

1 **Macroecological processes drive spiritual ecosystem services obtained from giant trees**

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12 **Author contributions**

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

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17 **Competing interests:** The author declares no conflicts of interest.

18 **Data availability:** Giant tree data were downloaded from the giant trees database in Japanese  
19 (<https://kyoju.biodic.go.jp/>) on February 27, 2022. Climate data were downloaded from Mesh  
20 Climate Data 2010 (Japan Meteorological Agency,  
21 <http://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html>). The complete dataset will be  
22 available in figshare after the acceptance of the manuscript.

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

25

26

27 **Abstract**

28 Giant trees that have come to have their own unique identities, are often named by local  
29 people and can inspire a sense of awe and become objects of faith. Although these giant trees  
30 provide various kinds of spiritual ecosystem services that are beneficial to the spiritual well-  
31 being of the human society, the drivers of these services remain unclear. Using structural

32 equation modeling with 5,353 giant tree records of 101 species across Japan, this study  
33 showed that macroecological processes, such as annual precipitation and temperature, drive  
34 spiritual ecosystem services obtained from giant trees directly and indirectly via tree sizes.

35

## 36 **Main**

37 Giant trees are the largest and longest living organisms on the planet and play an important  
38 ecological role in the natural world<sup>1,2</sup>. Moreover, human societies recognize trees that have  
39 become relatively large, and will position them for their sociocultural significant roles<sup>1,3,4</sup>. For  
40 instance, the Celts, Druids, and many other societies in ancient Europe venerated trees, and  
41 oak (*Quercus* spp.) and spruce (*Picea* spp.) trees were of special significance in old Germanic  
42 rituals, the source of the tradition of the Christmas tree<sup>4</sup>. These trees have come to have their  
43 own unique names, and occasionally, they inspire a sense of awe in people, eventually become  
44 objects of faith (i.e., animism)<sup>3,5</sup>. In this manner, giant trees have a spiritual connection with  
45 local people and encourage social cohesion among them; therefore, attachments to and  
46 identification with giant trees by people facilitate their spiritual well-being<sup>1,7,8</sup>. In other words,  
47 giant trees provide various spiritual ecosystem services that are beneficial to the spiritual well-  
48 being<sup>8</sup> of human societies worldwide<sup>1,3,6</sup>. However, the natural drivers and processes that  
49 influence the provision of spiritual ecosystem services have rarely been studied<sup>9</sup> and the  
50 mechanisms behind giant trees and their relationship with human society remains unclear as  
51 well.

52 The size and distribution of organisms are influenced by geography and climate, and a main  
53 topic in macroecology is of describing patterns and revealing background processes<sup>10</sup>. In this  
54 context, giant trees are no exception, and their age, size, and other properties are influenced by  
55 geography and climate<sup>11</sup>. In addition, previous studies have suggested that trees with  
56 extraordinary properties (e.g., large size and old age) tend to be given unique names<sup>1</sup> and are  
57 recognized as sacred<sup>4</sup>. Specifically, researchers have argued that human attachment to such  
58 “charismatic” organisms has resulted in many individual large old trees being given unique  
59 names such as Centurion, Methuselah, and General Sherman<sup>1</sup>. Matui reviewed previous  
60 studies and summarized that some Japanese religions are related to the natural environment  
61 (e.g., wind festival, thunder faiths, and mountain faiths) and topography (e.g., rivers, lakes,  
62 and marshes)<sup>12</sup>, and thus, climate and geography are related to religion. I hypothesized that the

63 sizes and distributions of trees and the provision of spiritual ecosystem services are possibly  
64 influenced by macroecological processes (e.g., temperature and precipitation) related to the  
65 properties of each tree<sup>1,4</sup>. Therefore, these unknown processes could be revealed from a  
66 macroecological perspective using appropriate methodology.

