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1 ***Title: Do the rich get richer? Varying effects of tree species identity and diversity on the***
2 ***richness of understory taxa.***

3 *Running title: Tree diversity effects on understory diversity*

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13

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1 **ABSTRACT**

2 Understory herbs and soil invertebrates play key roles in soil formation and nutrient cycling
3 in forests. Studies suggest that diversity in the canopy and in the understory are positively
4 associated, but they often confound the effects of tree diversity with those of tree species
5 identity and abiotic conditions. We combined extensive field sampling with structural
6 equation modeling to evaluate the simultaneous effects of tree diversity on the species
7 diversity of understory herbs, beetles, and earthworms. The diversity of earthworms and
8 saproxylic beetles was directly and positively associated with tree diversity, presumably
9 because species of both these taxa specialize on certain species of trees. Tree identity also
10 strongly affected diversity in the understory, especially for herbs, likely as a result of
11 interspecific differences in canopy light transmittance or litter decomposition rates. Our
12 results suggest that changes in forest management will disproportionately affect certain
13 understory taxa. For instance, changing canopy diversity will affect the diversity of
14 earthworms and saproxylic beetles more than changes in tree species composition, whereas
15 the converse would be expected for understory herbs and detritivorous beetles. We conclude
16 that the effects of tree diversity on understory taxa can vary from positive to neutral and may
17 affect biogeochemical cycling in temperate forests. We recommend to maintain high tree
18 diversity, thereby promoting the diversity of multiple understory taxa, and to reduce the
19 abundance of tree species that may reduce understory diversity.

20

21

1 INTRODUCTION

2 The ongoing loss of biodiversity induced by human activities has led ecologists to
3 assess its consequences for ecosystems, and the services that they provide humanity (Naeem
4 et al. 2009, Rockström et al. 2009, Cardinale et al. 2012). In grasslands, increased plant
5 diversity is often associated with increased productivity and decomposition (Hooper et al.
6 2012). The positive effect of diversity arises from both among-species complementarity and
7 species-specific impacts on ecosystem processes (Loreau and Hector 2001). Although the
8 importance of forests for both biodiversity and ecosystem services is widely recognized,
9 biodiversity studies are more difficult to mount in forests due the great size and lifespan of
10 trees (Nadrowski et al. 2010). Though recent work has shown that biodiversity in forests
11 promotes tree growth and ecosystem stability (Zhang et al. 2012, Jucker et al. 2014), the
12 relationships between tree diversity and the diversity of understory organisms such as soil
13 invertebrates and herbaceous plants are little known (Wardle et al. 2004, van der Heijden et
14 al. 2008).

15 Earthworms and other soil invertebrates play crucial roles in litter decomposition, a
16 key process for nutrient and carbon cycling in most terrestrial ecosystems (Aerts 1997). They
17 affect plant growth directly by feeding on roots (Scheu 2003), and indirectly by altering soil
18 structure, nutrient availability and the activity of soil microorganisms (Wardle 1999, Scheu
19 2003, Wurst et al. 2003, Partsch et al. 2006). Understory herbaceous plants, though they
20 contribute only 0.2% of total forest biomass (Gilliam 2007), generate 4% of forest net
21 primary production and up to 16% of foliar litter, with greater nutrient content and more
22 rapid decomposition than the tree-leaf litter (Muller 2003). As a result, impacts of tree
23 diversity on the diversity of understory organisms have the potential to alter forest carbon and
24 nutrient cycling.

1 Tree diversity often positively affects the diversity of understory invertebrates and
2 herbs (Nadrowski et al. 2010). For example, herb species richness increased with increasing
3 tree diversity in a central European forest, and decreased with canopy cover and humus mass
4 (Vockenhuber et al. 2011). Tree diversity was also associated with increased earthworm and
5 beetle diversity (Cesarz et al. 2007, Sobek et al. 2009b). The two mechanisms invoked to link
6 their diversity are an increase in the heterogeneity of soil conditions (Cesarz et al. 2007,
7 Sobek et al. 2009b, Vockenhuber et al. 2011), and differential facilitation effects of each tree
8 species on certain understory species (Augusto et al. 2003, Lassau et al. 2005).

9 The identity of tree species can indirectly affect understory diversity by altering
10 abiotic conditions. Tree species that differ in their rates of crown light transmittance, litter
11 chemistry, and decomposition also differ in their impact on forest soil, litter, and light
12 properties (Hobbie et al. 2006, Barbier et al. 2008). In Europe, for instance, European beech
13 (*Fagus sylvatica* L.) and conifers are generally associated with low herbaceous-plant
14 diversity (Cesarz et al. 2007, Barbier et al. 2008, Sobek et al. 2009b). Soil and litter
15 properties significantly impact the diversity of earthworms, soil beetles, and herb species
16 (Ponge et al. 1999, Wardle et al. 2004, Vockenhuber et al. 2011), and light availability often
17 limits herb species richness (Kirby 1988; Jennings et al. 1999; Hofmeister et al. 2009).

18 Tree diversity, tree species identity and abiotic conditions all affect the diversity of
19 understory organisms, yet no study has explored their simultaneous effects, rendering it
20 impossible to determine their relative importance (Mölder et al. 2008, Sobek et al. 2009a).
21 First, a dilution gradient, where one tree species is always present and is the only one found
22 in monocultures, is often used instead of a true diversity gradient, in which all possible
23 species combinations are represented (Cesarz et al. 2007, Sobek et al. 2009b). This makes it
24 difficult to distinguish the effects of tree diversity from those of tree identity. Second, studies

1 carried out in natural forests can confound diversity effects with variation in abiotic
2 conditions (Nadrowski et al. 2010). For example, a positive relationship between tree and
3 herb diversity could arise from soil fertility promoting the diversity of both trees and herbs.
4 In this contribution, we assess the effects of tree diversity on understory diversity while
5 controlling for the effects of tree identity and abiotic variables. We sampled 45 stands in a
6 managed forest of the Czech Republic, the canopy layers of which were dominated by all
7 possible combinations of four tree species, i.e. the composition ranged from the monoculture
8 of each species to the mixture of all four species. We investigated the effects of tree species
9 diversity, tree identity, and abiotic conditions on the diversity of three taxa that are important
10 for ecosystem functioning: litter-dwelling earthworms, litter-dwelling beetles, and understory
11 herbs. Using structural equation modeling (Grace et al. 2012), we distinguished the direct
12 effects of trees on the understory from those mediated by abiotic conditions. We
13 hypothesized that tree diversity would directly promote the diversity of all understory taxa.
14 Such relationships have been reported for herbs (Vockenhuber et al. 2011), earthworms
15 (Cesarz et al. 2007) and beetles (Sobek et al. 2009b) in single-taxon studies. We expected
16 tree diversity and density to increase canopy cover, and canopy cover to decrease herb
17 diversity (Vockenhuber et al. 2011). We also predicted the effect of soil variables on the
18 diversity of all taxa. Soil N content is likely to increase the diversity of herbs (as long as there
19 is no excess N accumulation, Gilliam 2006) and soil invertebrates, whereas humus mass
20 should reduce them (Curry 2004; Vockenhuber et al. 2011). Soils with higher pH can harbor
21 higher diversities of herbs (Augusto et al. 2003) and earthworms (Cesarz et al. 2007). Thus,
22 we expected soil quality (which is related to higher pH and N content, and lower humus
23 mass) to support increased diversity of all understory groups. Finally, we predicted that herb
24 diversity would drive the diversity of the invertebrate taxa due to increased food and habitat

1 diversity and that the diversity of predator beetle species would be affected with diversity of
2 other invertebrate taxa because they represent higher food diversity for the predators.

3 MATERIAL AND METHODS

4 Experimental design

5 The Training Forest Enterprise (TFE) is located north of Brno, Czech Republic:
6 49°3'N and 16°7'E, and 310 to 560 m above sea level (Figure 1). The annual mean
7 temperature is 7.5°C to 8.1°C, the average annual precipitation is 528 to 685mm, and 360mm
8 during the growing season, and Cambisol is the main soil type (Truhlář 1997). The forest has
9 been managed by Mendel University in Brno for a hundred years. Forest type, age, density,
10 and volumetric species composition are estimated in each of the 4000 stands every ten years,
11 and the data are publically available (www.mapserver-slp.mendelu.cz/). Forests of the TFE
12 are dominated by an evergreen conifer, *Picea abies* (Norway spruce), a deciduous conifer,
13 *Larix decidua* (European larch), and two broadleaved tree species, *Quercus petraea* and
14 *Fagus sylvatica* (Sessile oak and European beech, respectively). Out of the four species,
15 *Larix decidua* is the only non-native species, with the nearest native locality being in the
16 extreme north-east of the Czech Republic (approximately 150 km away from FTE). In the
17 most recent forest inventory (2012), these four species jointly represented 75% of timber
18 volume of the TFE. We selected three stands to represent each of the 15 possible
19 combinations of the four focal species (45 stands, total). The stands were chosen in a way to
20 minimize the range of abiotic features: all had Cambisol as a soil type, were flat or with a
21 slight slope (<10%), and were planted 50 to 100 years ago. Stands averaged 0.24 ha and
22 ranged from 0.07 to 0.6 ha.

1 **Data collection**

2 In each stand, six trees of every focal species were targeted, and the positions of
3 targets and their neighbors in a 10-m radius were mapped with Field-Map technology
4 (<http://www.fieldmap.cz/>). Every mapped tree was identified, and its diameter at breast
5 height (DBH) measured. Tree diversity was calculated as the effective number of species, or
6 the exponent of the Shannon index $e^{H'}$ (Magurran 2004), which accounts for both species
7 richness and evenness. Canopy tree density and the relative abundance of each species was
8 calculated on basal area.

9 A 40 x 20 m transect was established in the understory of every stand, along which
10 herbs, beetles, earthworms, and abiotic conditions were assessed (Figure 1). The direction of
11 each transect was randomly determined. For herbs, 41 1-m² randomly located plots, divided
12 into 20 by 20 cm sub-grids (i.e., 25 sub-grids per plot), were established along all transects.
13 In each plot, the relative abundance of each herb species was estimated by counting the
14 number of sub-grids in which the species was present. A pilot study showed that sampling 41
15 plots was sufficient to saturate the species-accumulation curve.

16 Beetles and earthworms were sampled in 5 m-radius plots at the ends and middle of
17 each transect (Figure1). For each invertebrate sample, we collected humus (ground litter and
18 leaf mold) in five randomly selected 30 by 30 cm subplots. Humus was sifted using an
19 entomological sifter with a 10-mm wire-mesh screen bottom. Material sifted through the
20 screen was exposed to the sun on a white cloth for about 15 minutes, and beetles were
21 manually collected. Large earthworms were collected prior to sifting, and small ones
22 following sun exposure. We classified beetles by their feeding habits because we expected
23 their responses to the tested variables to differ (Lassau et al. 2005). The three functional
24 groups were predators, which feed on other animals; detritivores, which consume detritus;

1 and saproxylics, which live and feed on dead wood. For herbs, earthworms, and each
2 functional group of beetles, gamma diversity was calculated as the total species richness per
3 stand.

4 Finally, we assessed abiotic conditions including humus mass, canopy cover and soil
5 characteristics (Figure 1). We assessed the mass of the humus layer by collecting, drying, and
6 weighing humus from the top litter layer to the mineral soil from 100-cm² quadrats at nine
7 points along each transect. Canopy cover was measured using hemispherical photographs taken
8 with a Canon EOS 550 camera with Sigma circular fish-eye lens (Sigma 4.5 mm F2.8 EX DC
9 Circular Fisheye HSM) at five points along each transect. The hemispherical photographs were
10 then analyzed using the Can-Eye V6.36 software. Finally, soil samples were taken at both ends
11 of each transect to assess nitrogen and phosphorus content, pH, and catalase activity (i.e., the
12 activity of microbial organisms). Herb, humus and canopy cover data were collected between
13 July and August 2012, and beetles and earthworms in June 2012.

