

1 Macroecological processes drive spiritual ecosystem services obtained from giant trees

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10

11 Abstract

12 Giant trees that have come to have their own unique identities are often named by local people
13 and can inspire a sense of awe and become objects of faith. Although these giant trees provide
14 various kinds of spiritual ecosystem services that are beneficial to the spiritual well-being of
15 the human society, the drivers of these services remain unclear. Using structural equation
16 modeling with 38,994 giant tree records of 237 species across Japan, this study showed that
17 macroecological processes, such as annual precipitation and temperature, may drive spiritual
18 ecosystem services obtained from giant trees directly and indirectly via tree properties such as
19 sizes and ages.

20

21 Main

22 Giant trees are the largest and longest living organisms on the planet and play an important
23 ecological role in the natural world^{1,2}. Moreover, human societies recognize trees that have
24 become relatively large, and position them for their sociocultural significant roles^{1,3,4}. For
25 instance, the Celts, Druids, and many other societies in ancient Europe venerated trees, and
26 oak (*Quercus* spp.) and spruce (*Picea* spp.) trees were of special significance in old Germanic
27 rituals, the source of the tradition of the Christmas tree⁴. These trees have come to have their
28 own unique names, and occasionally, they inspire a sense of awe in people, eventually become
29 objects of faith (i.e., animism)^{3,5}. In this manner, giant trees have a spiritual connection with
30 local people and encourage social cohesion among them; therefore, attachments to and
31 identification with giant trees by people facilitate their spiritual well-being^{1,7,8}. In other words,

32 giant trees provide various spiritual ecosystem services that are beneficial to the spiritual well-
33 being⁸ of human societies worldwide^{1,3,6}. However, the natural drivers and processes that
34 influence the provision of spiritual ecosystem services have rarely been studied⁹ and the
35 mechanisms behind giant trees and their relationship with human society remain unclear as
36 well.

37 The size and distribution of organisms are influenced by geography and climate, and a main
38 topic in macroecology is describing patterns and revealing background processes¹⁰. In this
39 context, giant trees are no exception, and their age, size, and other properties are influenced by
40 geography and climate¹¹. In addition, previous studies have suggested that trees with
41 extraordinary properties (e.g., large size and old age) tend to be given unique names¹ and are
42 recognized as sacred⁴. Specifically, researchers have argued that human attachment to such
43 “charismatic” organisms has resulted in many individual large old trees being given unique
44 names such as Centurion, Methuselah, and General Sherman¹. Matui reviewed previous
45 studies and summarized that some Japanese religions are related to the natural environment
46 (e.g., wind festival, thunder faiths, and mountain faiths) and topography (e.g., rivers, lakes,
47 and marshes)¹², and thus, religion is related to climatic and geographical context. I
48 hypothesized that the sizes and distributions of trees and the provision of spiritual ecosystem
49 services are possibly influenced by macroecological processes (e.g., temperature and
50 precipitation) related to the properties of each tree^{1,4}. Therefore, these unknown processes
51 could be revealed from a macroecological perspective using appropriate methodology.

52 Here, I aimed to test whether spiritual ecosystem services provided by giant trees are driven
53 by macroecological processes on a regional scale depending on the properties of each tree.
54 Moreover, I considered the possibility that geographical and climatic factors directly affect
55 spiritual ecosystem services by changing the relationship between giant trees and human
56 society¹². To test the hypothesis, I compiled a comprehensive dataset of 38,994 individual
57 giant trees with a trunk circumference ≥ 300 cm across the Japanese archipelago. For the
58 analysis, I selected the probabilities of being an object of faith and receiving a unique name as
59 variables related to spiritual ecosystem services; trunk circumference and tree age as variables
60 related to the properties of giant trees; and annual mean temperature, annual precipitation,
61 elevation, and latitude as variables related to macroecological processes. Specific hypotheses
62 were as follows: 1) larger circumference and older age of a tree tend to increase the probability

63 of it being an object of faith and receiving a unique name (i.e., properties of giant trees
64 influence spiritual ecosystem service)^{1,4}, 2) lower annual mean temperature and higher annual
65 precipitation facilitate larger trunk circumferences and older tree ages (i.e., macroecological
66 processes influence properties of giant trees)¹¹, and 3) geographical (i.e., latitude and
67 elevation) and climatic (i.e., annual mean temperature and precipitation) conditions alter the
68 probabilities of a tree being an object of faith and receiving a unique name (i.e.,
69 macroecological processes influence spiritual ecosystem services)¹². The overview of the
70 relationships and the general organization of the model is shown in Extended data Fig. 1. For
71 testing these hypotheses, I used piecewise structural equation modeling (SEM)¹³ to analyze
72 links among spiritual ecosystem services obtained from giant trees, individual tree properties,
73 and macroecological processes.