67 Here, I aimed to test whether spiritual ecosystem services provided by giant trees are driven  
68 by macroecological processes on a regional scale depending on the properties of each tree.  
69 Moreover, I considered the possibility that geographical and climatic factors directly affect  
70 spiritual ecosystem services by changing the relationship between giant trees and human  
71 society<sup>12</sup>. To test the hypothesis, I compiled a comprehensive dataset of 5,353 individual giant  
72 trees with a trunk circumference  $\geq 300$  cm across the Japanese archipelago. For the analysis, I  
73 selected the probabilities of being an object of faith and receiving a unique name as variables  
74 related to spiritual ecosystem services; trunk circumference and tree age as variables related to  
75 the properties of giant trees; and annual mean temperature, annual precipitation, elevation, and  
76 latitude as variables related to macroecological processes. Specific hypotheses were as  
77 follows: 1) larger circumference and older age of a tree tend to increase the probability of it  
78 being an object of faith and receiving a unique name (i.e., properties of giant trees influence  
79 spiritual ecosystem service)<sup>1,4</sup>, 2) lower annual mean temperature and higher annual  
80 precipitation facilitate larger trunk circumferences and older tree ages (i.e., macroecological  
81 processes influence properties of giant trees)<sup>11</sup>, and 3) geographical (i.e., latitude and  
82 elevation) and climatic (i.e., annual mean temperature and precipitation) conditions alter the  
83 probabilities of a tree being an object of faith and receiving a unique name (i.e.,  
84 macroecological processes influence spiritual ecosystem services)<sup>12</sup>. The overview of the  
85 relationships and the general organization of the model is shown in Extended data Fig. 1. For  
86 testing these hypotheses, I used piecewise structural equation modeling (SEM)<sup>13</sup> to analyze  
87 links among spiritual ecosystem services obtained from giant trees, individual tree properties,  
88 and macroecological processes.

89 The model outline and statistical analysis results are shown in Fig. 1 and Table 1,  
90 respectively. The piecewise SEM analysis showed that macroecological variables directly and  
91 indirectly affected spiritual ecosystem services obtained from giant trees through other  
92 variables (Global goodness-of-fit: Fisher's  $C = 8.269$  and  $P$ -value = 0.875, Table 1). Trunk  
93 circumference was influenced positively by tree age and annual precipitation, and negatively

94 by annual mean temperature; however, there was no relationship between tree age and  
95 macroecological processes, and hypothesis 1 was partially supported. The probabilities of  
96 being an object of faith and receiving a unique name were both positively correlated with giant  
97 tree trunk circumference. Conversely, the probabilities of being an object of faith and getting a  
98 unique name were negatively and positively correlated with tree age, respectively. Therefore,  
99 hypothesis 2 was partly supported, except for the link between faith and tree age. Additionally,  
100 the probability of being an object of faith was positively correlated with latitude and  
101 negatively correlated with annual precipitation and elevation. Furthermore, the probability of  
102 getting a unique name was positively correlated with latitude and elevation and negatively  
103 correlated with annual precipitation, thereby supporting hypothesis 3. Trunk circumference  
104 was the strongest explaining variable for both probabilities of being an object of faith and  
105 receiving a unique name (Table 1). A positive correlation between both probabilities of being  
106 an object of faith and receiving a unique name was observed (Table 1). Annual mean  
107 temperature was negatively influenced by both latitude and elevation, and annual precipitation  
108 was negatively influenced by latitude (Table 1).

109 This study clearly showed that macroecological processes (i.e., geographical and climatic  
110 factors) determined patterns of tree size, and, consequently, the occurrence probability of  
111 spiritual ecosystem services provided. Few studies have been conducted on the driving factors  
112 of cultural ecosystem services, which include spiritual services<sup>7</sup>, because the processes by  
113 which nature supplies these services are unknown. Thus, giant tree size is a simple and ideal  
114 property for clarifying these mechanisms. Generally, larger giant trees have stronger  
115 relationships with human society and, thus, provide a spiritual ecosystem service. Most of the  
116 results are consistent with the hypotheses, except for paths related to tree age. The negative  
117 influence of tree age on the probability of being an object of faith was particularly the most  
118 unexpected result. Tree age was a variable which had only four ranks based on estimated age  
119 and depending on the person reporting, the reported information was possibly different from  
120 the actual tree age.

