

1 **Title: Assessing the Utility of SoilGrids250 for Biogeographic Inference of Plant
2 Populations**

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13

14 **Abstract**

15 Inclusion of edaphic conditions in biogeographical studies typically provides a better fit and
16 deeper understanding of plant distributions. Increased reliance on soil data calls for easily
17 accessible data layers providing continuous soil predictions worldwide. Although SoilGrids
18 provides a potentially useful source of predicted soil data for biogeographic applications, its
19 accuracy for estimating the soil characteristics experienced by individuals in small-scale
20 populations is unclear. We used a biogeographic sampling approach to obtain soil samples from
21 212 sites across the midwestern and eastern United States, sampling only at sites where there was
22 a population of one of the 22 species in *Lobelia* sect. *Lobelia*. We analyzed six physical and
23 chemical characteristics in our samples and compared them with predicted values from
24 SoilGrids. Across all sites and species, soil texture variables (clay, silt, sand) were better
25 predicted by SoilGrids (R^2 : 0.25–0.46) than were soil chemistry variables (carbon and nitrogen,
26 $R^2 \leq 0.01$; pH, R^2 : 0.19). While SoilGrids predictions rarely matched actual field values for any
27 variable, we were able to recover qualitative patterns relating species means and population-level
28 plant characteristics to soil texture and pH. Rank order of species mean values from SoilGrids
29 and direct measures were much more consistent for soil texture (Spearman r_s =0.74–0.84; all
30 $P < 0.0001$) and pH (r_s =0.61, P =0.002) than for carbon and nitrogen ($P > 0.35$). Within the species
31 *L. siphilitica*, a significant association, known from field measurements, between soil texture and
32 population sex ratios could be detected using SoilGrids data, but only with large numbers of
33 sites. Our results suggest that modeled soil texture values can be used with caution in
34 biogeographic applications, such as species distribution modeling, but that soil carbon and
35 nitrogen contents are currently unreliable, at least in the region studied here.

36 *Keywords:* Plant species distribution modeling, SoilGrids, Digital soil model, Edaphic niche
37 properties

38

39 **Introduction**

40 Characterizing species distributions in geographic and environmental space can help us
41 understand a species' niche, evolutionary history, and potential for interactions with co-occurring
42 species (Kozak et al., 2008; Elith & Leathwick, 2009; Pollock et al., 2014). One important
43 component of predicting a species distribution is the inclusion of ecologically relevant predictors
44 (Dormann, 2007; Mod et al. 2016). Modeled climate data has a long history of use in ecological
45 modeling but for plant distributions, incorporating soil characteristics can further improve model
46 accuracy (Dubuis et al., 2013; Figueiredo et al., 2013; Thuiller, 2013; Velazco et al., 2017;
47 Zuquim et al., 2020; Roe et al., 2022). The inclusion of soil data has created the need to enhance
48 the quality and availability of data on soil characteristics on a global scale.

49 To incorporate accurate soil data into ecological and biogeographic inference of plant
50 species, soil characteristics would ideally be measured from cores collected at presence points
51 across the full species range. Predictions for soil characteristics derived from digital soil maps
52 may be useful substitutes, reducing the labor and cost of direct soil core analysis at range-wide
53 scales, as well as providing interpolated soil data for areas with limited accessibility (McBratney
54 et al., 2003; Grunwald et al., 2011; Minasny & McBratney, 2016). The International Soil
55 Reference Information Centre (www.isric.org) developed SoilGrids as a global collection of
56 model-predicted soil data for ease of use in a variety of settings, including soil erosion, food and
57 water security, and modeling biodiversity and effects from climate change (Hengl et al., 2014;
58 Poggio et al., 2021). The newest version of SoilGrids combined machine learning, 150,000 soil

59 profiles for training, and 158 environmental covariates to provide global predictions at a scale of
60 250 x 250 m (Hengl et al., 2017). Comparing cross-validation measures, R^2 values ranged from
61 56% (coarse soil fragments) to 83% (soil pH) across different soil variables (Hengl et al., 2017).
62 However, the utility of SoilGrids data needs additional validation for its appropriateness in the
63 development of species distribution models, particularly for low abundance plant species that are
64 moderate habitat specialists.

65 The use of digital soil maps for biogeographic applications comes with clear limitations.
66 First, the accuracy for modeling each soil characteristic varies, such that some soil variables will
67 be more reliable than others (Poggio et al., 2021). Along with issues of model accuracies, there
68 are scaling issues associated with the soil environment. For instance, climatological conditions
69 are likely to be quite similar at the local scale (e.g., 1 km² or smaller), whereas soil conditions
70 can exhibit substantial heterogeneity at much finer scales (Heuvelink & Webster, 2001; Malone
71 et al., 2017). Fine-scale variation in soil characteristics created by microtopography and
72 hydrology would not be captured in 250 x 250 m grid cells, and this is still much larger than the
73 scale experienced by individual plants or even whole populations. Furthermore, SoilGrids does
74 not predict soil conditions at locations with surface water or in cities (Poggio et al., 2021),
75 potentially yielding missing or inaccurate data for wetland and aquatic habitats, even where
76 plants of interest are dominant within the community.