1 *Soil quality*

2 To reduce the complexity of the model, we used Principal Components Analysis (PCA) to
3 reduce the number of soil variables. The first axis of a PCA that included pH, Nitrogen and
4 Humus content explained 59% of the variation in these variables and was highly correlated
5 with each of them (pH, $r = 0.88$; %N, $r = 0.64$; Humus, $r = -.77$). The scores from this axis
6 were used as a single indicator of soil quality.

7 **Statistical analysis**

8 *Causal hypotheses*

9 We used structural equation modeling (SEM, Grace et al. 2012) to quantify the direct and
10 indirect effects of canopy tree diversity, identity and density on the species richness of
11 earthworms, beetles and herbs. We began by developing a causal diagram, which captured
12 hypothesized causal relationships between the variables (Figure 2) that are developed in the
13 introduction. In addition, we included correlations between all pairs of tree species, because
14 an increase in one species' abundance implies a reduction in the others in these closed-
15 canopy forests. The variables at this point are concepts, regardless if we have the data to feed
16 into the concepts.

17

18 *Model updating and selection*

1 The analyses were conducted as follows. For each concept in Figure 2, we assigned one or
2 more variable from our observed dataset (or calculated combination of these) to represent that
3 concept (Figure S1 in supplementary material). For each node in the model representing a
4 random variable (i.e., a measured quantity; not one calculated without error from other
5 measured quantities), we estimated its expected value as a function of each of the arrows
6 pointing at it. Next, since the diagram is meant to capture all causal effects, each pair of
7 variables not connected by an arrow are hypothesized to be conditionally independent (i.e.,
8 independent after accounting for the effect indicated by the arrows pointing at them). We
9 used the set of pairs not connected by arrows to test the hypothesized structure. Pairs that
10 were not conditionally independent were interpreted as errors in the hypothesized causal
11 structure of the model. To test the conditional independence claims implied by the causal
12 diagram, we chose the likely direction of causation between them, and we then parameterized
13 the relationship between the variables and the probability that it differed from zero. We used
14 Fisher's Combined Test (Fisher 1950) to combine these probabilities into a single test of the
15 null hypothesis that the observed data were generated by a set of mechanisms given by the
16 causal diagram (Shipley 2000). We then used the feedback obtained from fitting the initial
17 model to update it. That is, we added arrows between pairs of variables that we first thought
18 independent but were not, and we removed arrows between variables that we thought
19 dependent but were not. Fitting the model in this manner, as opposed to using an automated
20 SEM procedure, allowed us to choose appropriate error distributions for random variables.

1 All parameter estimation was performed in the R language and environment, version 3.1.2 (R
2 Development Core Team 2011). We use generalized linear models to estimate the parameters
3 of the random variables in Figure S1. The distributions and link functions used for each
4 variable are listed in Table S2 (Supplementary material). For each of the species richness
5 variables, we attempted to fit a negative binomial distribution using the `glm.nb()` function
6 from the MASS package (Venables and Ripley 2002). In a few cases, this function failed to
7 converge on stable estimates. When this occurred, we fit a Poisson distribution using the
8 `glm()` function. We used Akaike information criterion (AIC) for model comparison. AIC was
9 calculated using the log-likelihood of the joint distribution factorized by the causal graphical
10 model. For these calculations, the basal area of each tree species assumed to follow a zero-
11 inflated lognormal distribution. In the final model, we calculated R^2 for each endogenous
12 (response) variable. For non-Gaussian models, we calculated a pseudo- R^2 as
13 $1 - e^{-2(LL_{full} - LL_{null})/n}$, where LL_{full} is the log-likelihood of the full model, LL_{null} is the log
14 likelihood of the intercept only model and n is the sample size (Shtatland and Barton 1998).

15 **RESULTS**

16 In total, we found 181 herb species (mean per stand 26.8, range 1-50), 6 earthworm species
17 (mean 2.4 per stand, range 0-4), and 98 beetle species (mean 8.7, range 3-16), of which 42
18 were detritivores (mean 2.8, range 0-11), 37 were predators (mean 2.4, range 0-5), and 19
19 were saproxylics (mean 0.9, range 0-4).

20 **Model selection**

1 Our initial causal network model was poorly supported by the data and was rejected ($\chi^2 =$
2 208.9, $df = 126$, $p < 0.001$, $AIC = 2503.6$); the tests of conditional independence were predicted
3 from the initial model in Table S3 (Supplementary material). Of the 63 conditional
4 independence tests indicated by the missing pairwise links in the initial model, nine failed
5 (i.e. $p < 0.05$). Six of these nine represented species-specific effects on other variables;
6 specifically soil quality, understory herb richness, canopy cover and detritus. We used this
7 feedback to modify the original causal network (Figure S4 in supplementary material).
8 Including the links indicated in Figure S4 resolved the discrepancy between the model and
9 the data ($\chi^2 = 94.1$, $df = 112$, $p = 0.889$). To arrive at the final data-informed model, we
10 removed the links for which there was little statistical support (Figure 3). The hypothesis that
11 the data were generated by a causal structure shown in Figure 3 could not be rejected ($\chi^2 =$
12 104.9, $df = 124$, $p = 0.891$, $AIC = 2436.6$). The final parameter estimates are shown in Table 1,
13 and the corresponding relationships are depicted in the Figure S5 in supplementary material.
14 The results of the conditional independence test for this final model are shown in Table S6 in
15 supplementary material.

16 **Effects on understory**

17 *Herbs*

18 Understory herb richness increased with increasing soil quality, and decreased with canopy
19 cover and *Larix* basal area (standardized coefficients [SC]: 0.11, -1.75 and -0.06,
20 respectively, $R^2 = 0.56$). Increasing *Fagus* basal area further reduced herb species richness
21 (SC: -0.09) by increasing canopy cover (SC: 0.05). *Picea* and *Quercus* basal area also had
22 indirect effects on herb species richness (SC: -0.02 and SC: 0.02, respectively), which were
23 mediated by their negative (*Picea*) and positive (*Quercus*) effects on soil quality (SC: -0.20
24 and SC: 0.18, respectively, $R^2 = 0.43$). Contrary to our expectations, tree diversity had no
25 direct or indirect effect on herb species richness.

1 *Invertebrates*

2 The diversity of saproxylic beetles and earthworms was positively and solely affected by tree
3 diversity (SC = 0.35, $R^2 = 0.15$ for saproxylic beetles, SC: 0.18, $R^2 = 0.10$ for earthworms).
4 Increasing soil quality and *Larix* basal area reduced the diversity of detritivorous beetles (SC:
5 -0.28 and -0.1, respectively).

6 **DISCUSSION**

7 Using a fully replicated study design and an appropriate analysis, we demonstrate that
8 tree diversity promoted the species richness of earthworms and saproxylic beetles, but
9 contrary to our expectations, did not affect the diversity of other invertebrate groups or
10 understory herbs (Figure 3). To our knowledge, this is the first multi-taxon study to
11 distinguish the effects of diversity from those of tree identity, and to account for the
12 potentially confounding effects of environmental heterogeneity (Nadrowski et al. 2010).

13 *Effects on invertebrate diversity*

14 We found that tree diversity had direct positive effects on the diversity of earthworms
15 and saproxylic beetles, whereas, surprisingly, they were independent of tree identity, abiotic
16 conditions and stand properties. A positive effect of tree diversity on earthworms was also
17 found by Cesarz et al. (2007) in natural forests, who reasoned that increasing litter diversity
18 increased the diversity of food available to earthworms. In contrast, Schwarz et al. (2015)
19 found a weak effect of tree identity, but no effect of tree diversity, on earthworm species
20 richness. However, their study was carried in forest stands so young (8 to 10 years old) that
21 the trees might have had insufficient time to generate the changes in soil properties that
22 would facilitate higher earthworm diversity. In addition, the tree-identity effect in their study
23 was site-specific and limited to two of 18 tree species. In combination with our results, this
24 suggests that earthworm diversity is largely independent of tree identity. Similarly, the

1 species richness of saproxylic beetles has been found to increase with dead wood diversity
2 (Similä et al. 2003), which is likely to correlate with tree species diversity. Surprisingly, we
3 found no relationship between tree and detritivore diversity, even though trees are the main
4 producers of leaf litter. This lack of effect could have arisen if the detritivorous beetles were
5 generalist consumers, and therefore not as responsive to litter composition and diversity as
6 saproxylic beetles or earthworms (Lassau et al. 2005).

7 Detritivore beetles were the only group of invertebrates whose diversity was significantly
8 affected by tree identity and abiotic conditions. Their species richness decreased with soil
9 quality and with increasing *Larix* abundance. The effect of *Larix* is likely to be caused by
10 unfavorable properties of its litter, which has higher N immobilization and lower
11 concentrations of Ca and K compared to the other studied tree species (Hobbie et al. 2006).
12 The mechanism behind the negative effect of soil quality is less clear. Soil quality in our
13 model was represented by scores of PCA axis which were positively correlated with N
14 content and pH but negatively with humus mass. Therefore, the negative effect of soil quality
15 implies a positive effect of humus mass on detritivore diversity, probably because of an
16 increase in the amount of detritus on which this group feeds. In addition, greater amounts of
17 slowly decomposing humus due to lower nutrient content probably creates a more stable
18 environment for these beetles, because it is likely to moderate temporal temperature and
19 humidity variation, and is also less likely to completely decompose or be removed by soil
20 disturbances. Surprisingly, the difference in litter quality caused by differences in species
21 identity did not affect earthworm or saproxylic beetle diversity, though tree diversity did. We
22 speculate that this could happen if earthworm and saproxylic beetle species were more
23 specific to certain tree species, and if all tree species hosted the same average number of
24 invertebrates. Finally, the lack of significant relationships between understory diversity and
25 most of the abiotic factors we measured may be attributable to the short gradients captured in

1 our study. We selected our 45 study stands to be as similar as possible in terms of altitude,
2 topology, and soil type, which limited our power to detect the effects of soil characteristics on
3 the diversity of understory taxa.

4 *Tree effects on herb diversity*

5 We found that herb diversity was most strongly affected by canopy cover and more
6 weakly by tree identity and soil quality, but not, contrary to our prediction, by tree diversity
7 (Figure 3). We had also expected herb diversity to be reduced by tree diversity, through an
8 increased canopy cover, due to denser canopy packing (Jucker et al. 2015). In this study we
9 found a positive relationship between total stand basal area and canopy cover. Because this
10 basal area measurement is calculated from the basal areas of the measured tree species, it is
11 not an independent variable and we could not test for the relationship between tree diversity
12 and total basal area that other studies have reported (Paquette and Messier 2011, Barrufol et
13 al. 2013, Vilà et al. 2013). It has been found that forests with high tree diversity have greater
14 structural complexity and canopies that capture more light (Morin et al. 2011). This in turn
15 reduces the amount of light reaching the understory, which limits herb growth and decreases
16 herb diversity (Kirby 1988; Jennings et al. 1999; Barbier et al. 2008). Although this causal
17 reasoning makes intuitive sense, it contradicts previous studies that detected positive or
18 neutral effects of tree diversity on herb diversity (Ingerpuu et al. 2003, Mölder et al. 2008,
19 Nadrowski et al. 2010, Vockenhuber et al. 2011). Those studies however, were carried out in
20 natural or semi-natural forests, where variation in abiotic conditions has the potential to
21 confound the effects of tree diversity on herb diversity (Vockenhuber et al. 2011).