121 The results showed that climatic and geographic factors are related to spiritual ecosystem  
122 services. The most prominent relationships were that both the probabilities of being an object  
123 of faith and receiving a unique name tended to increase with lower annual precipitation (Table  
124 1). The worship of giant trees in Japan is partly related to “pray for rain” (雨乞い; “Amagoi”

125 in Japanese)<sup>14,15</sup> and some trees even have names related to this. Considering these facts, the  
126 piecewise SEM results are strongly consistent with previous empirical findings that suggest  
127 the probability of having a unique name or being an object of faith increases when  
128 precipitation is low<sup>14,15</sup>. Originally, rice cultivation was the foundation of the traditional  
129 Japanese society, and the abundance or failure of the rice crop was a matter of the greatest  
130 concern that was directly linked to life and death<sup>15</sup>. Among various climatic factors, drought  
131 was the strongest causality of a devastating decline in rice yields. Therefore, future changes in  
132 rainfall may alter the provision of spiritual services obtained from giant trees.

133 Results related to elevation showed a contrasting relationship with the two types of  
134 variables related to spiritual ecosystem services (Table 1 and Fig. 1). Specifically,  
135 probabilities of being an object of faith and receiving a unique name tend to be lower and  
136 higher with a higher elevation, respectively (Table 1 and Fig. 1). Both shrines and temples,  
137 including sacred trees, are generally located close to human residential area (i.e., villages and  
138 village mountains) in Japan, with the exception of mountain worship<sup>12</sup>. This is probably owing  
139 to easier accessibility, as a remote place is difficult to visit routinely. Similarly, giant trees are  
140 less likely to be objects of faith in remote areas that are difficult to visit. Contrarily, if giant  
141 trees are visible from far off places, human society will give them unique names as a signpost  
142 or symbol without having to visit them daily. Moreover, giant trees should be more visible  
143 from a long distance at higher elevations, such as on top of a mountain. Therefore, the  
144 contrasting relationship can be due to differences in provision of two types of spiritual  
145 ecosystem services.

146 Interestingly, species information as a random effect was only selected among paths related  
147 to trunk circumferences and not among paths related to the provision of spiritual ecosystem  
148 services (Table 1). Although these results may seem to contradict the view of some previous  
149 studies, in which certain species were recognized as sacred trees<sup>4</sup>, they are consistent with the  
150 findings of other previous studies that trees with extraordinary properties are more likely to be  
151 recognized as sacred<sup>1,4</sup>. These two aspects have rarely been considered in a single framework  
152 related to spiritual ecosystem services. Therefore, differences in species in providing spiritual  
153 ecosystem services are due to interspecific size differences as shown by the result of this study  
154 (Table 1). However, further studies are required to reveal the importance of species  
155 differences with regard to factors other than size and longevity.

156 This study of giant trees in the Japanese archipelago is the first to clearly demonstrate the  
157 relationship between spiritual services and underlying macroecological processes, which have  
158 been difficult to evaluate quantitatively. Although comprehensively assessing spiritual and  
159 religious values across regions and countries is difficult<sup>16</sup>, future research on the drivers of  
160 non-material ecosystem services, including spiritual services, worldwide is necessary to  
161 accumulate knowledge on their similarities and differences and to prevent loss of spiritual  
162 ecosystem services, the roles of which in human society are ecologically unclear. In addition,  
163 although spiritual ecosystem services have been reported worldwide<sup>6,8</sup>, their cultural and  
164 psychological backgrounds are different among regions, countries, and continents<sup>17</sup>. Thus, an  
165 understanding of the backgrounds of spiritual ecosystem services for human society will  
166 change their directions, quantities, and qualities even if they originate from same natural  
167 phenomena as they are based on the relationships between nature and human perception.  
168 Therefore, comprehensive approaches including ecological, cultural, and psychological  
169 aspects are required to understand spiritual ecosystem services in one framework globally.