74 The model outline and statistical analysis results are shown in Fig. 1 and Table 1,
75 respectively. The piecewise SEM analysis showed that macroecological variables directly and
76 indirectly affected spiritual ecosystem services obtained from giant trees through other
77 variables (Global goodness-of-fit: Fisher's $C = 6.608$ and two-sided P -value = 0.579, Table 1).
78 Trunk circumference was influenced positively by tree age and annual precipitation, and
79 negatively by latitude, elevation, and annual mean temperature; tree age was negatively
80 influenced by annual mean temperature, and hypothesis 1 was supported. The probabilities of
81 being an object of faith and receiving a unique name were both positively correlated with both
82 trunk circumference and age of giant tree. Therefore, hypothesis 2 was supported.
83 Additionally, the probability of being an object of faith was positively correlated with latitude
84 and negatively correlated with annual mean temperature and annual precipitation.
85 Furthermore, the probability of getting a unique name was positively correlated with latitude,
86 elevation, and annual mean temperature and negatively correlated with annual precipitation,
87 thereby supporting hypothesis 3. Both trunk circumference and tree age were the top two
88 strongly influential explaining variables for both probabilities of being an object of faith and
89 receiving a unique name (Table 1). A positive correlation between both probabilities of being
90 an object of faith and receiving a unique name was observed (Table 1). Annual mean
91 temperature was negatively influenced by both latitude and elevation, and annual precipitation
92 was influenced negatively by latitude and positively by elevation (Table 1).

93 This study clearly showed that macroecological processes (i.e., geographical and climatic

94 factors) determined patterns of tree properties, and, consequently, the occurrence probability
95 of spiritual ecosystem services provided. Few studies have been conducted on the driving
96 factors of cultural ecosystem services, which include spiritual services⁷, because the processes
97 by which nature supplies these services are unknown. Thus, giant tree size is a simple and
98 ideal property for clarifying these mechanisms. Generally, larger and more long-lived giant
99 trees have stronger relationships with human society and, thus, provide a spiritual ecosystem
100 service. The results of this study are totally consistent with the hypotheses.

101 The results showed that climatic and geographic factors are related to spiritual ecosystem
102 services. The most prominent relationships were that both the probabilities of being an object
103 of faith and receiving a unique name tended to increase with lower annual precipitation (Table
104 1). The worship of giant trees in Japan is partly related to “pray for rain” (雨乞い; “Amagoi”
105 in Japanese)^{14,15} and some trees even have names related to this. Considering these facts, the
106 piecewise SEM results are strongly consistent with previous empirical findings that suggest
107 the probability of having a unique name or being an object of faith increases when
108 precipitation is low^{14,15}. Originally, rice cultivation was the foundation of the traditional
109 Japanese society, and the abundance or failure of the rice crop was a matter of the greatest
110 concern that was directly linked to life and death¹⁵. Among various climatic factors, drought
111 was the strongest causality of a devastating decline in rice yields. Therefore, future changes in
112 rainfall may alter the provision of spiritual services obtained from giant trees.

113 Results related to elevation showed different relationships with the two types of variables
114 related to spiritual ecosystem services (Table 1 and Fig. 1). Specifically, the probability of
115 receiving a unique name tends to be higher with a higher elevation, but no significant
116 relationship was observed between the probability of being an object of faith and elevation
117 (Table 1 and Fig. 1). Both shrines and temples, including sacred trees, are generally located
118 close to human residential areas (i.e., villages and village mountains) in Japan, with the
119 exception of mountain worship¹². This is probably owing to easier accessibility, as a remote
120 place is difficult to visit routinely. Similarly, giant trees are unlikely to be objects of faith in
121 remote areas that are difficult to visit, but this was not clear in the result. Contrarily, if giant
122 trees are visible from far off places, human society will give them unique names as a signpost
123 or symbol without having to visit them daily. Moreover, giant trees should be more visible
124 from a long distance at higher elevations, such as on top of a mountain. Therefore, different

125 relationships can be due to differences in provision of two types of spiritual ecosystem
126 services.

