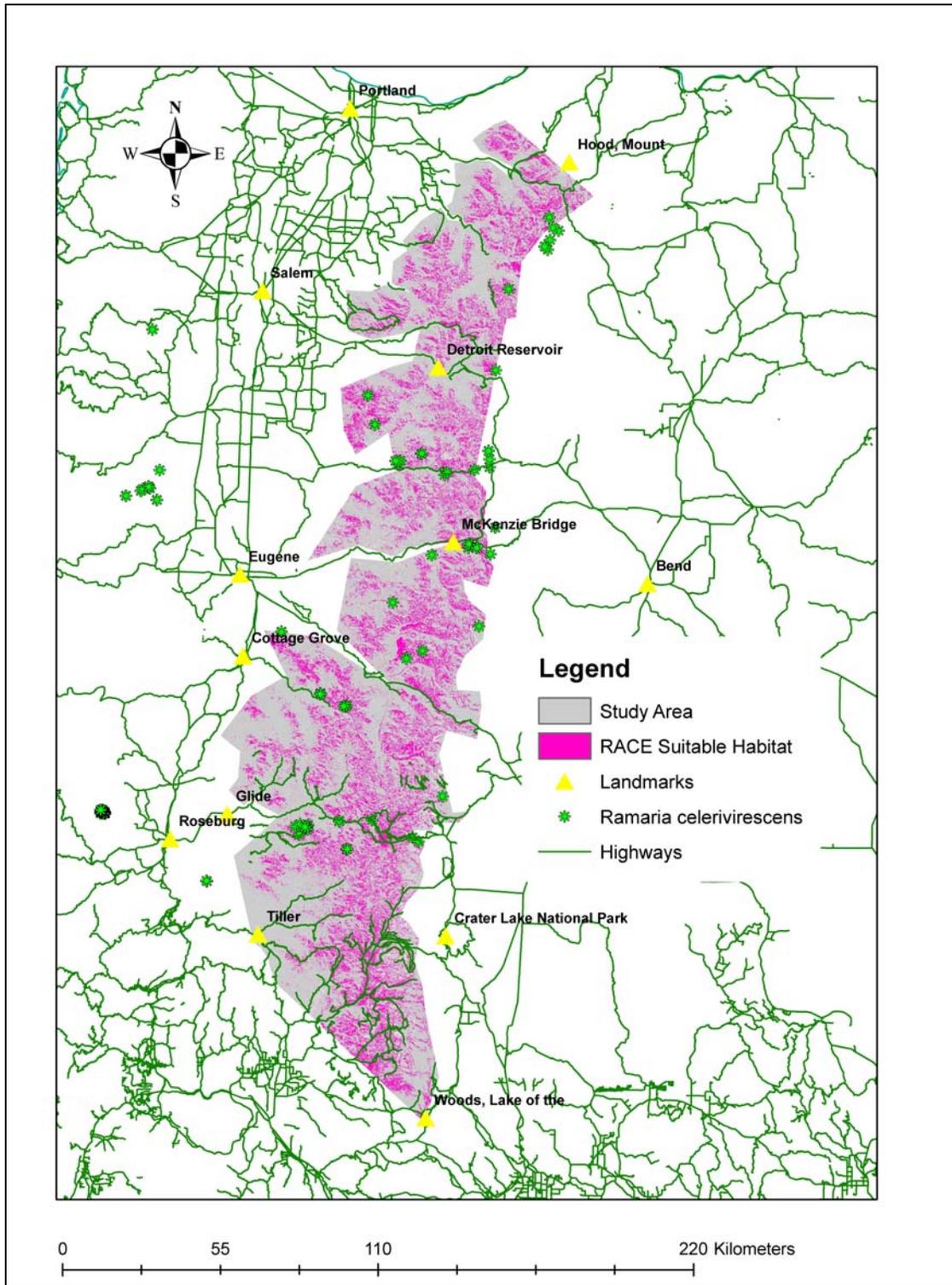
**Figure 2.** Habitat-suitability map for *Turbinellus kauffmanii* based on the median algorithm and suitability values above 50. Suitable habitat = 425 km<sup>2</sup>.



**Figure 3.** Habitat-suitability map for *Ramaria araiospora* based on the median algorithm and suitability values above 50. Suitable habitat = 821 km<sup>2</sup>.