170

## 171 **Methods**

### 172 **Definition of spiritual ecosystem services**

173 A spiritual ecosystem service is categorized as a part of cultural ecosystem services<sup>6</sup>. Previous  
174 studies have pointed out the fuzzy definition of spiritual ecosystem services as a critical  
175 problem<sup>6,16</sup>. In the present study, I define spiritual ecosystem services as ecosystem services  
176 that are beneficial to the spiritual well-being of human beings as stated by Irvine et al<sup>8</sup>.  
177 Furthermore, they summarized features of spiritual well-being for four relational domains of  
178 self, others, environment, and transcendent other(s) to interpret identified literature in terms of  
179 the relationships between biodiversity and spiritual well-being<sup>8</sup>. Obviously, provision of  
180 spiritual ecosystem services from giant trees can have various routes and it is difficult to  
181 identify one or two categories. Some parts of the provision processes of spiritual ecosystem  
182 services by giant trees can be recognized as place-based processes<sup>8,18</sup>, in which attachment to  
183 and place identity are known as measures of spiritual well-being<sup>8</sup>. The relationship between  
184 human attachments to giant trees and the trees receiving unique names has been suggested<sup>1</sup>. In  
185 addition, the religious part of the provision processes of spiritual ecosystem services by giant  
186 trees can foster connections with nature and feelings of transcendence, linking them implicitly

187 to spiritual well-being<sup>8</sup>. Therefore, in the present study, I considered the probabilities of being  
188 an object of faith and receiving a unique name as variables related to spiritual ecosystem  
189 services.

## 190 **Data preparation**

191 Animism was a primitive religion in ancient Japan, and sacred trees are frequently found at  
192 both shrines and temples and also remote places such as steep mountains in contemporary  
193 Japan<sup>5</sup>. Since the fourth National Survey of the Natural Environment in Japan (1988–1991),  
194 the Ministry of Environment conducted a survey of giant trees and forests across the Japanese  
195 archipelago, which is a long chain of continental islands located off the eastern coast of Asia  
196 and recognized as a biodiversity hotspot<sup>19</sup>. Therefore, the data I used for analysis was based on  
197 this survey (giant trees database, ‘巨樹・巨木林データベース’ in Japanese;  
198 <https://kyoju.biodic.go.jp/>). A single-trunk tree was considered giant when its trunk  
199 circumference exceeded 300 cm<sup>14,20</sup>. If a tree had multiple trunks originating from the same  
200 root system, individual trunk circumferences were measured and combined, and considered  
201 giant when the total circumference exceeded 300 cm. In the original dataset, the location of  
202 each giant tree was identified by its address in Japan. Based on these addresses, I geocoded the  
203 location of each giant tree using the Google Maps Geocoding API  
204 (<https://developers.google.cn/maps/documentation/geocoding>). However, records with only  
205 prefectural information were excluded from the main analysis because the resolution was  
206 insufficient. Based on both latitude and longitude, the elevation of each location was  
207 determined by the Google Maps Elevation API  
208 (<https://developers.google.cn/maps/documentation/elevation/overview>). For climatic variables,  
209 I used annual mean temperature and precipitation at the 1-km grid scale from Mesh Climate  
210 Data 2010 (Japan Meteorological Agency, [http://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-](http://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html)  
211 [G02.html](http://nlftp.mlit.go.jp/ksj/gml/datalist/KsjTmplt-G02.html)). The 1-km grids have 30-s latitude and 45-s longitude grid cells (the Japanese  
212 Standard Third Mesh). The package “jpmesh” (version 2.1.0)<sup>21</sup> was used in R software to  
213 convert the location of each giant tree to an identity number of the Japanese Standard Third  
214 Mesh. I linked the location of each giant tree with climatic variables using the mesh identity  
215 number.