127 Interestingly, species information as a random effect was not selected in all paths (Table 1).
128 Although these results may seem to contradict the view of some previous studies, in which
129 certain species were recognized as sacred trees⁴, they are consistent with the findings of other
130 previous studies that trees with extraordinary properties are more likely to be recognized as
131 sacred^{1,4}. These two aspects have rarely been considered in a single framework related to
132 spiritual ecosystem services. Therefore, differences in species in providing spiritual ecosystem
133 services are due to size differences as shown by the result of this study (Table 1). However,
134 further studies are required to reveal the importance of species differences with regard to
135 factors other than size and longevity.

136 This study of giant trees in the Japanese archipelago is the first to clearly demonstrate the
137 relationship between spiritual ecosystem services and underlying macroecological processes,
138 which have been difficult to evaluate quantitatively. Although comprehensively assessing
139 spiritual and religious values across regions and countries is difficult¹⁶, future research on the
140 drivers of non-material ecosystem services, including spiritual services, worldwide is
141 necessary to accumulate knowledge on their similarities and differences and to prevent loss of
142 spiritual ecosystem services, the roles of which in human society are unknown. In addition,
143 although spiritual ecosystem services have been reported worldwide^{6,8}, their cultural and
144 psychological context are different among regions, countries, and continents¹⁷. Thus, the
145 cultural and psychological context of each human society will impact the directions,
146 quantities, and qualities of spiritual ecosystem services even if the ecosystem services
147 originate from same natural phenomena as they are based on the relationships between nature
148 and human perception. Therefore, comprehensive approaches including ecological, cultural,
149 and psychological aspects are required to understand spiritual ecosystem services in one
150 framework globally.

151

152 **Methods**

153 **Definition of spiritual ecosystem services**

154 Spiritual ecosystem services belong to the category of cultural ecosystem services⁶. Previous
155 studies have pointed out the fuzzy definition of spiritual ecosystem services as a critical

156 problem^{6,16}. In the present study, I define spiritual ecosystem services as ecosystem services
157 that are beneficial to the spiritual well-being of human beings as stated by Irvine et al⁸.
158 Furthermore, they summarized features of spiritual well-being for four relational domains of
159 self, others, environment, and transcendent other(s) to interpret identified literature in terms of
160 the relationships between biodiversity and spiritual well-being⁸. Obviously, provision of
161 spiritual ecosystem services from giant trees can have various routes and it is difficult to
162 identify one or two categories. Some parts of the provision processes of spiritual ecosystem
163 services by giant trees can be recognized as place-based processes^{8,18}, in which attachment to
164 and place identity are known as measures of spiritual well-being⁸. The relationship between
165 human attachments to giant trees and the trees receiving unique names has been suggested¹. In
166 addition, the religious part of the provision processes of spiritual ecosystem services by giant
167 trees can foster connections with nature and feelings of transcendence, linking them implicitly
168 to spiritual well-being⁸. Therefore, in the present study, I considered the probabilities of being
169 an object of faith and receiving a unique name as variables related to spiritual ecosystem
170 services.

171 **Data preparation**

172 Animism was a primitive religion in ancient Japan, and sacred trees are frequently found at
173 both shrines and temples and also remote places such as steep mountains in contemporary
174 Japan⁵. Since the fourth National Survey of the Natural Environment in Japan (1988–1991),
175 the Ministry of Environment conducted a survey of giant trees and forests across the Japanese
176 archipelago, which is a long chain of continental islands located off the eastern coast of Asia
177 and recognized as a biodiversity hotspot¹⁹. Therefore, the data I used for analysis was based on
178 this survey (giant trees database, ‘巨樹・巨木林データベース’ in Japanese;
179 <https://kyoju.biodic.go.jp/>). A single-trunk tree was considered giant when its trunk
180 circumference exceeded 300 cm^{14,20}. If a tree had multiple trunks originating from the same
181 root system, individual trunk circumferences were measured and combined, and the tree was
182 considered giant when the total circumference exceeded 300 cm. In the original dataset, the
183 location of each giant tree was identified by its address in Japan. Based on these addresses, I
184 geocoded the location of each giant tree using the Google Maps Geocoding API
185 (<https://developers.google.com/maps/documentation/geocoding>). However, records with only
186 prefectural information were excluded from the main analysis because the resolution was

187 insufficient. Based on both latitude and longitude, the elevation of each location was
188 determined by the Google Maps Elevation API
189 (<https://developers.google.com/maps/documentation/elevation/overview>). For climatic
190 variables, I used annual mean temperature and precipitation at the 1-km grid scale from Mesh
191 Climate Data 2010 (Japan Meteorological Agency,
192 <http://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html>). The 1-km grids have 30-s latitude
193 and 45-s longitude grid cells (the Japanese Standard Third Mesh). The package “jpmesh”
194 (version 2.1.0)²¹ was used in R software to convert the location of each giant tree to an identity
195 number of the Japanese Standard Third Mesh. I linked the location of each giant tree with
196 climatic variables using the mesh identity number.