22 Our study confirms that abiotic conditions affect understory herb species richness
23 (Barbier et al. 2008). We showed that herb diversity not only decreases with increasing
24 canopy cover, but also with humus mass, corroborating research from other temperate forests

1 (Augusto et al. 2003, Gazol and Ibáñez 2009, Vockenhuber et al. 2011). The humus layer
2 represents a physical barrier for germinating plants (Sydes and Grime 1981, Dzwonko and
3 Gawroński 2002). Naturally, the tree species with greatest effects on canopy cover and
4 humus most strongly affected herb diversity. For example, *Fagus sylvatica* is one of the most
5 shade-casting species in European forests (Brzeziecki and Kienast 1994), and an increase in
6 its abundance indirectly decreased herb diversity via its positive effect on canopy cover.
7 *Quercus petraea*, on the other hand, produces a quickly decomposing litter (Cornelissen
8 1996), and its abundance indirectly enhanced herb diversity via its positive effect on soil
9 quality, corresponding to a negative effect on humus mass.

10 *Conclusions and implications for forestry*

11 Understanding the mechanisms underlying the effects of trees on the understory can help us
12 manage forests to simultaneously maximize multiple ecosystem functions. The positive effect
13 of tree diversity on the diversity of earthworms and saproxylic beetles is likely to affect
14 nutrient cycling and soil formation (Hättenschwiler et al. 2005, Cobb et al. 2010). By altering
15 the composition and activity of soil biota (Scheu et al. 2002), earthworms and saproxylic
16 beetles support the structure and functioning of the aboveground community, including plant
17 growth and productivity (Wardle et al. 2004). On the other hand, tree identity significantly
18 affected the diversity of herbs and detritivorous beetles, but not that of saproxylic beetles and
19 earthworms. This implies that changes in tree species composition would not affect the
20 diversity of earthworms and saproxylic beetles as long as tree diversity stayed unchanged,
21 whereas herb diversity would vary since it is highly dependent on tree identity. In addition,
22 except for the effect of *Quercus* on herb diversity, all tree identity effects were negative. This
23 implies that avoiding planting or keeping low density of some tree species, such as *Larix*
24 *decidua*, which was also the only non-native species of our study, may benefit several

1 understory taxa. Therefore, encouraging high tree diversity in planted forests may be
2 beneficial not only for timber production (Chamagne et al. 2016) but also for forest
3 biodiversity, which can be further promoted by the careful selection of tree species. Indeed,
4 we recommend maintaining high tree diversity overall, while maintaining at low abundance
5 tree species that may detrimentally impact understory diversity.

6

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13

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- 18

1 **TABLE LEGENDS**

- 2 Table 1: All coefficients in the final model, linking the response variables (rows) to all
- 3 explanatory variables (columns). The distribution error models (associated with the link
- 4 function) are also shown for each response variable.

1 TABLES

2 Table 1:

3

Response/Variable	Distribution(Link)	Intercept	Larix BA	Fagus BA	Picea BA	Quercus BA	Total BA	Tree Diversity	Canopy Cover	Soil Quality	Catalase Activity	Understory Herb Richness	Herbivorous Beetle Richness	Saproxyl Beetle Richness	Detritivorous Beetle Richness	Earthworm Richness	Predatory Beetle Richness
Canopy Cover	Normal(Log)	-3.28E-01		4.63E-02			1.20E-03										
Soil Quality	Normal(Identity)	1.44E-01			-2.04E-01	1.81E-01											
Catalase Activity	Normal(Identity)	6.99E+01															
Understory Herb Richness	Negative Binomial(Log)	4.81E+00	-6.10E-02						-1.75E+00	1.14E-01							
Herbivorous Beetle Richness	Poisson(Log)	7.68E-01															
Saproxyl Beetle Richness	Poisson(Log)	-1.07E+00						3.49E-01									
Detritivorous Beetle Richness	Negative Binomial(Log)	1.17E+00	-9.97E-02							-2.79E-01							
Earthworm Richness	Poisson(Log)	3.81E-01						1.76E-01									
Predatory Beetle Richness	Poisson(Log)	8.85E-01															

4

1 **FIGURE LEGENDS**

2 Figure 1: The Training Forest Enterprise (TFE) is a managed forest located north of Brno,
3 Czech Republic: 49°3'N and 16°7'E. The bottom panel pictures a map of an example forest
4 stand with three tree species dominating the canopy: *Fagus sylvatica*, *Larix decidua*, and
5 *Picea abies*. The points marking canopy tree locations are proportional to their DBH
6 (diameter at breast height; 1.3m). The 40 x 20 m understory transect is indicated by a green
7 rectangle, in which herbs were sampled at 41 plots. Invertebrates were sampled at both ends
8 and at the middle of the transect. Canopy cover, humus mass, and soil attributes were
9 collected at 5, 9, and 2 locations along the transect, respectively.

10

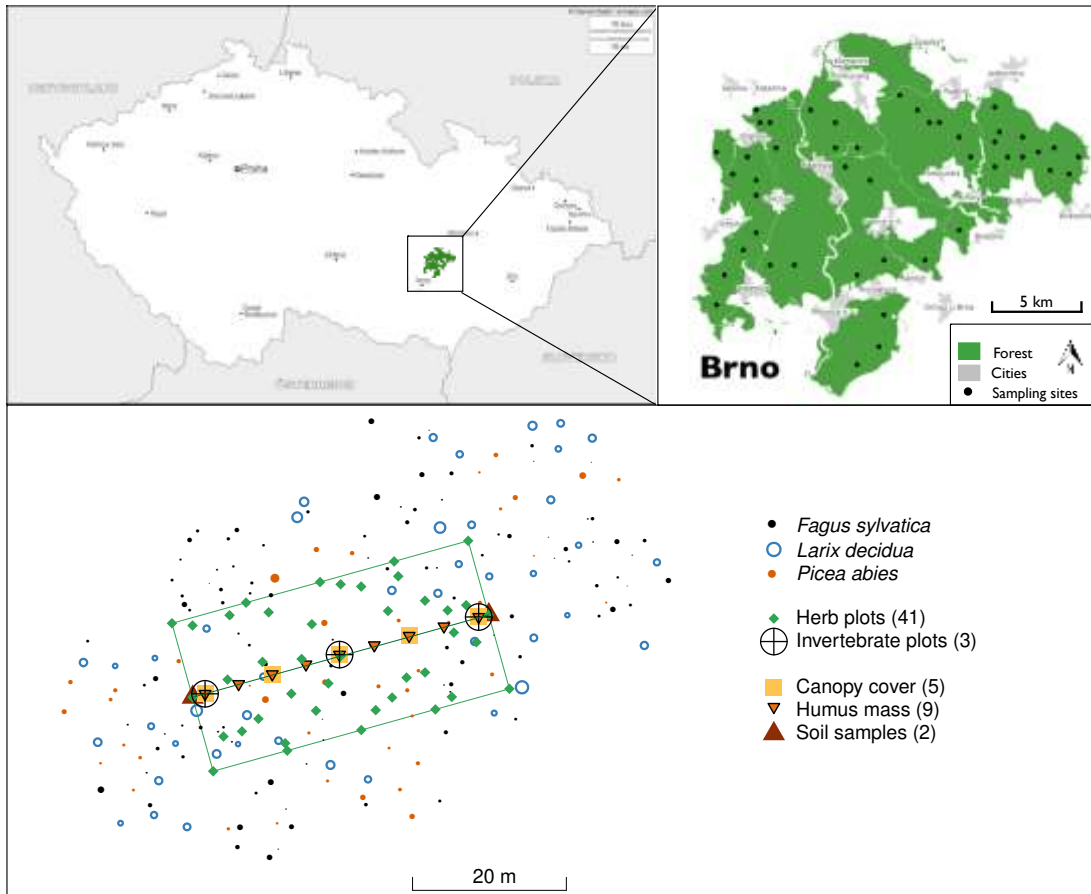
11 Figure 2: The *a priori* causal model of relationships between concepts (independent of data
12 availability). The arrows in this diagram represent a hypothesized direct causal effect of the
13 variable at the end of the arrow on the variable at the tip of the arrow. Double headed arrows,
14 such that those connecting tree basal areas, indicate correlation due to unmeasured shared
15 causes.

16

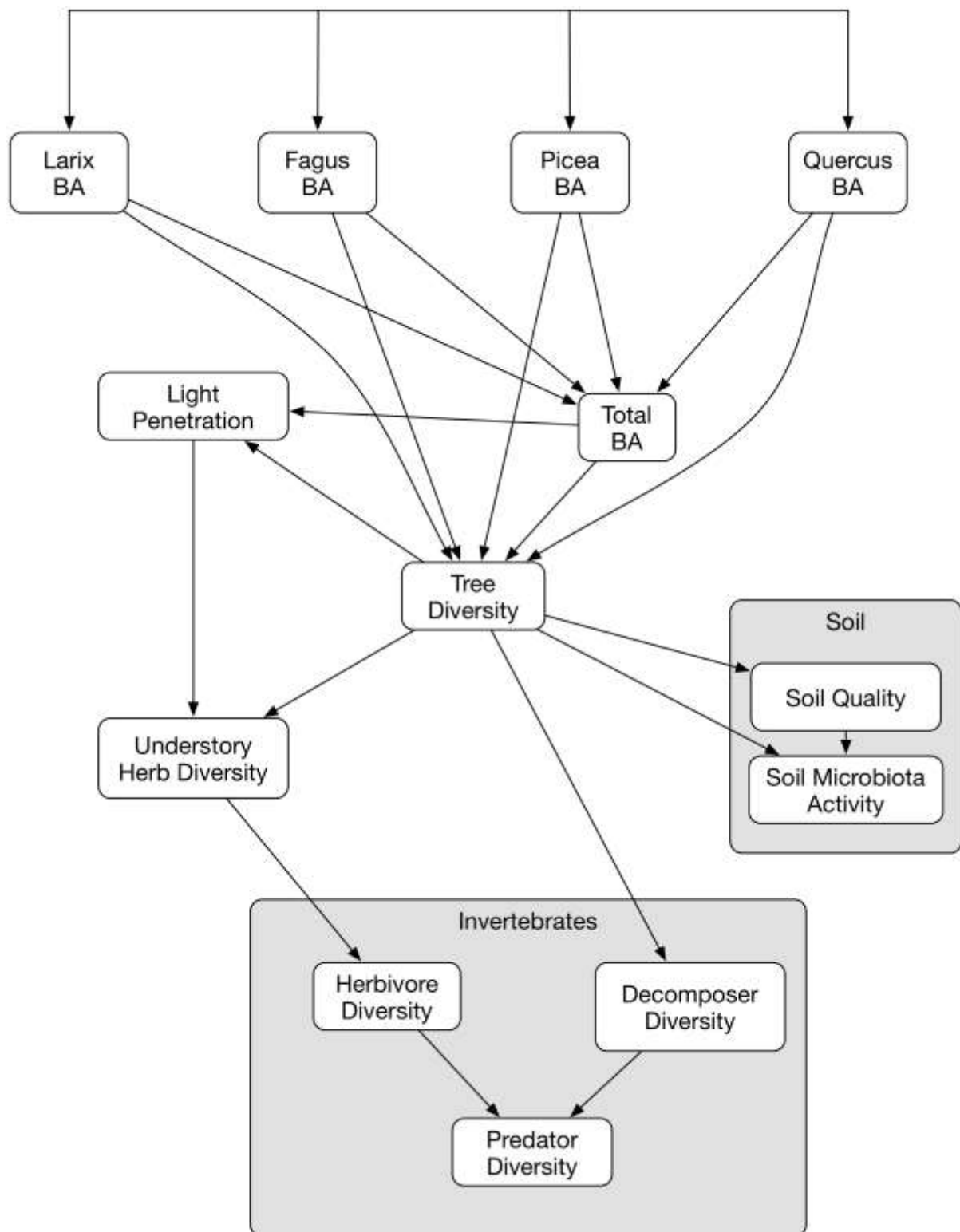
17 Figure 3: The final model ($\chi^2 = 104.9$, $df = 124$, $p=0.891$). Only relationships found to be
18 statistically significant ($P < 0.05$) were retained. Percentage variance explained (R^2) is
19 shown for random variables, i.e. the variables that were predicted from the model.