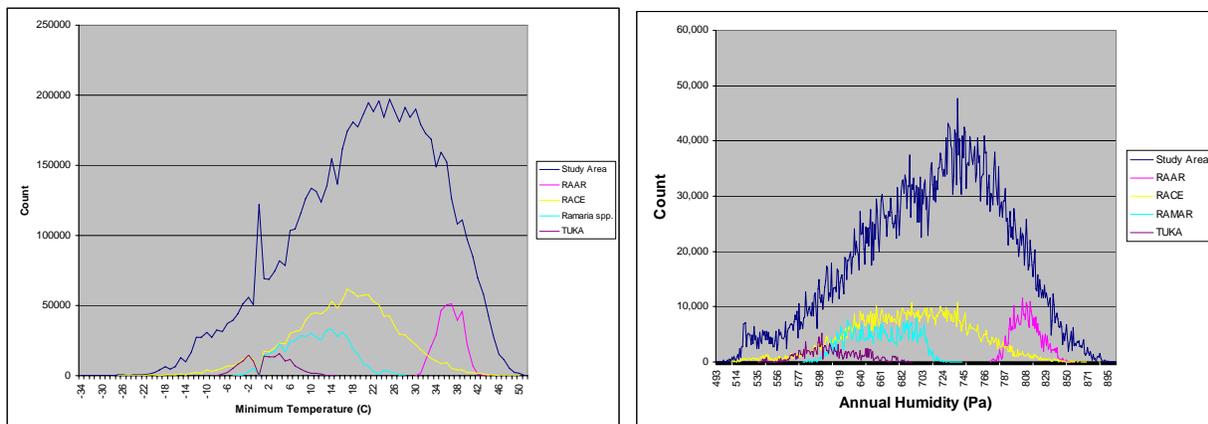


**Figure 4.** Habitat-suitability map for three *Ramaria* spp. based on the median algorithm and suitability values above 70. Suitable habitat = 1,301 km<sup>2</sup>.



**Figure 5.** Habitat-suitability map for *Ramaria celerivirescens* based on the median distance algorithm and suitability values above 50. Suitable habitat = 3,520 km<sup>2</sup>.

*Turbinellus kauffmanii* and *R. araiospora* produced the strongest models. Suitable habitat for the former taxon was confined to high elevations, mostly at the south end of the study area, while the later mapped exclusively at lower elevations with a more northerly predilection (Figures 2 & 3). Interestingly, the EGVs that most influenced both models were nearly identical but with inversed relationships. Where *T. kauffmanii* correlated with low humidity and low minimum temperature; *R. araiospora* required high humidity and high minimum temperature (Figures 6 & 7, Table 5). The inverse relationship with climatic variables resulted in a similarly inverse relationship with elevation. Both had high marginality values indicating that the habitat conditions they favor are different than the mean conditions within the study area. *Turbinellus kauffmanii*, in particular, also had a high overall specialization value indicating that it also occupies a particularly narrow range of habitat conditions. Both models are considered to be robust ( $P < 0.10$ ). Slope has a much different relationship across the fungi species than the other EGVs. Compared to the entire study area, suitable habitat for all the study species occur on flatter slopes.



**Figures 6 & 7.** Mean annual minimum temperature and annual humidity distribution of each model and the study area. RAAR = *Ramaria araiospora*, RACE = *R. celerivirescens*, RAMAR = *R. aurantiiscescens*, *R. amyloidea* and *R. largentii*, TUKA = *Turbinellus kauffmanii*

**Table 5.** Suitable habitat mean values for five EGVs.

EGV	Study Area	<i>Turbinellus kauffmanii</i>	Three <i>Ramaria</i> spp.	<i>Ramaria araiospora</i>	<i>Ramaria celerivirescens</i>
Elevation (m)	979	1,420	1,196	604	1,069
Frost Days	134	188	162	88	147
Mean Annual Humidity (Pa)	712	611	660	809	690
Slope (%)	42	37	40	41	37
Mean Annual Minimum Temp. (°C)	20	2	11	37	17

That the three *Ramaria* spp. should collectively exhibit such high specialization was a surprise, particularly since the attempt to model a larger number of species within the genus had failed. All three species have broad distributions within the Pacific Northwest. Although there are occasional instances where sites of the different taxa occur in proximity, there is no obvious pattern of similarity in their distribution. Unlike *T. kauffmanii* and *R. araiospora*, minimum temperature in August and temperature variability in both January and November were the principle EGVs influencing marginality, and precipitation was an important variable affecting

specialization. The high specialization value suggests that these three species share not only similar but narrowly-defined habitat requirements. However, this model did not validate as well as the first two models ( $R_s = 0.43$ ,  $P = 0.24$ ) so the HSM should be considered with appropriate caution. Because the mapped high-quality habitat bunched in a few very discrete clusters, the low validation score likely represents an overly conservative mapping of suitable habitat. Specifically, the model is presumably mapping only the overlapping habitat characteristics of the three species.