197 **Data filtering**

198 Based on information in the giant trees database, I summarized presence/absence of both
199 faith and unique name for each tree, because the original dataset included more detailed
200 information for some individuals (e.g., presence/absence of ritual and taboo). The records
201 targeting only individual giant trees were selected; thus, those targeting a row of trees or a
202 forest area were not considered. The range of trunk circumferences was 300–3,000 cm. Tree
203 ages were approximated based on local and traditional knowledge on giant trees, and they
204 were categorized into four ranks: 1) ≤ 99 years, 2) > 100 and ≤ 199 years, 3) > 200 and ≤ 299
205 years, and 4) > 300 years, as reported by the observed person of the records in the giant trees
206 database¹⁴. The original records use the Japanese name for each tree; therefore, I converted the
207 Japanese names to scientific names using a checklist of Japanese plant names²² and linked
208 them with a plant family. Unmatched individuals at the species level were removed prior to
209 statistical analysis. For individuals with overlapping data, complementary data were combined
210 into one species, while duplicate data about presence/absence mismatches were assumed to be
211 present, and newer data were prioritized. In addition, missing data (NA values) were deleted
212 list-wise. Finally, the dataset, containing 38,994 complete records of individual giant trees,
213 comprising 237 species, was compiled and used for the following statistical analysis.

214 **Piecewise SEM statistical analysis**

215 To explore direct and indirect relationships among spiritual ecosystem services obtained from
216 giant trees and macroecological processes, I performed the analysis using the “piecewiseSEM”
217 package (version 2.1.2) in R¹³. The SEMs included probabilities of being an object of faith and

218 receiving a unique name as variables related to spiritual ecosystem services, trunk
219 circumference and tree age as variables related to properties of giant trees, and annual mean
220 temperature, annual precipitation, elevation, and latitude as macroecological variables. First, I
221 constructed a model that included all hypothesized paths between macroecological processes,
222 properties of giant trees, and spiritual ecosystem services (Extended data Fig. 1). The model
223 was continuously updated by removing and adding potential paths until both of the following
224 criteria were satisfied: 1) no significant relationship in Shipley's test of directed separation,
225 and 2) no non-significant paths in the model. After finishing the updates, I compared models
226 with and without the plant species information of each giant tree as a random effect for the
227 response variables (i.e., trunk circumference, tree age, faith, and unique name) using Akaike's
228 Information Criterion. As a result, only paths with trunk circumference as explanatory variable
229 were included with the plant species as a random effect. After determining the best model, I
230 conducted a goodness-of-fit evaluation for piecewise SEM based on Fisher's C and chi-square
231 tests ($P > 0.05$). The final model satisfied the criteria for adequate model fit with Fisher's $C =$
232 6.608 and $P = 0.579$ (Table 1). The result is consistent in the case of changing the taxonomic
233 resolution from species to family because the model without random effects was finally
234 selected.

235
236 **Data availability:** Giant tree data were downloaded from the giant trees database in Japanese
237 (<https://kyoju.biodic.go.jp/>) on November 19, 2022. Climate data were downloaded from
238 Mesh Climate Data 2010 (Japan Meteorological Agency,
239 <http://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html>). The compiled dataset will be
240 available in Figshare after acceptance of the manuscript.

241
242 **Code availability:** The code for the piecewise structural equation modeling (SEM) statistical
243 analysis will be available in figshare after acceptance of the manuscript.

244
245 **Author contributions statement**

246 R.N. conceived the study, analyzed the empirical data, and wrote the manuscript.

247
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 251 Institute for Environmental Studies, Japan.

252

253 **Competing interests statement**

254 The author declares no conflict of interest.

255

256 **Table 1.** Global goodness-of-fit of the final model is an overview of piecewise structural
 257 equation modeling (SEM)¹³ results with Fisher's $C = 6.608$ and two-sided P -value = 0.579 on
 258 eight degrees of freedom, satisfying the criteria of adequate fit. Abbreviations: LAT, latitude;
 259 ELV, elevation; AMT, annual mean temperature; AP, annual precipitation; TC, trunk
 260 circumference; AGE, tree ages; FAI, probability of being an object of faith; NAM, probability
 261 of receiving a unique name.