1 FIGURES

2 Figure 1

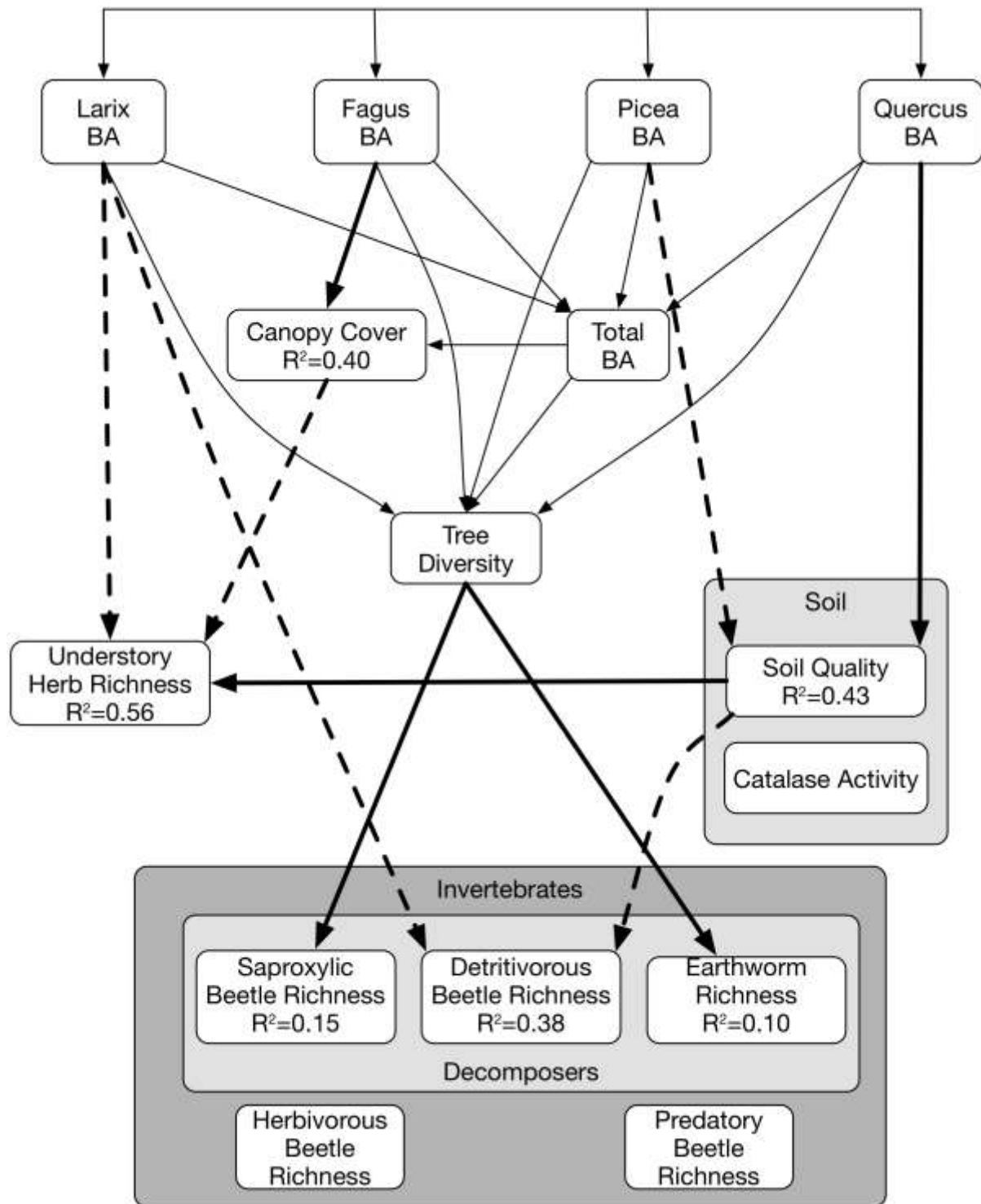


1 Figure 2:



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1 APPENDIX LEGENDS

2 Figure S1: A priori (initial) statistical model resulting from pairing concepts from the
3 causal diagram to variables represented with data.

4

5 Table S2: Coefficients of initial fitted model (see Figure S1), linking the response variables
6 (rows) to all explanatory variables (columns). Numbers in bold show significant
7 relationships. The distribution error models (and associated link function) are also shown for
8 each response variable.

9

10 Table S3: The results of the conditional independence test in the informed model. The rows
11 in bold show relationships that were not included in the informed model (Fig. S2) but that
12 appeared to be dependent. Those relationships were then included in the updated model (Fig.
13 S4).

14

15 Figure S4: The updated data-informed model ($\chi^2 = 94.1, df = 112, p=0.889$): after fitting the
16 initial model, we added the relationships that we were shown to be dependent but that we
17 hadn't included in our conceptual model.

18

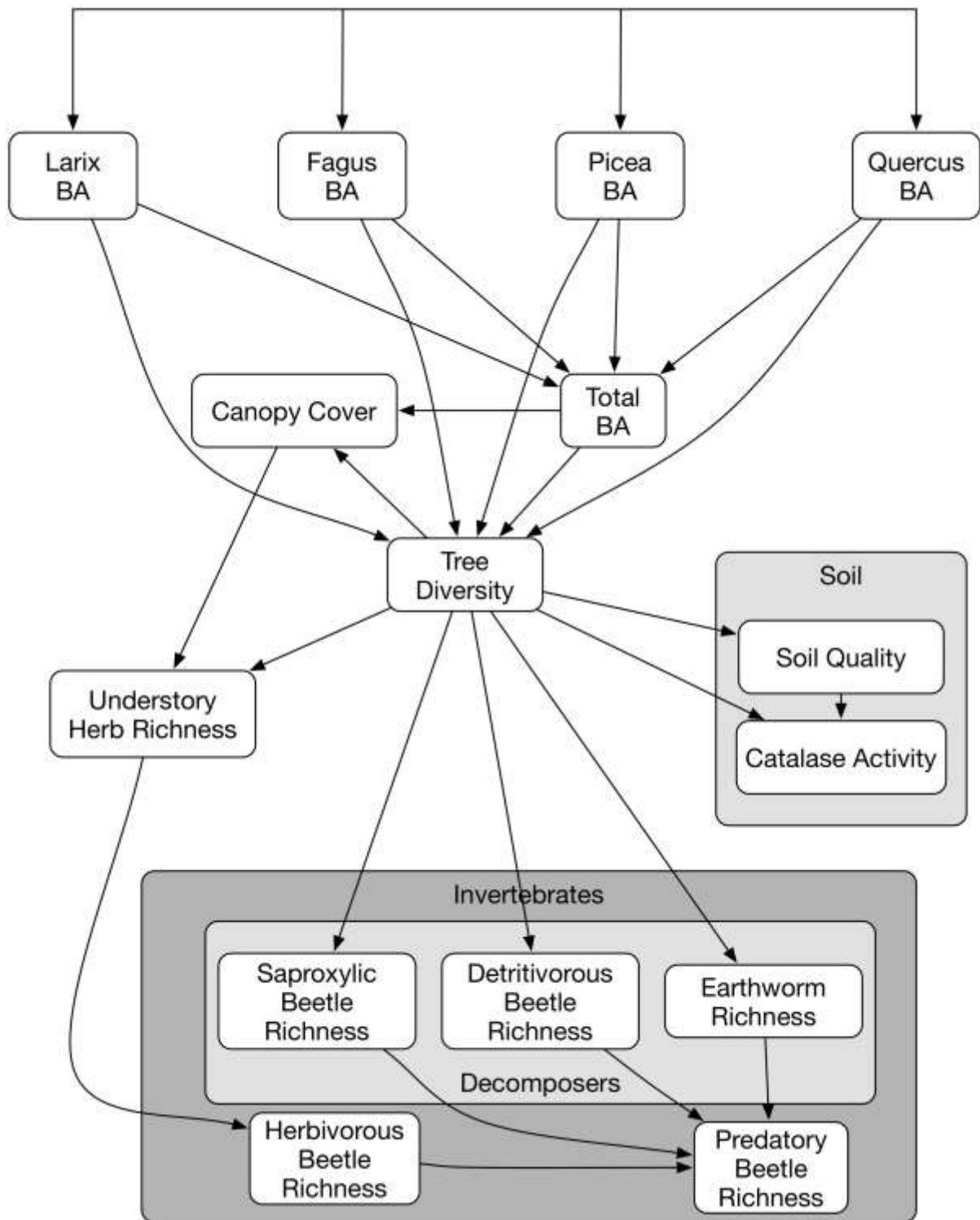
19 Figure S5: Scatterplot showing the response variables against all explanatory variables. The
20 significant relationships that were included in the final model include a prediction (mean +
21 $2*SE$, i.e. Standard Error).

22

23 Table S6: The results of the conditional independence test in the final model.

24

1 Figure S1:



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1 Table S2:

Response/Variable	Distribution(Link)	Intercept	Larix:BA	Fagus:BA	Picea:BA	Quercus:BA	Total:BA	Tree Diversity	Canopy Cover	Soil Quality	Catalase Activity	Understory ² Herb Richness	Herbivorous ² Beetle Richness	Saproxyllic ² Beetle Richness	Detritivorous ² Beetle Richness	Earthworm ² Richness	Predatory ² Beetle Richness
Canopy:Cover	Normal(Log)	-3.69E-01					7.34E-03	2.96E-02									
Soil:Quality	Normal(Identity)	-4.30E-01						1.63E-01									
Catalase:Activity	Normal(Identity)	6.45E+01						2.05E+00		5.55E+00							
Understory:Herb Richness	NegativeBinomial(Log)	4.63E+00						1.76E-02	-1.74E+00								
Herbivorous:Beetle Richness	Poisson(Log)	1.24E+00							-3.02E-01			-8.73E-03					
Saproxyllic:Beetle Richness	Poisson(Log)	-1.07E+00						3.49E-01									
Detritivorous:Beetle Richness	NegativeBinomial(Log)	1.16E+00						-5.62E-02									
Earthworm:Richness	Poisson(Log)	3.81E-01						1.76E-01									
Predatory:Beetle Richness	Poisson(Log)	6.36E-01										-5.34E-02	-4.65E-02	5.90E-02	9.70E-02		