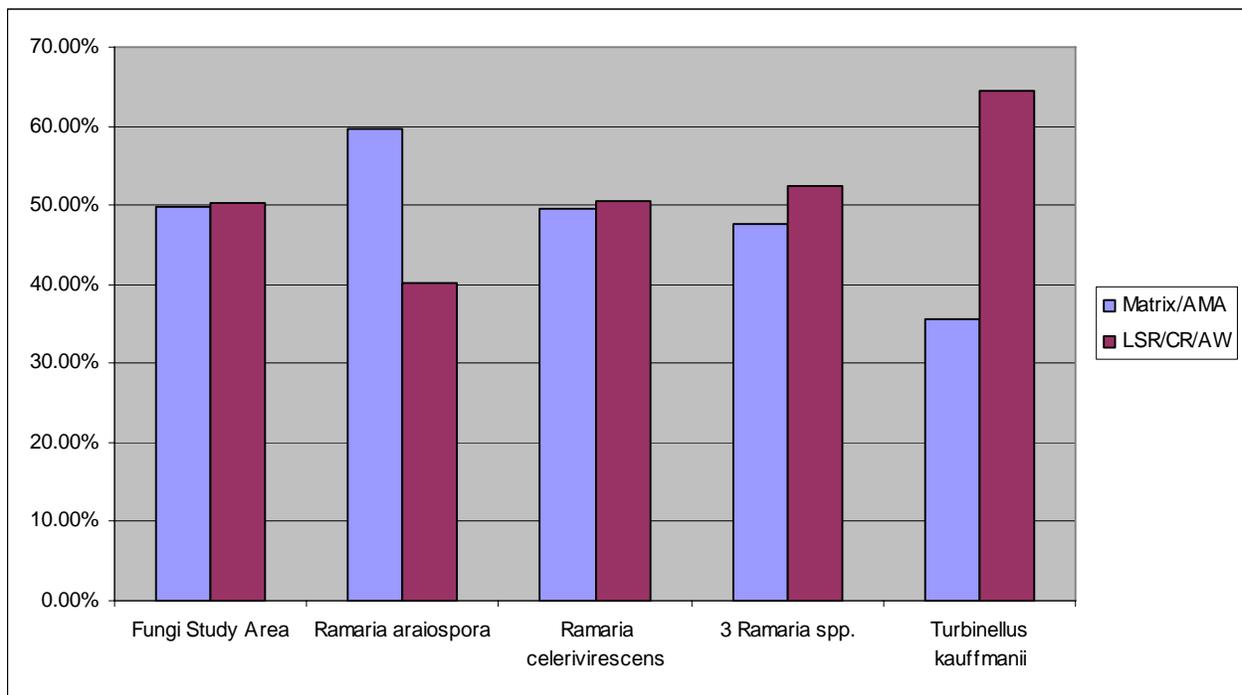
*Ramaria celerivirescens* had the most unique model in terms of the explanatory EGVs, however it was also the weakest model. The mapped suitable habitat for this species is scattered diffusely throughout the study area and the low marginality value indicates that habitat conditions where the known sites occur are similar to mean conditions within the study area. Slope, solar radiation in both August and December, and conifer quadratic mean diameter were the principle factors explaining marginality. The later EGV represents old-growth stand conditions and was completely uncorrelated in the other three models. The HSM produced is of little value, and subsequently had poor validation scores ( $R_s = 0.26$ ,  $P = 0.45$ ). However, when considered along with the other models, this does demonstrate how variable the habitat for these taxonomically related species is.