77 To test the utility of SoilGrids specifically for biogeographic inference, we focused on a
78 clade of wildflowers with highly variable geographic distributions and habitat types, including
79 wetland and emergent aquatic species. *Lobelia* sect. *Lobelia* L. (Campanulaceae) is comprised of
80 24 herbaceous species native to North and Central America. Some species are widespread across
81 the eastern United States and Canada, while other species are found in only a few states (Biota of

82 North America, BONAP, Kartesz, 2015; Spaulding & Barger, 2016). This clade provides an
83 opportunity to document potential scaling effects, as species frequently co-occur and appear to
84 be separated into different microhabitat conditions within 250 m (unpub. data). One species,
85 *Lobelia siphilitica* L., permits assessment of how soil conditions relate to trait variation among
86 populations within a species. *Lobelia siphilitica* is comprised of two sexes—females and
87 hermaphrodites—which are readily observable in the field. Females vary dramatically in their
88 frequency among *L. siphilitica* populations, and field data indicate that both population size and
89 population sex ratio vary with soil conditions (Hovatter, 2008; Hovatter et al., 2013).

90 We tested how estimates from SoilGrids compared with soil data collected in the field at
91 sites hosting *Lobelia* populations. The questions addressed here focus on: (1) the accuracy of
92 SoilGrids estimates in habitats occupied by a set of closely related plants and (2) whether
93 modeled soil values from SoilGrids lead to different inferences about species distributions and
94 ecology compared to direct measurements on soils collected *in situ*. First, we determined how
95 soil physical and chemical variables from SoilGrids compare to soil samples collected at sites
96 hosting *Lobelia* populations. Second, we looked for associations between deviations of SoilGrids
97 from measured field data and particular conditions (proximity to a water body or ecoregion).
98 Third, we used two datasets to examine the extent to which SoilGrids data would be useful in
99 understanding the biogeography of *Lobelia*. We collected and analyzed field soil from 22
100 *Lobelia* species at 212 population sites across the midwestern and eastern United States. We
101 compared direct measures of soil characteristics to modeled SoilGrids data to test whether: i)
102 modeled SoilGrids data could predict patterns in average edaphic conditions among 22 *Lobelia*
103 species, and ii) in polymorphic *L. siphilitica*, whether data from SoilGrids could predict
104 relationships between soil conditions and population sex ratios.

105

106 **Materials and Methods**

107 *Soil Field Data*

108 In the summers of 2017 and 2021, we visited a total of 212 populations of 22 *Lobelia*
109 species across the midwestern to eastern United States and Canada (Supplemental Table S1),
110 where we collected soil samples and GPS coordinates. Potential populations were identified from
111 personal communications and using the Southeast Regional Network of Expertise and
112 Collections (SERNEC; 2022). After removing any Oi horizon, soil samples were collected from
113 the top 10 cm of soil underneath individual *Lobelia* plants (five samples per site, or from each
114 plant if there were fewer than five present), which were bulked for analysis by population site
115 and species. Distances between bulked soil samples ranged from 1-30 meters. Population sizes
116 ranged widely by site and species, from single plants to over 1000 individuals. Although most
117 species prefer moist habitats, specific habitat conditions range widely among species and sites,
118 including roadsides, upland forests, bogs, prairies, riparian areas, and near-shore lacustrine
119 habitats (Spaulding & Barger 2016). Soil samples were allowed to air dry before passing through
120 a 2mm sieve, leaving only the fine-earth fractions (sand, silt, and clay). pH was measured using a
121 1:2.5 mass ratio of soil to water. Percent carbon and nitrogen were measured using an elemental
122 analyzer (Costech Analytical, Santa Clarita, USA). For texture analysis, sieved soils were first
123 pretreated with 30% hydrogen peroxide to remove organic matter, and then analyzed using a
124 laser-diffraction particle size analyzer (Mastersizer 2000, Malvern Panalytical, UK). Soil
125 aggregates were added to distilled water and broken up with one minute of ultrasonication. We
126 used a protocol measuring the texture distribution of three subsamples, each of which reached a
127 laser obscuration value between 12-16%, and obtained the mean distribution of subsamples. As

128 laser diffraction measurements underestimate clay and overestimate silt fractions in soil
129 compared to the sedimentation method, we applied a correction factor as described in DiStefano
130 et al. (2010), which was confirmed for our laboratory (Supplemental Figure S1), multiplying the
131 clay fraction 1.9X and subtracting the resulting difference from the silt fraction.

132 *SoilGrids Data*

133 Using population GPS coordinates, SoilGrids250 data were obtained for pH, carbon,
134 nitrogen, and each of the three fine-earth fractions (sand, silt, and clay). The data were accessed
135 directly from the SoilGrids website in December 2022 (Poggio et al. 2021). In some cases, GPS
136 coordinates landed in a grid cell with no SoilGrids data. In these cases, we used the nearest grid
137 cell with data.