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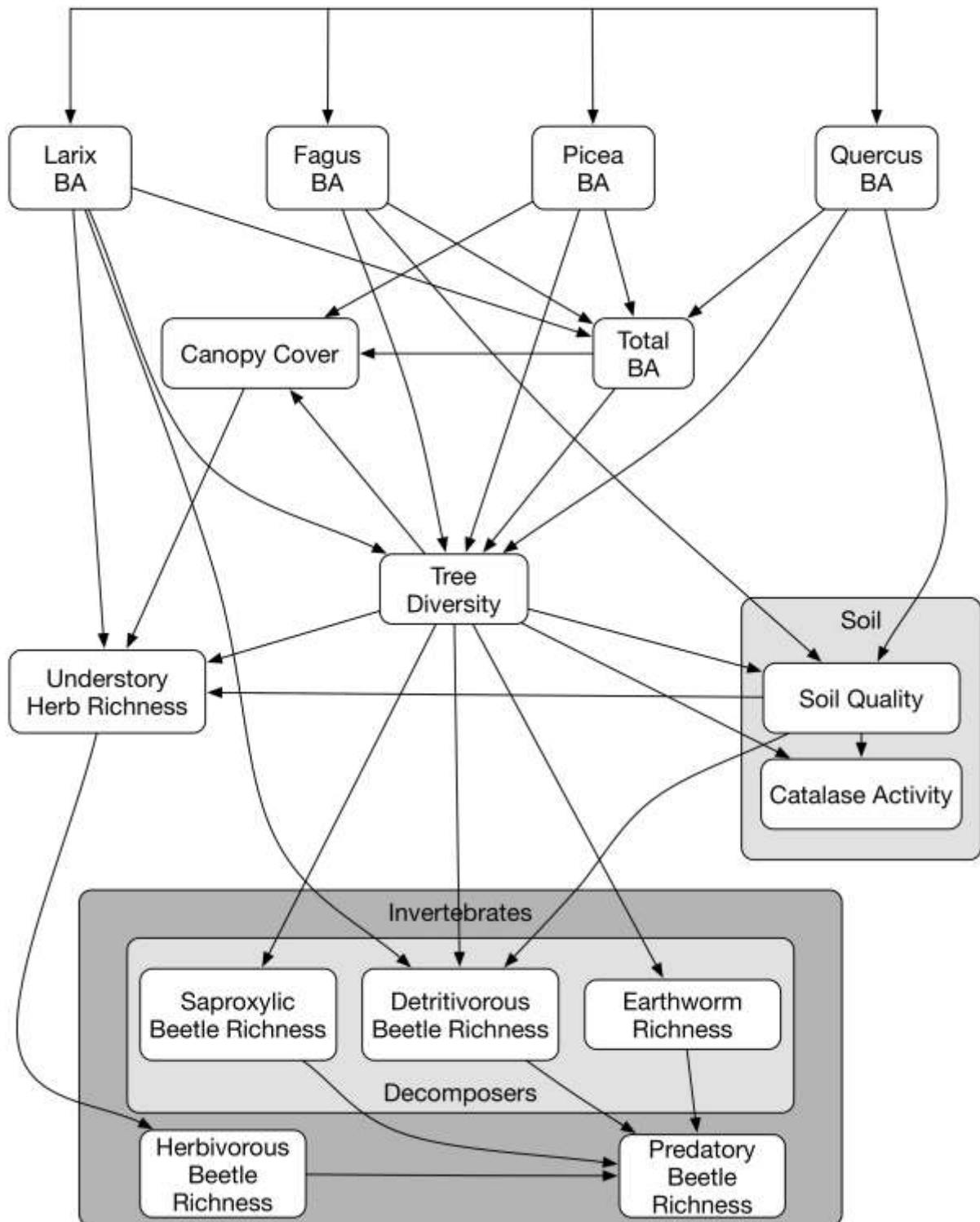
1 Table S3:

Predictor	Response	p-value
LarixBA	SoilQuality	2.67E-01
FagusBA	SoilQuality	2.46E-01
PiceaBA	SoilQuality	9.12E-06
QuercusBA	SoilQuality	3.86E-04
LarixBA	CanopyCover	7.66E-02
FagusBA	CanopyCover	2.02E-05
PiceaBA	CanopyCover	3.71E-01
QuercusBA	CanopyCover	8.00E-01
LarixBA	CatalaseActivity	6.99E-01
FagusBA	CatalaseActivity	8.26E-01
PiceaBA	CatalaseActivity	8.79E-01
QuercusBA	CatalaseActivity	7.43E-01
TotalBA	CatalaseActivity	9.46E-01
LarixBA	UnderstoryHerbRichness	7.42E-04
FagusBA	UnderstoryHerbRichness	1.59E-01
PiceaBA	UnderstoryHerbRichness	7.77E-01
QuercusBA	UnderstoryHerbRichness	4.64E-01
TotalBA	UnderstoryHerbRichness	6.04E-03
SoilQuality	UnderstoryHerbRichness	6.63E-03
LarixBA	HerbivorousBeetleRichness	9.10E-01
FagusBA	HerbivorousBeetleRichness	1.04E-01
PiceaBA	HerbivorousBeetleRichness	3.15E-01
QuercusBA	HerbivorousBeetleRichness	2.93E-01
TotalBA	HerbivorousBeetleRichness	4.93E-01
TreeDiversity	HerbivorousBeetleRichness	4.60E-01
SoilQuality	HerbivorousBeetleRichness	1.32E-01
LarixBA	SaproxyllicBeetleRichness	5.43E-01
FagusBA	SaproxyllicBeetleRichness	2.59E-01
PiceaBA	SaproxyllicBeetleRichness	8.99E-02
QuercusBA	SaproxyllicBeetleRichness	9.98E-01
TotalBA	SaproxyllicBeetleRichness	3.63E-01
SoilQuality	SaproxyllicBeetleRichness	1.67E-01
CanopyCover	SaproxyllicBeetleRichness	2.64E-01
CatalaseActivity	SaproxyllicBeetleRichness	8.53E-01
LarixBA	DetritivorousBeetleRichness	4.73E-02
FagusBA	DetritivorousBeetleRichness	5.23E-01
PiceaBA	DetritivorousBeetleRichness	2.03E-02
QuercusBA	DetritivorousBeetleRichness	4.77E-01
TotalBA	DetritivorousBeetleRichness	8.25E-01
SoilQuality	DetritivorousBeetleRichness	2.51E-03
CanopyCover	DetritivorousBeetleRichness	6.03E-01
CatalaseActivity	DetritivorousBeetleRichness	6.08E-01
UnderstoryHerbRichness	DetritivorousBeetleRichness	2.40E-01
LarixBA	EarthwormRichness	7.84E-01
FagusBA	EarthwormRichness	6.57E-01
PiceaBA	EarthwormRichness	3.71E-01
QuercusBA	EarthwormRichness	8.01E-01
TotalBA	EarthwormRichness	6.97E-01
SoilQuality	EarthwormRichness	5.26E-01
CanopyCover	EarthwormRichness	9.03E-01
CatalaseActivity	EarthwormRichness	3.21E-01
UnderstoryHerbRichness	EarthwormRichness	6.69E-01
HerbivorousBeetleRichness	EarthwormRichness	3.46E-01
LarixBA	PredatoryBeetleRichness	7.62E-01
FagusBA	PredatoryBeetleRichness	5.58E-01
PiceaBA	PredatoryBeetleRichness	5.77E-01
QuercusBA	PredatoryBeetleRichness	8.89E-01
TotalBA	PredatoryBeetleRichness	7.90E-01
TreeDiversity	PredatoryBeetleRichness	3.83E-01
SoilQuality	PredatoryBeetleRichness	2.69E-01
CanopyCover	PredatoryBeetleRichness	9.74E-01
CatalaseActivity	PredatoryBeetleRichness	1.86E-01
UnderstoryHerbRichness	PredatoryBeetleRichness	2.83E-01