It was unexpected that *R. celerivirescens* would be the only model that showed any correlation with old-growth conditions. Numerous studies have reiterated the relationship of fungal species richness to old-growth (Kranabetter et al. 2005, Roberts et al. 2004), and many *Ramaria* species, including *R. celerivirescens*, tend to only be detected in old-growth stands (Kranabetter et al. 2005, Norvell and Exeter 2004, Smith et al. 2002). However, in no published studies that we are aware of are there sufficient detections of individual *Ramaria* spp. that would allow for analysis of individual species relationship to old-growth stands. Other studies generally collect stand attribute data as part of the study rather than rely on landscape-scale data generated through remote sensing technologies. It is possible that the lack of old-growth relationship exhibited in this study is simply a shortcoming in the accuracy of these data at the scale of the EM fungi location data. However, this same dataset was of sufficient resolution to demonstrate relationships with other organisms in the Pacific Northwest (Davis and Lint 2005, Helliwell and York 2005). Furthermore, the coefficient values are so low as to suggest that an old-growth correlation is indeed absent for these species other than possibly with *R. celerivirescens*.

Although a fair amount of research has been devoted to studying EM fungi relationships with host species and stand types (Kranabetter et al. 2005, Norvell and Exeter 2004, Roberts et al. 2004, Smith et al. 2002), there has been little research into the evaluation of species distribution relative to regional climatic variables. One exception is Odell et al. (1999) who established a correlation with species richness and sporocarp standing crop within a moisture gradient on the Olympic Peninsula. Luoma (1991) also demonstrated a precipitation relationship; in this case, of hypogeous fungi to mesic, old-growth forest. Precipitation was a relatively insignificant factor for each of the four models in our study although annual precipitation was an important specialization variable for the three *Ramaria* spp. and *R. celerivirescens* models. In Australia, Claridge et al. (2000) demonstrated environmental correlations with models of several species of hypogeous fungi. In their study, mean minimum temperature of the coldest month and annual mean moisture index were the key environmental variables in their species occurrence models.

A relationship with minimum temperature in winter is corroborated to varying degrees in all four of the models in the present study. This is particularly true for the two strongest models (*T. kauffmanii* and *R. araiospora*). It is interesting that the same relationship with minimum temperature should be constant for both hypogeous, spring-fruited fungi in Australian eucalyptus forests and epigeous, fall-fruited fungi in Northwestern United States Douglas-fir forests.

The models were generally more parsimonious than was expected since ENFA has been reported to over-represent habitat (Pearce and Boyce 2005, Engler et al. 2004). The three *Ramaria* spp., *R. araiospora* and *T. kauffmanii* mapped suitable habitat across 7.9%, 5.0%, and 2.6% of the study area, respectively. Even if ENFA is not over-predicting suitable habitat for these species, their suitable habitat appears to be quite rare at the landscape scale. On the other hand, the HSMs were based only on sporocarp distribution. Had non-fruited populations been represented it is possible that a larger distribution would have been portrayed in the HSMs. Although *R. celerivirescens* mapped by far the most suitable habitat at 21.5% of the total study area, the poor validation of the model does not allow for meaningful evaluation of its relative rarity.



**Figure 8.** Suitable habitat by land use allocations on federal lands (private lands are excluded) within the study area.

The Northwest Forest Plan was intended to represent a conservation plan for old-growth associated species. Conservation elements of the plan principally involve adaptation of a series of land allocations with differing management emphasis and standards for management actions within each of these land allocations (USDI and USDA 1994). Because only *R. celerivirescens* exhibited any preference for old-growth stands, it is unclear whether standards for preserving old-growth *per se* would confer the intended benefit upon these species. However, assuming that

relative stability of the habitat is beneficial to these species, land allocation designations that mandate less intrusive management actions should provide greater protection for these species and their habitats. This contention is supported by Luoma et al. (2006) who determined that retention of living trees enhances diversity of EM fungi. Across the study area overall, there is an almost identical amount of habitat in the “reserved” land allocations (i.e., congressionally withdrawn, Late Successional Reserve &c.) as in the “non-reserved” land allocations (i.e., matrix and Adaptive Management Areas). However, because there appears to be a greater percentage of reserved land allocations at higher elevations within the study area, *T. kauffmanii* is much less at risk from disturbance than *R. araiospora* (Figure 8) based solely on land allocation.

Climatic variables were the principle explanatory factors in predicting suitable habitat for EM fungi. The principle EGVs that accounted for most of the marginality and specialization were similar among the models although the EGVs’ relationship to individual species may be inverse. Evaluation of the physiological response of fungi to regional climatic variables is beyond the scope of this study; however the ENFA results suggest that this may be an area that merits further research.

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