138 Because our *in situ* soil samples included the top 10 cm, we averaged SoilGrids layers for
139 the surface horizon (0-5 cm) and the first subsurface horizon (5-15 cm) for our analyses using
140 equal weights for each horizon. The 0-5 cm and 5-15 cm layers were strongly correlated for clay,
141 sand, silt, and pH ($r>0.98$), while the correlation between layers was weaker for nitrogen ($r: 0.8$)
142 and weakest for carbon ($r: 0.5$). To further explore this, we conducted separate regressions
143 comparing the field data with each individual horizon, and the results were similar as the average
144 values (Supplemental Table S2).

145 *Comparison of SoilGrids Predictions to Field-Collected Soil Measurements*

146 To investigate the relationship between SoilGrids data and field-collected data, we conducted
147 linear regressions for each variable using field-collected measurements as the independent
148 variable. We then examined goodness-of-fit measurements (R^2), slopes, root mean squared error
149 (RMSE), and mean bias error (MBE) to determine agreement between SoilGrids predictions and
150 observations obtained in the field. RMSE and MBE are expressed in the same units as the

151 response variable (here, SoilGrids values). RMSE is used in comparing measured values with
152 predicted values by using the square root of the sum of the squared residuals of the model. MBE,
153 on the other hand, calculates the mean of the residuals and indicates whether variables are under-
154 or over-predicted.

155 *Investigating Environmental Correlates of Deviations between Field and Modeled Data*

156 The difference between measured and modeled values were calculated by subtracting SoilGrids
157 values from field values. We then tested for associations between these SoilGrids-measured
158 differences and two environmental variables: proximity of the sample site to water bodies and
159 ecoregion designation. Some GPS coordinates for populations near water bodies had no
160 corresponding data from SoilGrids due to issues like shifting boundaries of water bodies. Sites
161 close to water bodies may also be affected by flooding and hydrology that vary over small scales
162 (i.e., a few meters). Thus, we tested whether the distance of a population to a water body affected
163 the magnitude of SoilGrids-measured differences. Water body data were obtained from the
164 National Hydrography Dataset managed by the United States Geological Survey (USGS, 2019).
165 We used QGIS 3.6 to determine the distance a population point was from the nearest body of
166 water (QGIS, 2019). Linear regressions were used to investigate whether larger SoilGrids-
167 measured differences were associated with distance to the nearest water body.

168 We also used ecoregions to see if SoilGrids-measured differences were associated with
169 our sampling points being embedded in any particular habitat conditions. Data on ecoregions
170 were obtained from the US Environmental Protection Agency (US EPA, 2022; Omernik, 1987;
171 Omernik & Griffith, 2014). We conducted the analyses using level-2 ecoregions because many
172 sampled populations fell into a single category of level-1 ecoregions (eastern temperate forests;
173 Supplemental Table S2). To test for significant differences in SoilGrids-measured differences

174 across ecoregions, we used the non-parametric Kruskal-Wallis one-way ANOVA followed by
175 the Steel-Dwass pairwise comparison method that controls for multiple comparisons and is
176 robust to imbalanced sampling (Morley, 1982; Neuhäuser & Bretz, 2001).

177 *Inferring Ecological Relationships Between Soil Conditions and Lobelia Species*

178 The utility of SoilGrids data for inferring soil conditions at *Lobelia* population sites was tested
179 using two approaches. First, for each of 22 *Lobelia* species, we calculated the mean and standard
180 error of field soil measurements and SoilGrids modeled data for each soil characteristic. Species
181 were then ranked by mean field soil measurement to determine whether the ranking according to
182 SoilGrids data would be consistent with measured habitat values. This procedure was used to see
183 if SoilGrids could capture ecologically relevant but very broad, qualitative characteristics of the
184 dataset without influence of outliers or noise introduced by individual site data. Congruence of
185 species ranks was assessed by a Spearman rank correlation test (Spearman correlation shown
186 below as r_S).

187 Second, to compare how SoilGrids and field-collected data associated with *L. siphilitica*
188 population sex ratios, we conducted Spearman rank tests between each soil characteristic and the
189 percent females in a population. This dataset was confined to 30 populations for which we had
190 obtained both soil samples and population sex ratios for *L. siphilitica*. Sex ratios were calculated
191 by sexing and counting all female and hermaphrodite plants at each site and are reported here as
192 the percent of all censused plants that were female. In a second analysis, we used an expanded
193 set of population sex ratios at 195 sites where *L. siphilitica* sex ratios and GPS coordinates had
194 been recorded *in situ*, but no physical soil samples were available. This latter analysis was done
195 to determine whether the associations between population female frequency and soil
196 characteristics known from empirical measurements (n=30) could be recovered by using

197 modeled SoilGrids variables with an increased sample size. As sex-ratio data are non-normally
198 distributed, we used Spearman rank tests. All statistics were calculated using JMP Version 14
199 (JMP Statistical Discovery, SAS, 2019). Soil data was extracted using QGIS 3.6 (QGIS, 2019).