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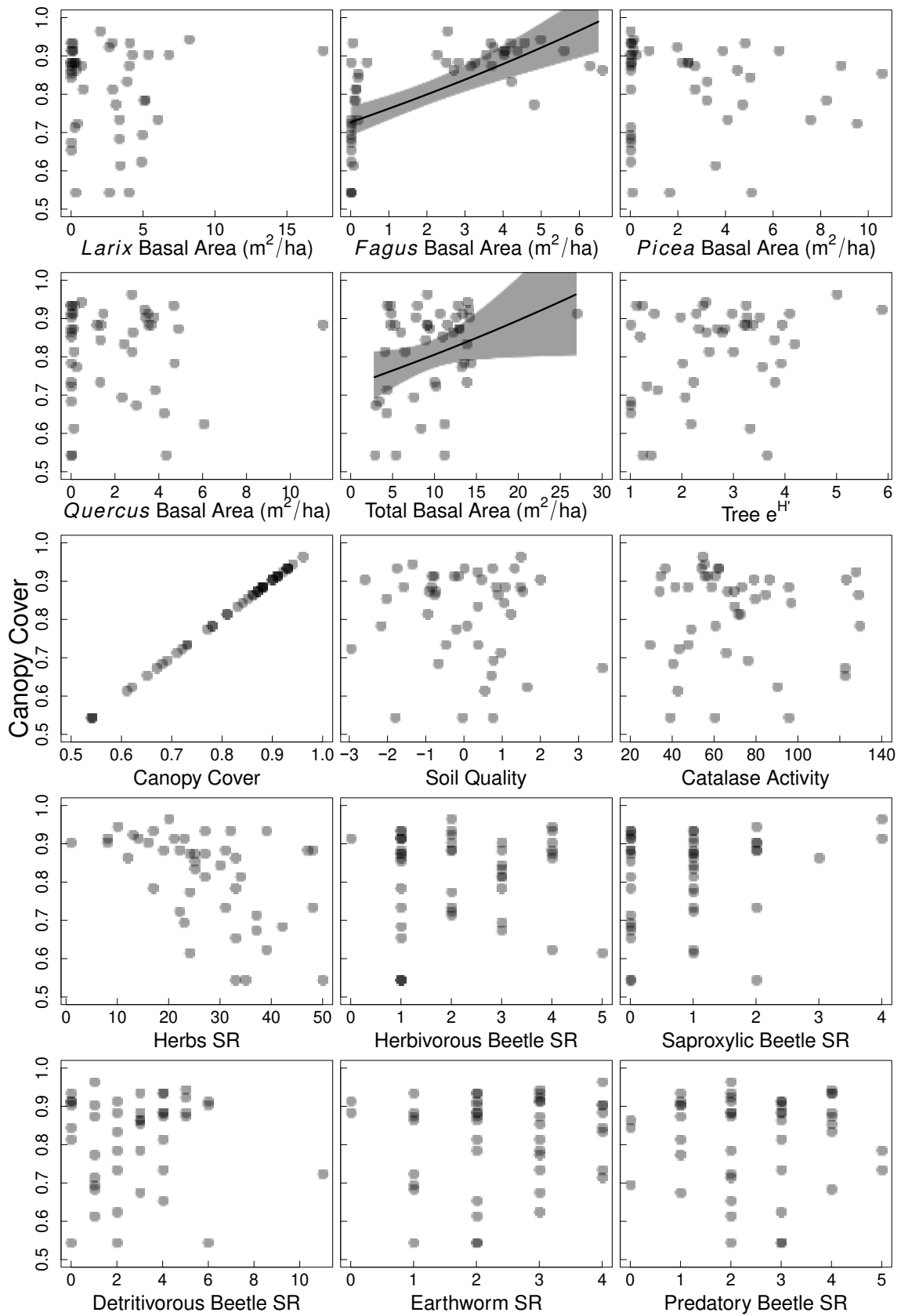
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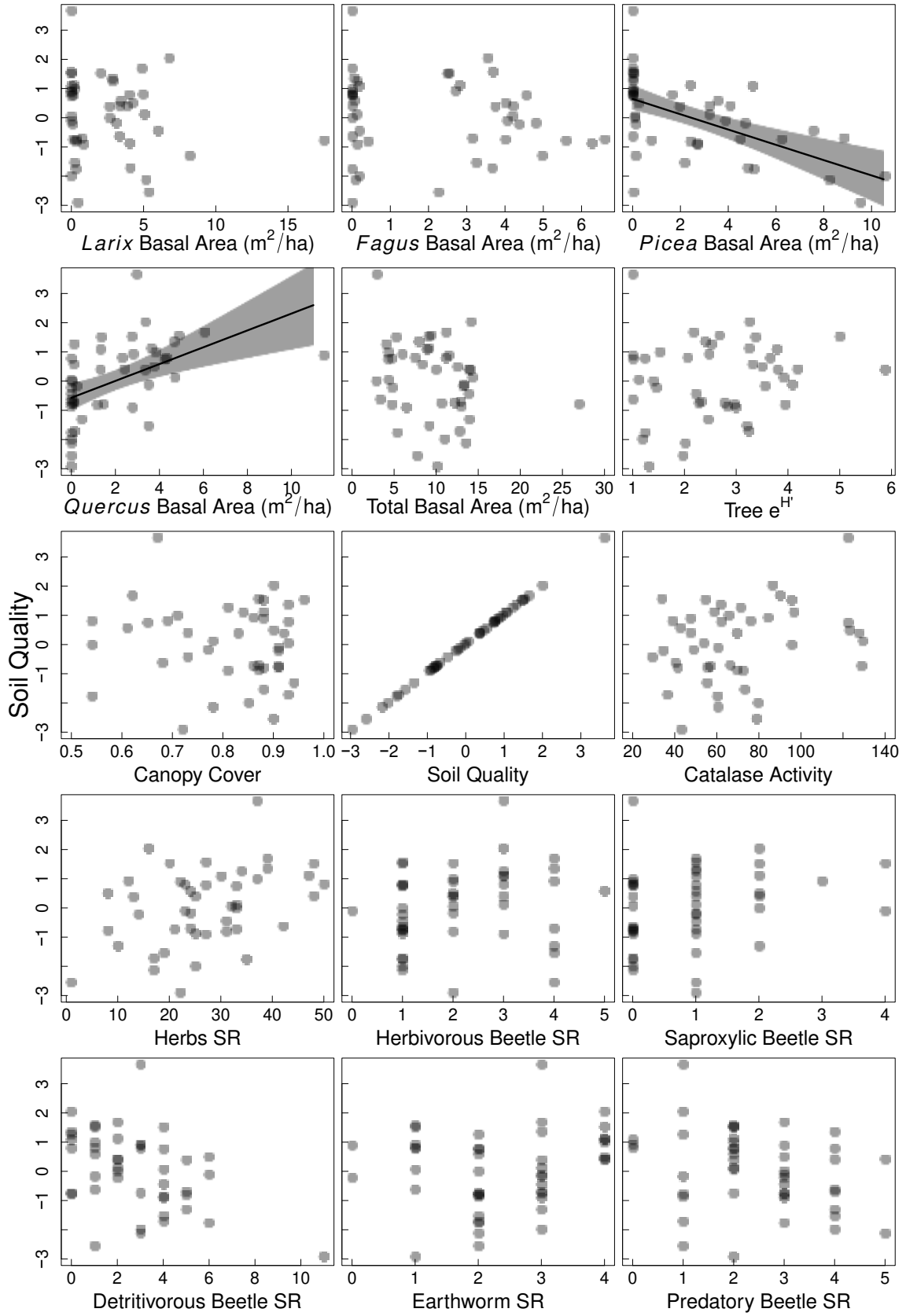
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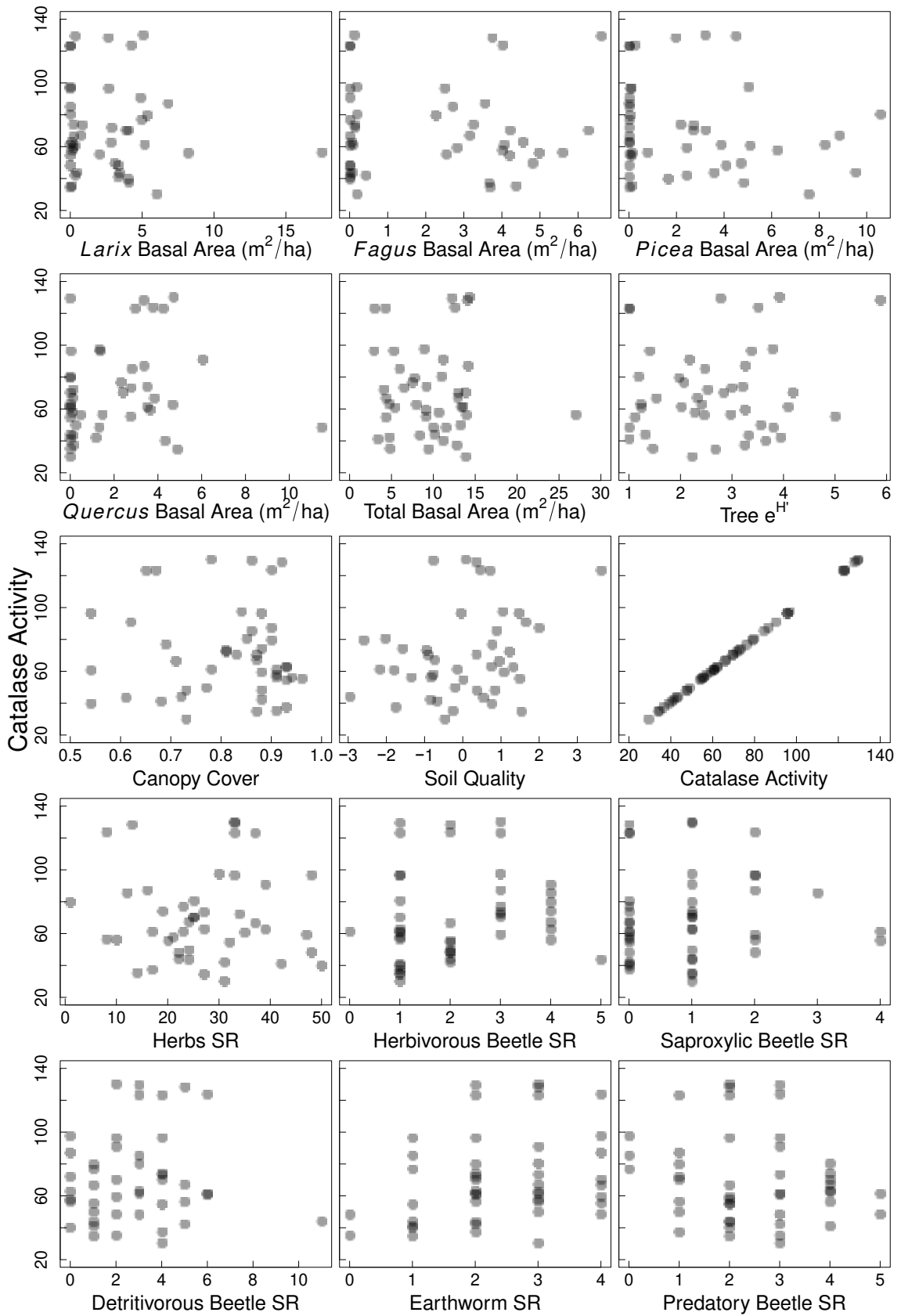
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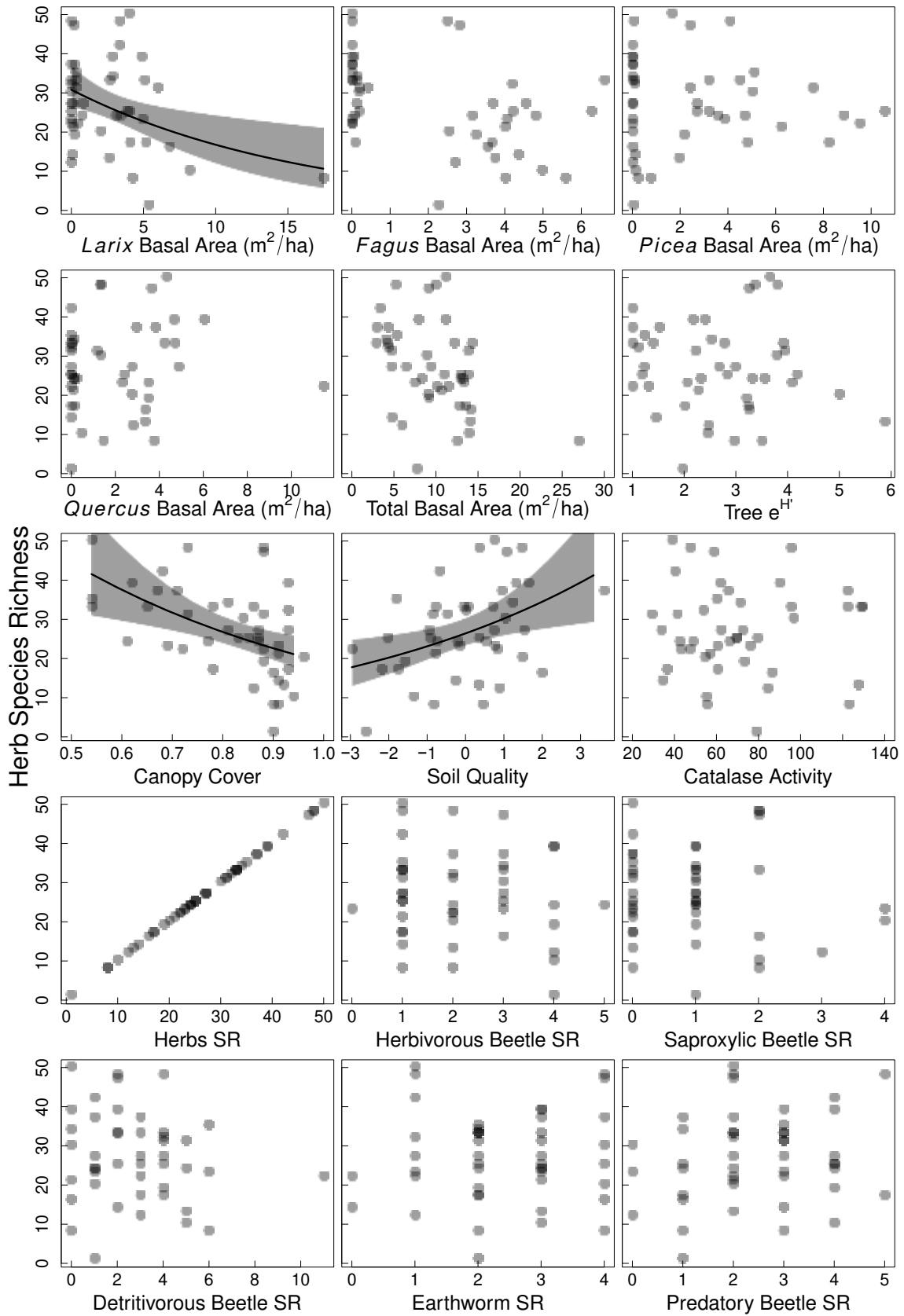
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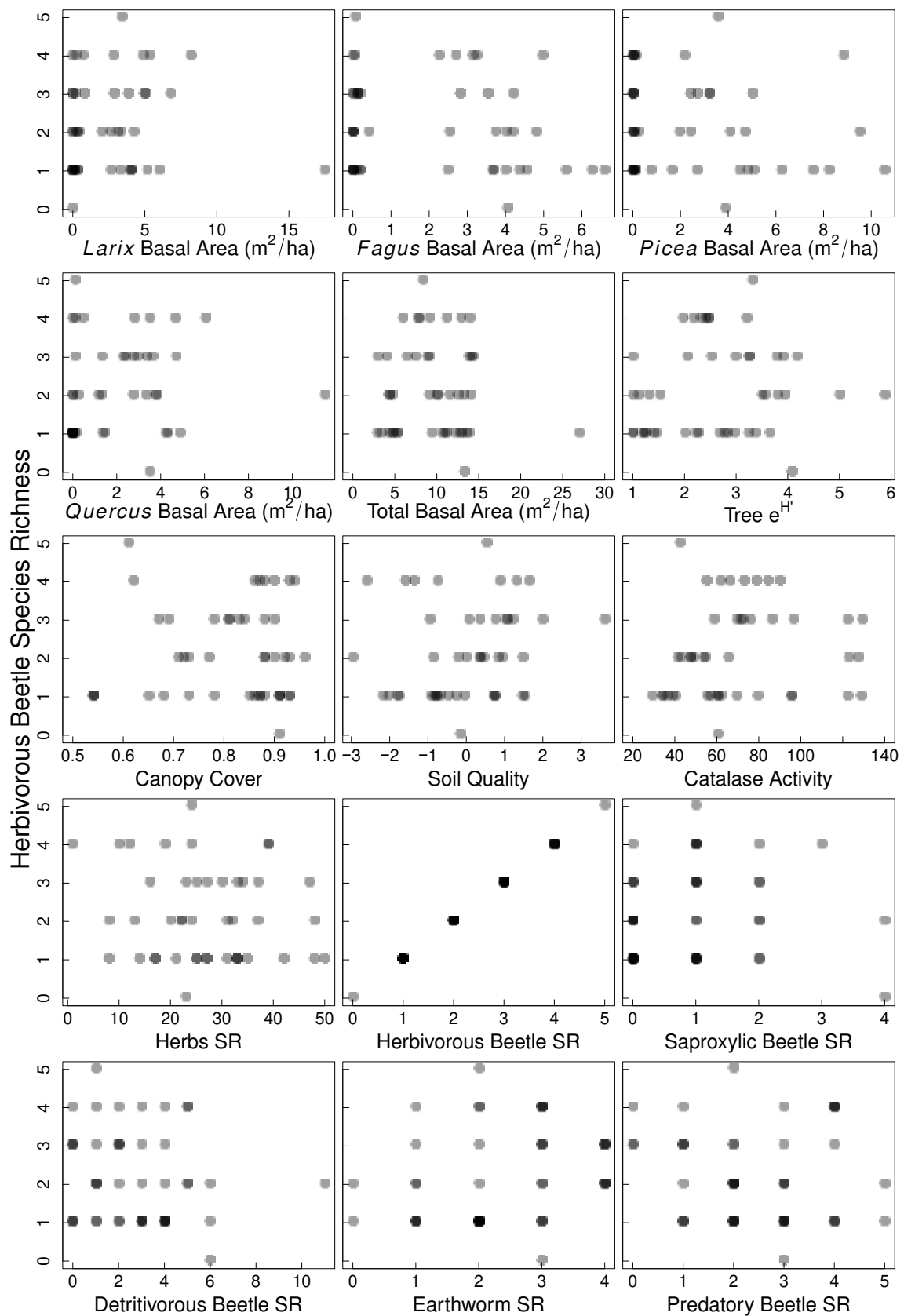