Response	Explanatory variable	Standardized coefficient (r)	Coefficient	Degrees of freedom	two-sided P -value
Causal effect					
AMT	LAT	-0.7327	-0.8528	38991	<0.0001
AMT	ELE	-0.6532	-0.0060	38991	<0.0001
AP	LAT	-0.3881	-89.9245	38991	<0.0001
AP	ELV	0.1879	0.3441	38991	<0.0001
TC	LAT	-0.1183	-7.9795	38988	<0.0001
TC	ELV	-0.0660	-0.0352	38988	<0.0001
TC	AMT	-0.0975	-5.6519	38988	<0.0001
TC	AP	0.0485	0.0141	38988	<0.0001
TC	AGE	0.2509	47.4205	38988	<0.0001
AGE*	AMT	-	-0.0124	38992	<0.0001
FAI	LAT	-0.0760	-0.0622	38988	<0.0001
FAI	TC	0.1474	0.0018	38988	<0.0001
FAI	AGE	0.2202	0.5045	38988	<0.0001
FAI	AMT	-0.0304	-0.0214	38988	0.0007
FAI	AP	-0.0301	-0.0001	38988	<0.0001

NAM	LAT	0.1879	0.1693	38987	<0.0001
NAM	ELE	0.1746	0.0012	38987	<0.0001
NAM	TC	0.3481	0.0046	38987	<0.0001
NAM	AGE	0.2273	0.5737	38987	<0.0001
NAM	AMT	0.1284	0.0994	38987	<0.0001
NAM	AP	-0.1100	-0.0004	38987	<0.0001
Covariance					
FAI	NAM	0.0832	0.0832	38994	<0.0001
AMT	AP	-0.1354	-0.1354	38994	<0.0001

262 *The standardized coefficient could not be calculated due to analytical limitation.

263

264 **Figure legend**

265 **Figure 1.** Relationship diagram of piecewise structural equation modeling (SEM) explaining
 266 links among macroecological processes, giant trees, and spiritual ecosystem services. Green and
 267 red arrows indicate significant positive and negative correlations, respectively. Path thickness
 268 indicates the strength (absolute value) of the standardized coefficients at three levels: ≤ 0.3 , $>$
 269 0.3 , and > 0.6 . Abbreviations: LAT, latitude; ELV, elevation; AMT, annual mean temperature;
 270 AP, annual precipitation; TC, trunk circumference; AGE, tree age; FAI, probability of being an
 271 object of faith; NAM, probability of receiving a unique name. The path between annual mean
 272 temperature and tree age is shown as a dashed line because the standardized coefficient could not
 273 be calculated due to analytical limitation.