200 **Results**

201 *Accuracy of SoilGrids—Soil Physical Characteristics*

202 The estimated particle-size fractions from SoilGrids were all positively correlated with the
203 corresponding measurement from field-collected soils (Fig. 1). Of the three texture variables
204 analyzed, the weakest relationship was in the clay fraction (Fig. 1a, R^2 : 0.25). Silt fractions and
205 sand fractions showed relatively strong relationships between SoilGrids predictions and field-
206 collected data (Figs. 1b & 1c, R^2 : 0.42 & 0.46, respectively). Clay and silt fractions tended to be
207 over-estimated, as many of the data points fell above the 1:1 line (MBE: 8.5% and 12.3%,
208 respectively; Fig. 1). Sand fractions were under-estimated, with most points falling below the 1:1
209 line (MBE: -21%). Overall, SoilGrids texture predictions were most accurate for soils with
210 relatively high clay and silt but low sand (closest to the 1:1 line in Fig. 1).

211 *Accuracy of SoilGrids—Soil Chemical Characteristics*

212 The soil pH from field-collected soils had a weak, positive relationship with SoilGrids pH
213 predictions (Fig. 1d, R^2 : 0.19). The range of SoilGrids pH values was much smaller (ranging
214 from 4.4 to 6.6) than for field soils (ranging from <4 to >8). SoilGrids tended to over-estimate
215 pH for soils with pH below 5 and under-estimate pH above 5.

216 For nitrogen and carbon, there was no relationship between field data and predicted data
217 from SoilGrids (Figs. 1e & 1f, R^2 : < 0.01, and R^2 : 0.01, respectively). The relationship was not
218 improved by removing outliers (identified using the quantile range method in JMP), or
219 examination of carbon to nitrogen ratio (R^2 : < 0.01).

220 *Investigating Environmental Correlates of Variation between Field and Modeled Data*
221 The distance to the nearest water body did not account for discrepancies between field and
222 SoilGrids data for any of the soil variables analyzed ($P > 0.4$ for each variable). Across
223 ecoregions, we found significant differences for all variables of interest (Supplemental Figure
224 S2). Of note is that mean carbon SoilGrids-measured differences can either be positive or
225 negative depending in which ecoregion the soil core was collected. The SoilGrids-measured
226 differences for nitrogen were lowest in the southeast USA plains (Supplemental Figure S2 panel
227 e). However, even when conducting linear regression using only the southeast USA plains
228 populations, the relationship for nitrogen concentration in the field and predicted from SoilGrids
229 was still not significant ($R^2 < 0.01$).

230 *Inferring Ecological Relationships Between Soil Conditions and Lobelia Species*
231 Comparing the rank order of the *Lobelia* species, the SoilGrids predictions do not mirror ranks
232 based on field-collected data. Comparisons for sand, pH, and nitrogen (Fig. 2) illustrate strong,
233 medium, and weak correlations between predictions and field data. Spearman correlation tests
234 indicate that the rankings of species means are significantly related for soil texture (clay $r_s=0.74$,
235 silt $r_s=0.79$, sand $r_s=0.84$; all $P < 0.0001$) and pH ($r_s=0.61$, $P=0.002$). However, while rankings of
236 species means may be partially consistent, SoilGrids species means do not often reflect true field
237 values. For example, species that affiliate with alkaline soil pH show highly underestimated soil
238 pH means from modeled SoilGrids data (e.g., *L. siphilitica* soils have a mean pH of 7.0 but the
239 SoilGrids estimate is 5.6). In contrast to soil texture and pH, species means for soil C and N
240 calculated from SoilGrids data appear to be completely unrelated to values measured from the
241 field (carbon $r_s=0.21$ $P=0.35$; nitrogen $r_s=-0.06$ $P=0.79$).

242 The relationships between SoilGrids data and *L. siphilitica* sex ratios did not match
243 relationships between field data and sex ratios (Table 1). Using field data from 30 population
244 sites, percentage of females in a population was positively associated with clay content and
245 negatively associated with sand content. Silt and pH showed no relationship with the percent of
246 females in a population. Using SoilGrids predictions for these same 30 populations, no
247 associations were significant, but clay content and pH were marginally positively associated with
248 female percentage ($P<0.1$). When expanding the sample to 195 populations with known sex
249 ratios, the association of modeled SoilGrids clay and sand content became significant, better
250 matching the results from the empirical dataset based on direct measures of both soil and female
251 frequency at 30 population sites.

252 **Discussion**

253 Plant distributions are commonly constrained by soil properties (e.g., nutrient availability
254 and water holding capacity), making digital soil maps a potentially valuable resource for
255 improving plant species distribution mapping, forecasting, and making inferences about plant
256 species' niches (Mod et al. 2016; Velazco et al., 2017; Zuquim et al., 2020; Roe et al. 2022). In
257 this study, we explored the utility of SoilGrids for investigating biogeographic patterns within
258 and among species using soil samples from 212 *Lobelia* population sites representing a broad
259 range of habitats. Most datasets that have been used to evaluate SoilGrids predictions are derived
260 from random or systematic soil sampling distributed across a geographic area of interest (Tifafi
261 et al. 2018; Caubet et al., 2019; Cramer et al. 2019; Liang et al. 2019; Dharumarajan et al. 2021;
262 Bodenstein et al., 2022; Dandabathula et al., 2022; Huang et al., 2022; Radočaj et al. 2023). Our
263 test incorporated constraints that are inherent in 'presence' datasets for modeling the
264 distributions of individual species (Jeliazkov et al. 2021). Our study organisms determined the

265 locations of soil sampling sites, introducing constraints on the specific types of habitats sampled
266 and their distribution across the landscape.