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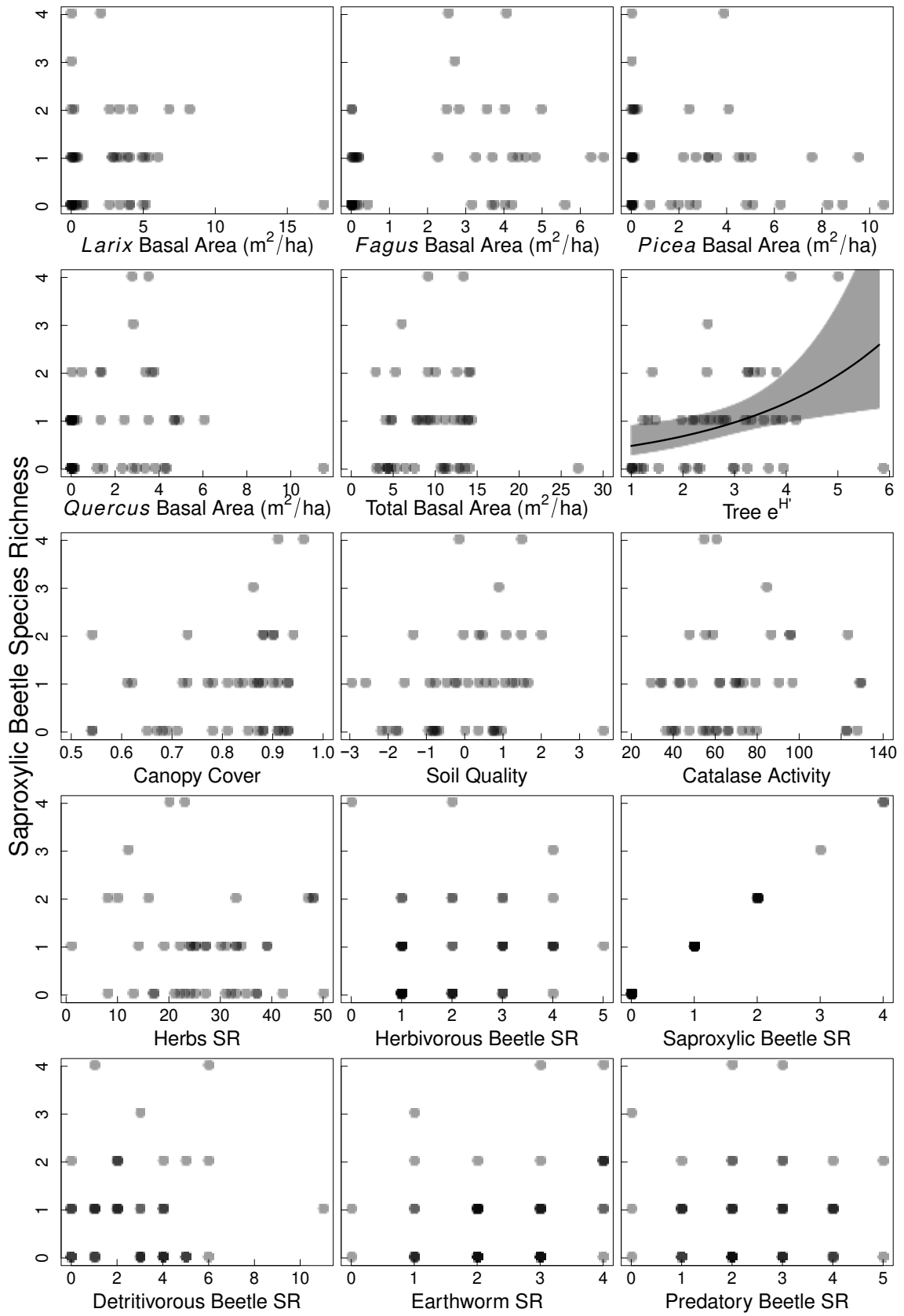
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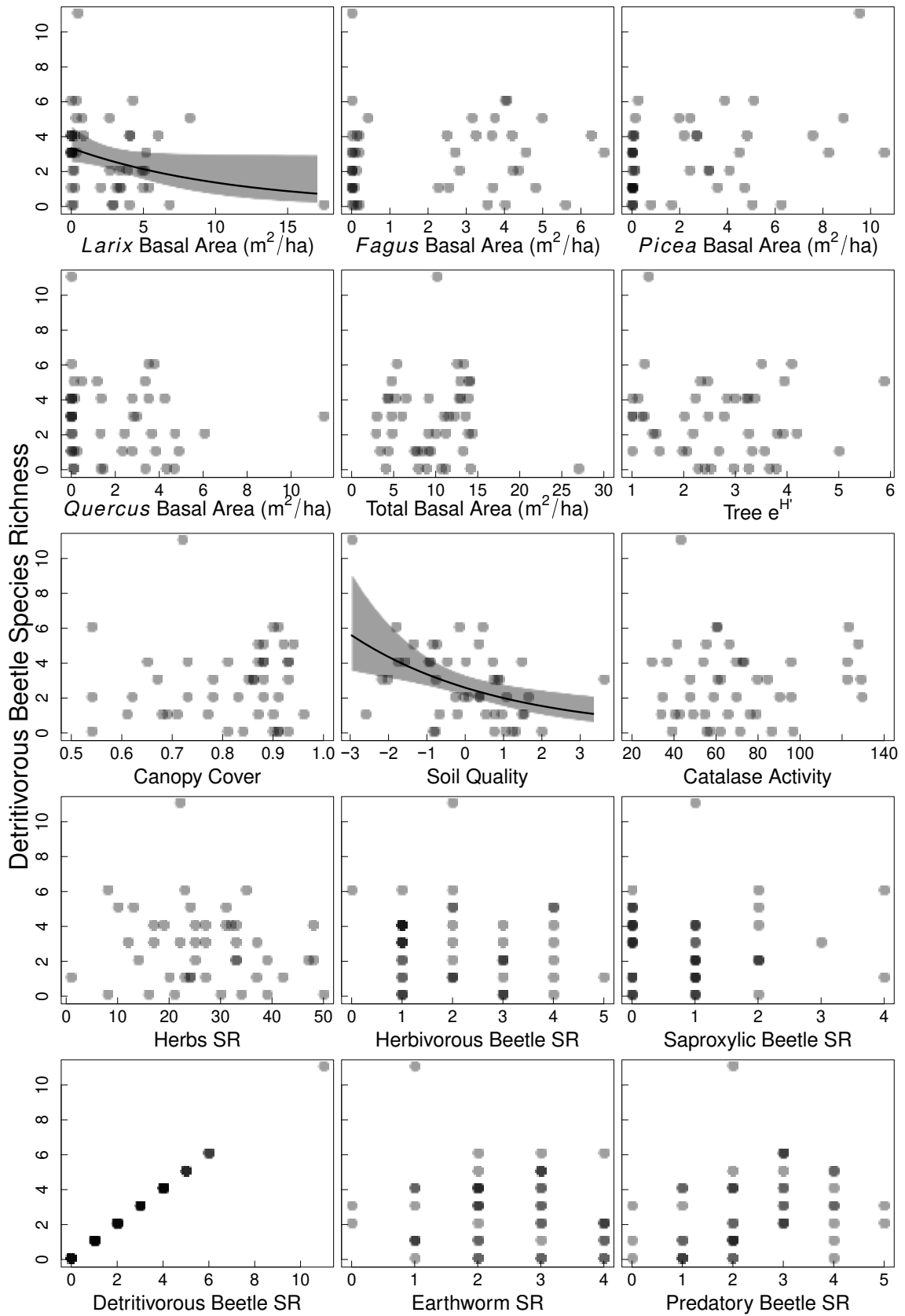
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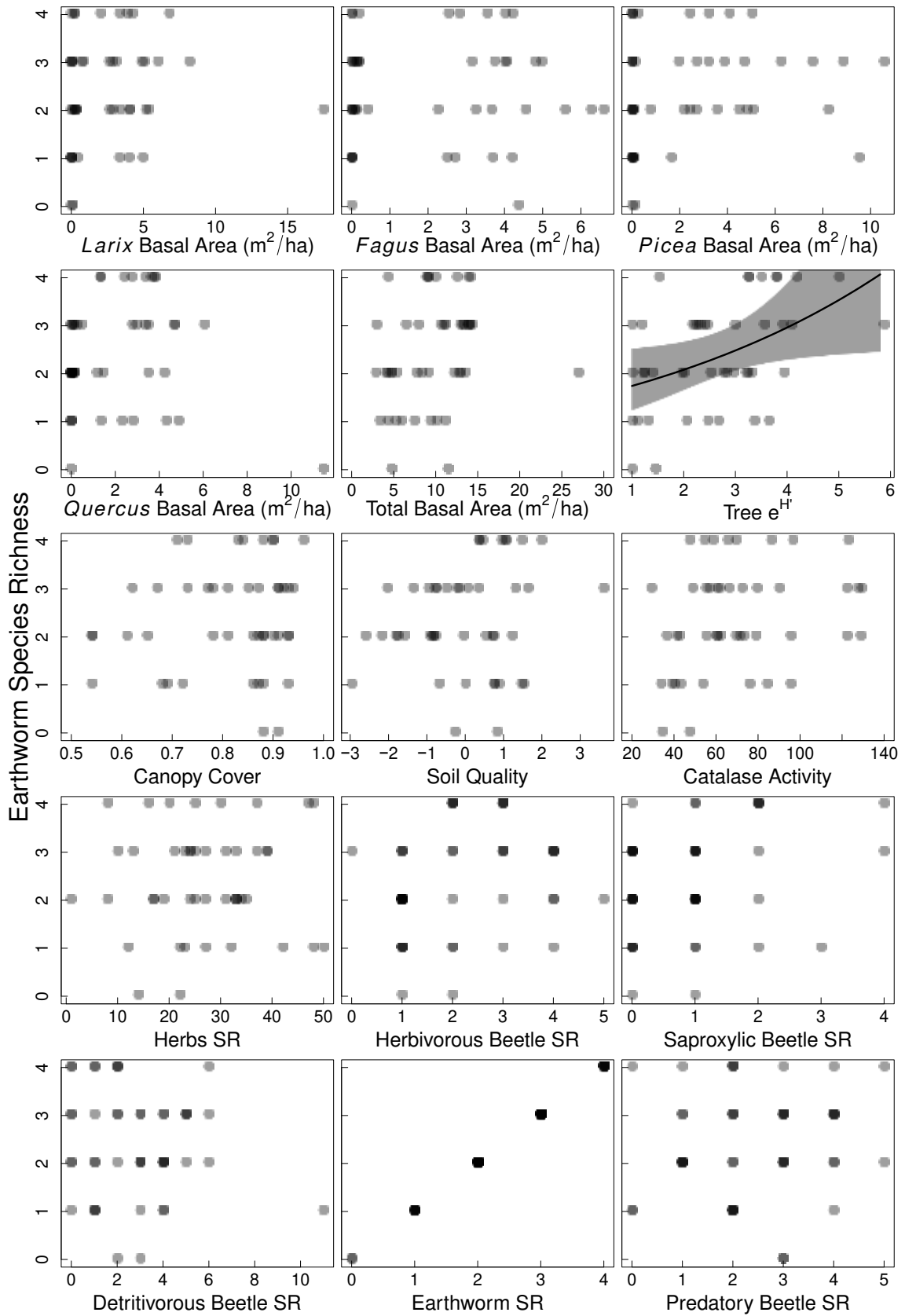
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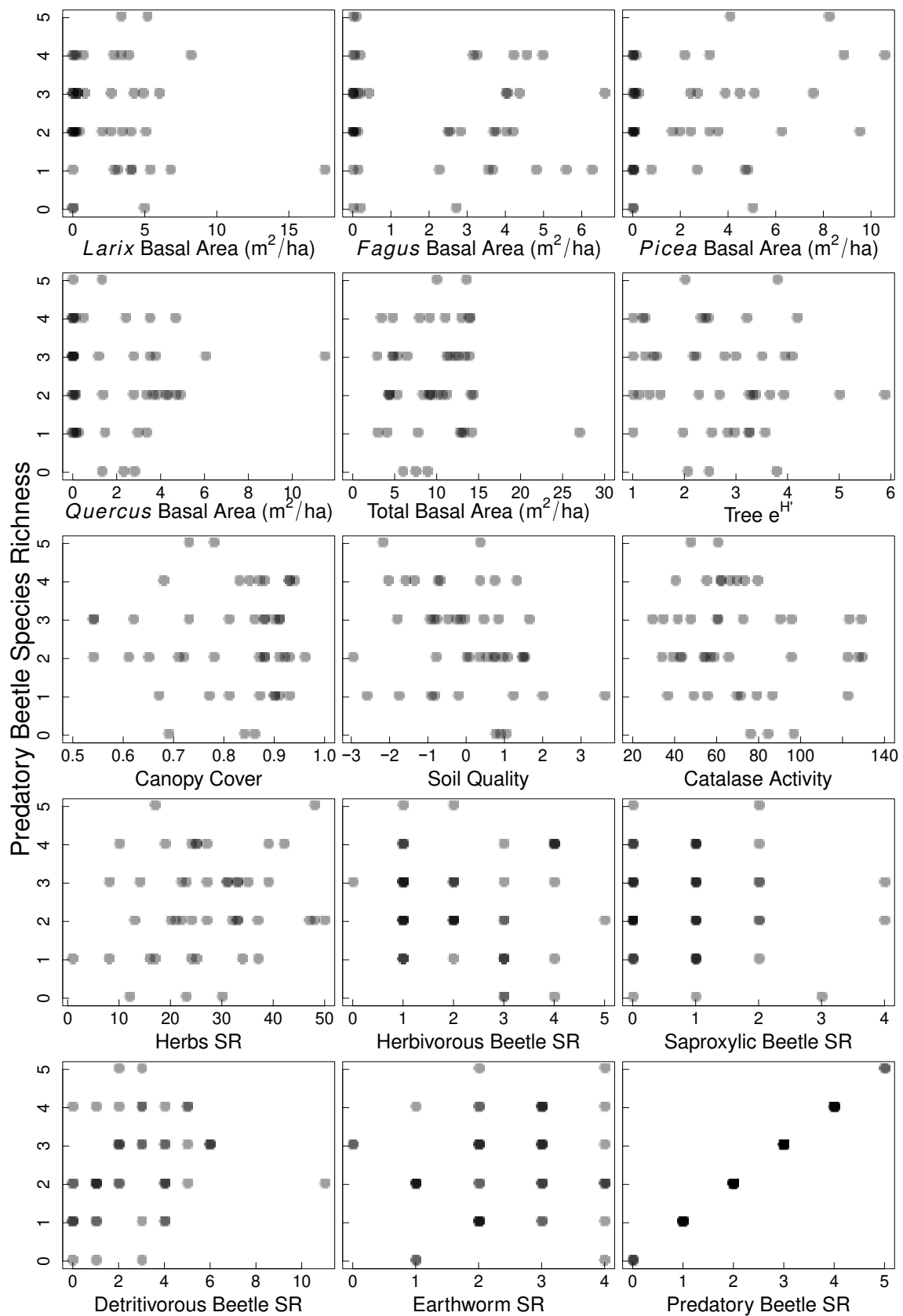
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1 Figure S5 (continued):