274

275

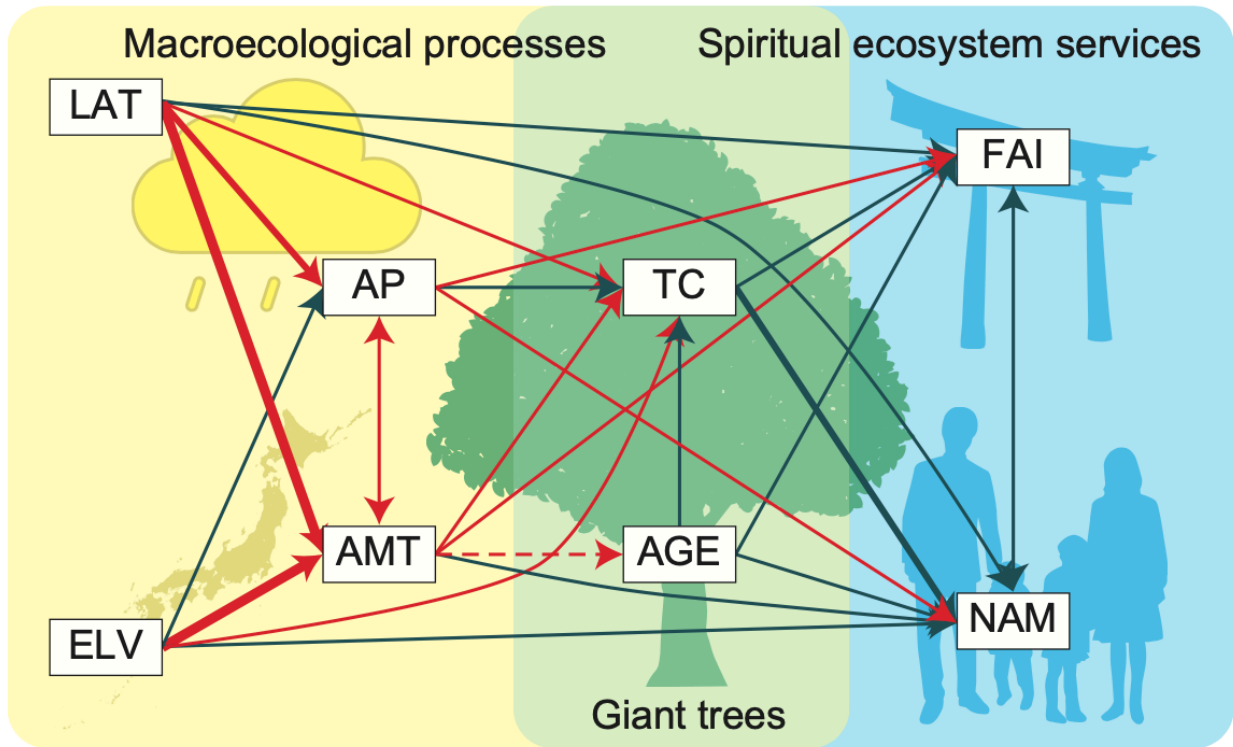
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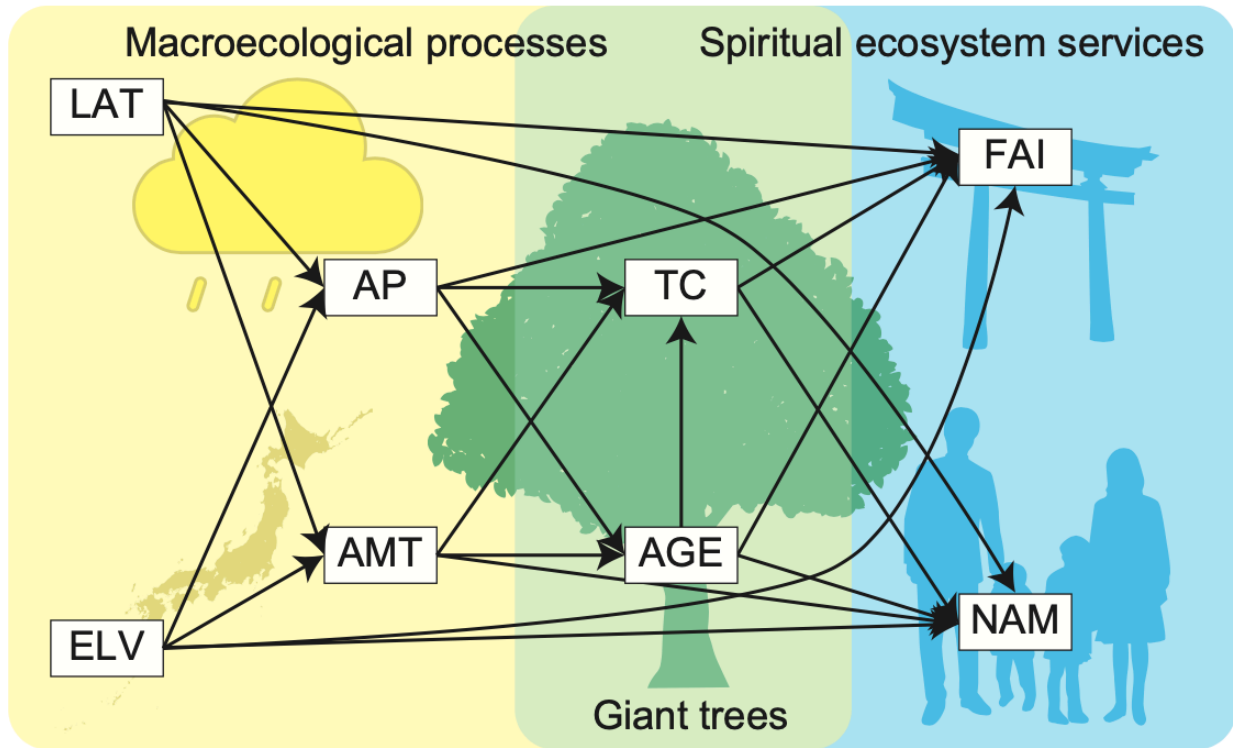
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- 326

327 **Figure 1**



328

329 **Extended data Figure 1.** Initial model structure for piecewise SEM analysis.



330