267 Of the six soil variables predicted by SoilGrids, soil texture variables (percent sand, silt,
268 and clay) were most similar to measurements taken on field samples. pH values showed a poor
269 but significant relationship, and soil carbon and nitrogen predictions did not correspond with
270 direct measurements at all. Although the slopes of these relationships were significantly different
271 from 1.0, our analysis indicates that certain SoilGrids variables may be of some usefulness for
272 biogeographic analyses. For example, when comparing edaphic conditions among species,
273 texture and pH may provide a broad indication of species rank-orders, albeit not actual field
274 values. In our analysis of *L. siphilitica* population sex ratios, we also found that noise in
275 predicted soil texture variables may be overcome by increasing sample size, potentially revealing
276 similar associations as those found using a smaller dataset (Table 1). Although not directly tested
277 in this study, the lack of fit between predicted and actual values is likely to be even greater when
278 population presence information is taken from online databases (e.g., GBIF) rather than taken *in*
279 *situ*, as error rates in location data tend to be extremely high across taxa (Zizka et al., 2020).
280 Overall, our results indicate that caution should be exercised, but that using predicted data from
281 SoilGrids may still be helpful in generating hypotheses about the importance of soil texture and
282 pH in species biogeography, as long as the number of accurate presence points is sufficient.
283 *Use of SoilGrids in Ecological Inference and Statistical Modeling*
284 Our results have important consequences for using SoilGrids to assess variable
285 importance in constructing species distribution models, mapping habitat suitability, and revealing
286 ecological relationships. Even in cases where modeled predictor variables have a decent
287 relationship with underlying true values (e.g., best shown here for soil texture variables), error in

288 predictor variables leads to lack of statistical power and biased parameter estimates and
289 projections. In some cases, it may be possible to reduce the effects of predictor-variable
290 uncertainty by taking advantage of spatial autocorrelation and joint species distributions, or by
291 statistically propagating known variance in predictor values as part of the SDM (McInerny and
292 Purves 2011, Stoklosa et al. 2015). The latter methods may prove useful and should be explored
293 further for SoilGrids data because the database provides a measure of model prediction
294 uncertainty (Poggio et al. 2021).

295 Problems using SoilGrids variables are likely to remain particularly acute for several
296 common situations. Mismatches between grain size resolution of predictor variable estimates and
297 the scales at which individual organisms or populations respond to the environment are known to
298 be problematic (Moulatlet et al. 2017, Moudry et al. 2023). As shown here, even the 250m
299 SoilGrids predictions may not be fine enough resolution to use with species that have small
300 population sizes or species that specialize on soil types that either occur on a small scale or are
301 difficult to predict using a digital soil model.

302 In addition, if true conditions are poorly reflected by interpolated predictor variables,
303 SDMs can provide misleading inferences, even in cases where algorithms generate a model with
304 high predictive accuracy (Smith and Santos 2020). We found that SoilGrids frequently failed to
305 predict values that are extreme but not uncommon in soils, or predicted extreme values in
306 incorrect locations. For instance, the extremely low variation in pH estimates from SoilGrids is
307 likely to result in reduced discrimination among sites and lower weighting in a SDM, whereas
308 the increased variation in soil N will likely result in misleading predictions and variable
309 importance. The exceptionally narrow range of soil pH values predicted by SoilGrids at our

310 sampling sites compared to measured values (as well as in Cramer et al. 2019) is particularly
311 problematic given its importance as a driver of variation in nutrient and biotic soil properties.

312 *Comparison to Other SoilGrids Validation Studies*

313 Despite our biogeographically focused sampling design, our results are broadly similar to
314 previous studies that used systematic or random sampling to assess the accuracy of SoilGrids
315 over larger landscape scales. SoilGrids predictions of texture data appear more reliable than
316 predictions of soil carbon and nitrogen, and silt and sand have stronger relationships than clay,
317 including in the cross-validation performed on the newest iteration of SoilGrids (Poggio et al,
318 2021). Because the United States contains many soil cores that were used as training data for the
319 SoilGrids algorithm, our study assessed the accuracy of SoilGrids under a favorable scenario,
320 compared to regions with limited training data. The relationships for soil texture found here were
321 similar to those reported in France (Caubet et al., 2019), another area with high density of
322 training data. Results in regions with fewer training points are more variable: no relationships
323 were found between SoilGrids texture predictions and field textures in Norway or Croatia
324 (Huang et al., 2022; Radočaj et al. 2023), whereas results in arid regions in India were similar to
325 what we observed here (Dandabathula et al., 2022). This suggests that biases or noise in
326 SoilGrids predictions of soil texture may be related to regional differences in drivers of soil
327 texture variation rather than the density of training data. Indeed, based on our comparison of the
328 clay fraction, there may be certain ecoregions where SoilGrids predictions would be more
329 suitable for use (e.g., the Ozark/Ouachita Appalachian forests and southeastern USA plains).