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1 Table S6:

Predictor	Response	p-value
LarixBA	SoilQuality	1.47E-01
FagusBA	SoilQuality	3.78E-01
LarixBA	CanopyCover	1.44E-01
PiceaBA	CanopyCover	9.84E-01
QuercusBA	CanopyCover	1.94E-01
LarixBA	CatalaseActivity	6.21E-01
FagusBA	CatalaseActivity	8.93E-01
PiceaBA	CatalaseActivity	2.47E-01
QuercusBA	CatalaseActivity	2.17E-01
TotalBA	CatalaseActivity	8.07E-01
TreeDiversity	CatalaseActivity	4.10E-01
FagusBA	UnderstoryHerbRichness	4.06E-01
PiceaBA	UnderstoryHerbRichness	1.04E-01
QuercusBA	UnderstoryHerbRichness	4.69E-01
TotalBA	UnderstoryHerbRichness	7.20E-01
TreeDiversity	UnderstoryHerbRichness	4.56E-01
LarixBA	HerbivorousBeetleRichness	6.66E-01
FagusBA	HerbivorousBeetleRichness	3.27E-01
PiceaBA	HerbivorousBeetleRichness	3.32E-01
QuercusBA	HerbivorousBeetleRichness	3.52E-01
TotalBA	HerbivorousBeetleRichness	7.38E-01
TreeDiversity	HerbivorousBeetleRichness	4.90E-01
SoilQuality	HerbivorousBeetleRichness	2.96E-01
CanopyCover	HerbivorousBeetleRichness	8.89E-01
LarixBA	SaproxyllicBeetleRichness	5.43E-01
FagusBA	SaproxyllicBeetleRichness	2.59E-01
PiceaBA	SaproxyllicBeetleRichness	8.99E-02
QuercusBA	SaproxyllicBeetleRichness	9.98E-01
TotalBA	SaproxyllicBeetleRichness	3.63E-01
SoilQuality	SaproxyllicBeetleRichness	1.67E-01
CanopyCover	SaproxyllicBeetleRichness	2.64E-01
CatalaseActivity	SaproxyllicBeetleRichness	8.53E-01
FagusBA	DetritivorousBeetleRichness	4.30E-01
PiceaBA	DetritivorousBeetleRichness	9.51E-01
QuercusBA	DetritivorousBeetleRichness	3.67E-01
TotalBA	DetritivorousBeetleRichness	2.70E-01
TreeDiversity	DetritivorousBeetleRichness	4.91E-01
CanopyCover	DetritivorousBeetleRichness	7.80E-01
CatalaseActivity	DetritivorousBeetleRichness	1.18E-01
UnderstoryHerbRichness	DetritivorousBeetleRichness	4.04E-01
LarixBA	EarthwormRichness	7.84E-01
FagusBA	EarthwormRichness	6.57E-01
PiceaBA	EarthwormRichness	3.71E-01
QuercusBA	EarthwormRichness	8.01E-01
TotalBA	EarthwormRichness	6.97E-01
SoilQuality	EarthwormRichness	5.26E-01
CanopyCover	EarthwormRichness	9.03E-01
CatalaseActivity	EarthwormRichness	3.21E-01
UnderstoryHerbRichness	EarthwormRichness	6.69E-01
HerbivorousBeetleRichness	EarthwormRichness	3.46E-01
LarixBA	PredatoryBeetleRichness	5.76E-01
FagusBA	PredatoryBeetleRichness	6.30E-01
PiceaBA	PredatoryBeetleRichness	1.67E-01
QuercusBA	PredatoryBeetleRichness	8.72E-01
TotalBA	PredatoryBeetleRichness	9.73E-01
TreeDiversity	PredatoryBeetleRichness	5.09E-01
SoilQuality	PredatoryBeetleRichness	1.14E-01
CanopyCover	PredatoryBeetleRichness	9.84E-01
CatalaseActivity	PredatoryBeetleRichness	3.08E-01
UnderstoryHerbRichness	PredatoryBeetleRichness	3.42E-01
HerbivorousBeetleRichness	PredatoryBeetleRichness	5.27E-01
SaproxyllicBeetleRichness	PredatoryBeetleRichness	8.70E-01