330 Although valuable in global analyses and modeling, the SoilGrids estimates of soil
331 carbon stocks are often found to be inaccurate when compared to direct measurements. We
332 found a very poor relationship between direct measurements of soil carbon and nitrogen contents

333 and estimates in SoilGrids. This finding resembles several other studies finding essentially no
334 relationship ($R^2 < 0.15$) between SoilGrids250 carbon values and independent regional datasets
335 generated using non-biogeographic sampling approaches in China (Liang et al. 2019) and
336 Western Ghats, India (Dharumaranjan et al. 2021). Somewhat better results have been obtained in
337 southern Africa (Cramer et al. 2019; Bodenstein et al., 2022) and European countries (Tifafi et
338 al. 2018), but these analyses still suggest that extreme caution must be used in using point
339 estimates from SoilGrids as an indicator of soil carbon at any particular location. In addition to
340 limited utility in biogeographic modeling, this may also explain the consistent overestimation of
341 regional carbon stocks by SoilGrids (Liang et al. 2019, Silatsa et al. 2020, Duarte et al. 2022).

342 *Conclusions*

343 The importance of suitable soil characteristics in determining plant species presence
344 motivates the use of digital soil predictions for species distribution modeling. Our sampling
345 scheme represents a best-case scenario for assessing the accuracy of SoilGrids in modeling the
346 environmental conditions associated with widespread, low-abundance plant species, but we
347 recommend that extreme caution must be used even under these circumstances. Our findings
348 confirm that soil texture variables are often better predicted than chemistry variables, with two
349 additional insights. First, our analysis of *L. siphilitica* sex ratios indicated that having a sufficient
350 number of precise sampling locations appears to be more important for enhancing signal-to-noise
351 than having a higher density of training points within a region. Second, while SoilGrids estimates
352 may not reflect actual field values, rank ordering of mean species values may be somewhat
353 reliable from predicted data. Soil texture may be easier to predict because it varies more
354 gradually over time and space compared to chemical properties, which can be extremely
355 dynamic, especially with changes in land use (Guo and Gifford, 2002). Incorporating additional

356 drivers of soil properties (e.g., disturbance, edge effects) into digital soil models may be helpful
357 in improving accuracy of chemical predictions and increase reliability of modeled soil data for
358 uncovering biogeographic patterns.

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368 **Author Contributions**

369 John Miller: conceptualization (equal); data curation (lead); formal analysis (lead); investigation
370 (lead); methodology (equal); software (lead); validation (equal); visualization (equal);
371 writing – original draft preparation (lead); writing – reviewing and editing (equal).

372 Christopher Blackwood: conceptualization (equal); formal analysis (supporting); funding
373 acquisition (equal); investigation (supporting); methodology (equal); resources
374 (supporting); software (supporting); validation (supporting); visualization (equal); writing
375 – original draft preparation (supporting); writing – reviewing and editing (equal).

376 Andrea Case: conceptualization (equal); data curation (supporting); formal analysis (supporting);
377 funding acquisition (equal); investigation (supporting); methodology (supporting);

378 project administration (lead); supervision (lead); validation (equal); visualization (equal);
379 writing – original draft preparation (supporting); writing – reviewing and editing (equal).

380 **Competing Interests Statement**

381 The authors of this manuscript declare that there are no competing interests.

382 **Data Accessibility Statement**

383 The raw data and figures are available to download through Open Science Framework:

384 https://osf.io/wf3ad/?view_only=a91dfa7c9d874776abb0df3396285435

385 **Supporting Information**

386 Supplemental Figure S1: Relationship between clay values obtained from the laser diffraction
387 method (Malvern) and from the sieve hydrometer method (hydrometer)

388 Supplemental Figure S2: Comparing SoilGrids-measured differences across ecoregions

389 Supplemental Table S1: Population locations and species information

390 Supplemental Table S2: Ecoregions used in the current study

391

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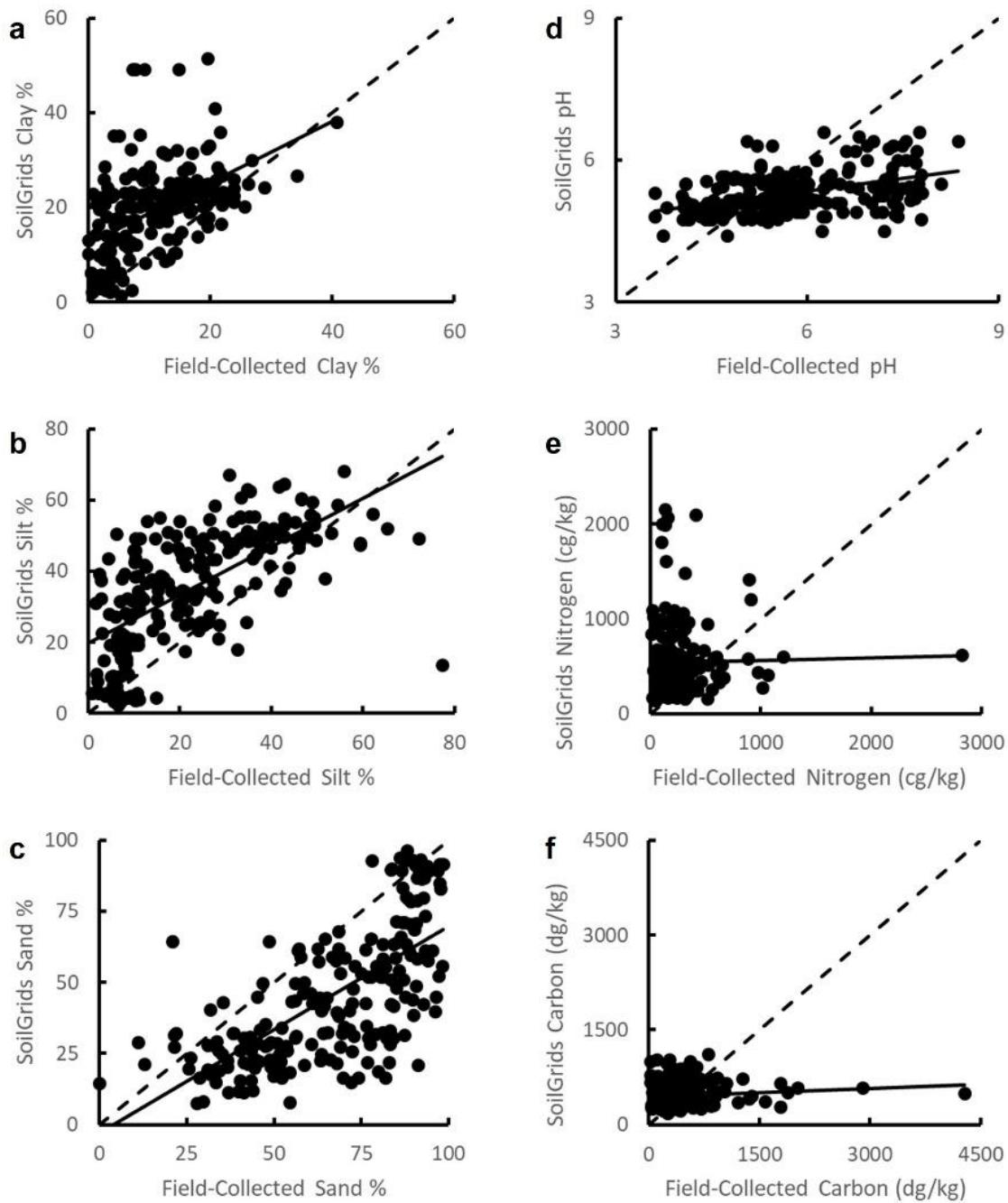
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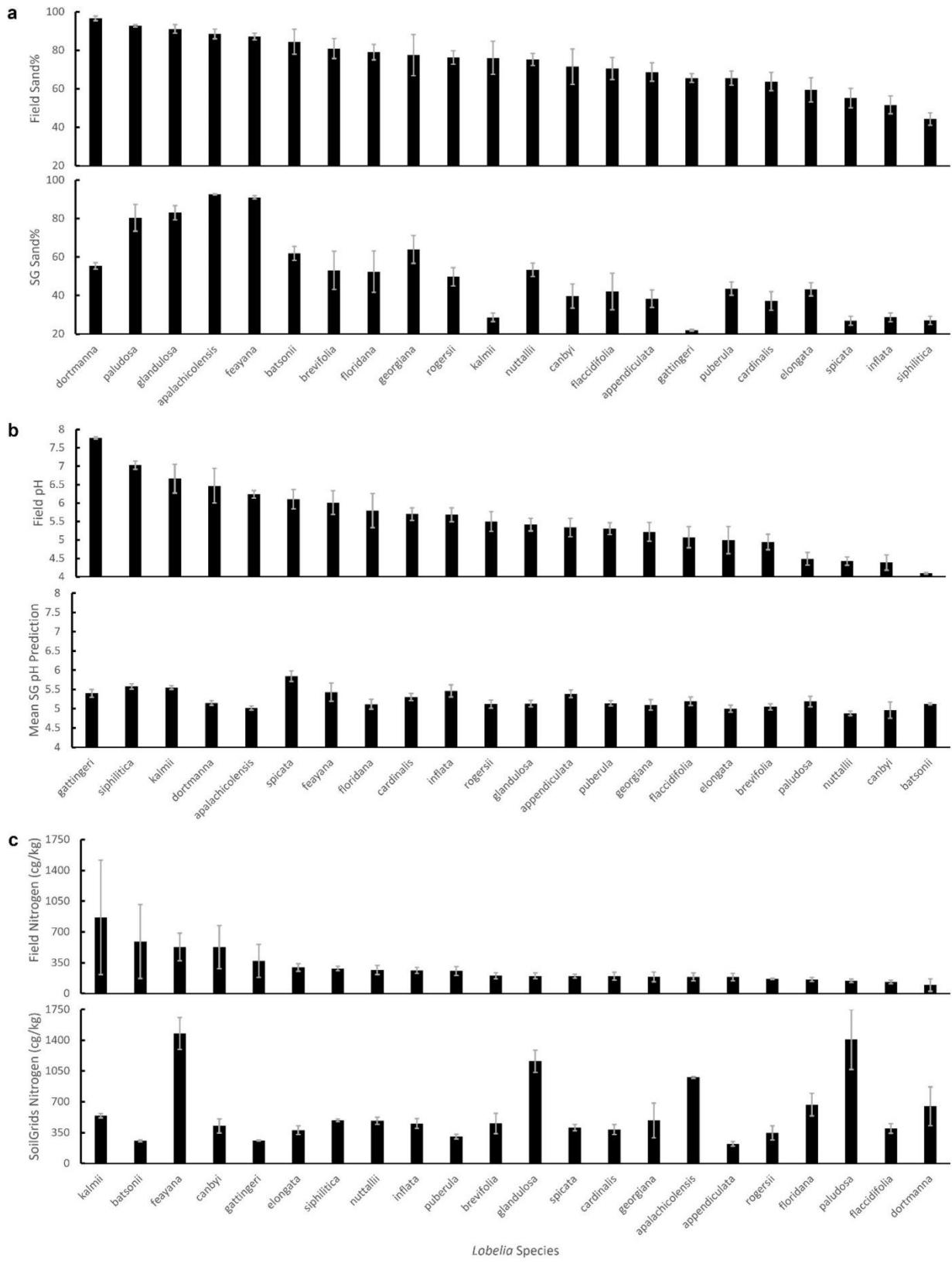


534

535 **Figure 1. Relationships between field-collected soil measurements and predicted soil**
 536 **measurements from SoilGrids.** Solid lines represent relationships between the field-collected
 537 data with the SoilGrids predicted data. Dashed lines represent a 1:1 line, which would be
 538 expected if the field collections and predictions have perfect agreement. (a) clay ($R^2: 0.25$;

539 Slope: 0.65 +/- 0.08; $P < 0.01$; RMSE: 12; MBE: 8) **(b)** silt (R^2 : 0.42; Slope: 0.67 +/- 0.05; $P <$
540 0.01; RMSE: 18; MBE: 12) **(c)** sand (R^2 : 0.46, Slope: 0.73 +/- 0.05; $P < 0.01$; RMSE: 28; MBE:
541 -21) **(d)** pH (R^2 : 0.19; Slope: 0.17 +/- 0.02; $P < 0.01$; RMSE: 1.1; MBE: -0.45) **(e)** nitrogen (R^2 :
542 0.0004; Slope: 0.030 +/- 0.1; $P = 0.07$; RMSE: 525; MBE: 280) **(f)** carbon (R^2 : 0.01; Slope:
543 0.044 +/- 0.03; $P = 0.13$; RMSE: 472; MBE: 19)

544



546 **Figure 2 Comparing ranked species means derived from field-collected soil measurements**
547 **and SoilGrids predictions.** The top graph within each panel shows the mean (\pm standard error)
548 of measurements on field-collected soil ranked in order from highest to lowest on the x-axis. The
549 bottom graph within each panel shows the mean (\pm standard error) of SoilGrids predictions for
550 the variables, while maintaining the same order on the x-axis to compare ranks. (a) % Sand ($r_s =$
551 0.84) (b) pH ($r_s = 0.61$) (c) % Nitrogen ($r_s = -0.06$)

552

553 **Table 1** Associations of population sex ratios of *L. siphilitica* with soil data collected from
 554 the field *versus* predicted from SoilGrids. Spearman's correlation (r_s) and p-values are
 555 provided for assessing the relationship between the proportion of females within populations and
 556 field-collected soil samples (A) or SoilGrids predictions (B,C). Significant relationships are
 557 shown in bold. A. Field data from 30 populations where soil samples and sex ratios were both
 558 collected. B. Data from SoilGrids predictions for the same 30 populations as in A. C. Data from
 559 SoilGrids predictions for 195 populations where sex ratios were observed but soil samples were
 560 not collected.

561
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	A. Field soil samples from population sites (n=30)		B. SoilGrids matching field samples (n=30)		C. SoilGrids matching sites with sex-ratio data only (n=195)	
Soil variable	r_s	p-value	r_s	p-value	r_s	p-value
Clay	0.45	0.01	0.31	0.09	0.19	<0.001
Silt	0.23	0.2	-0.002	0.98	0.37	<0.0001
Sand	-0.37	0.03	-0.23	0.2	-0.40	<0.0001
pH	0.07	0.6	0.28	0.1	0.08	0.2

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