## 216 **Data filtering**

217 Based on information in the giant trees database, I summarized presence/absence of both

218 faith and unique name for each tree, because the original dataset included more detailed  
219 information for some individuals (e.g., presence/absence of ritual and taboo). The records  
220 targeting only individual giant trees were selected; thus, those targeting a row of trees or a  
221 forest area were not considered. The range of trunk circumferences was 300–2830 cm. Tree  
222 ages were approximated based on local and traditional knowledge on giant trees, and they  
223 were categorized into four ranks: 1)  $\leq 99$  years, 2)  $> 100$  and  $\leq 199$  years, 3)  $> 200$  and  $\leq 299$   
224 years, and 4)  $> 300$  years, as reported by the observed person of the records in the giant trees  
225 database<sup>14</sup>. The original records use the Japanese name for each tree; therefore, I converted the  
226 Japanese names to scientific names using a checklist of Japanese plant names<sup>22</sup> and linked  
227 them with a plant family. Unmatched individuals at the species level were removed prior to  
228 statistical analysis. For individuals with overlapping data, complementary data were combined  
229 into one species, while duplicate data about presence/absence mismatches were assumed to be  
230 present, and newer data were prioritized. In addition, missing data (NA values) were deleted  
231 list-wise. Finally, the dataset, containing 5,353 complete records of individual giant trees,  
232 comprising 101 species, was compiled and used for the following statistical analysis.

### 233 **Piecewise SEM statistical analysis**

234 To explore direct and indirect relationships among spiritual ecosystem services obtained from  
235 giant trees and macroecological processes, I performed the analysis using the “piecewiseSEM”  
236 package in R<sup>13</sup>. The SEMs included probabilities of being an object of faith and receiving a  
237 unique name as variables related to spiritual ecosystem services, trunk circumference and tree  
238 age as variables related to properties of giant trees, and annual mean temperature, annual  
239 precipitation, elevation, and latitude as macroecological variables. First, I constructed a model  
240 that included all hypothesized paths between macroecological processes, properties of giant  
241 trees, and spiritual ecosystem services (Extended data Fig. 1), which included the plant species  
242 information of each giant tree as a random effect. The model was continuously updated by  
243 removing and adding potential paths until both of the following criteria were satisfied: 1) no  
244 significant relationship in Shipley’s test of directed separation, and 2) no non-significant paths  
245 in the model. After finishing the updates, I compared models with and without the plant  
246 species information of each giant tree as a random effect for the response variables (i.e., trunk  
247 circumference, tree age, faith, and unique name) using Akaike's Information Criterion. As a  
248 result, only paths with trunk circumference as explanatory variable were included with the



249 plant species as a random effect. After determining the best model, I conducted a goodness-of-  
 250 fit evaluation for piecewise SEM based on Fisher's  $C$  and chi-square tests ( $P > 0.05$ ). The final  
 251 model satisfied the criteria for adequate model fit with Fisher's  $C = 8.269$  and  $P = 0.875$   
 252 (Table 1). The result is almost consistent in the case of changing the taxonomic resolution  
 253 from species to family (Extended data Table 1).

254

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292

293 **Table 1.** Global goodness-of-fit of the final model is an overview of piecewise structural  
 294 equation modeling (SEM)<sup>13</sup> results with Fisher's  $C = 8.269$  and  $P$ -value = 0.875, satisfying the  
 295 criteria of adequate fit. Abbreviations: LAT, latitude; ELV, elevation; AMT, annual mean  
 296 temperature; AP, annual precipitation; TC, trunk circumference; AGE, tree ages; FAI,  
 297 probability of being an object of faith; NAM, probability of receiving a unique name.

Response	Explanatory variable	Standardized coefficient ( $r$ )	P-value
Causal effect			
AMT	LAT	-0.7625	<0.001

AMT	ELE	-0.7266	<0.001
AP	LAT	-0.3491	<0.001
TC†	AMT	-0.0888	<0.001
TC†	AP	0.0832	<0.001
TC†	AGE	0.2025	<0.001
FAI	LAT	0.0727	<0.001
FAI	TC	0.3224	<0.001
FAI	AGE	-0.1141	<0.001
FAI	AP	-0.1370	<0.001
FAI	ELE	-0.0867	<0.001
NAM	LAT	0.1126	<0.001
NAM	TC	0.4110	<0.001
NAM	AGE	0.1051	<0.001
NAM	AP	-0.0689	<0.001
NAM	ELE	0.1459	<0.001
Covariance			
FAI	NAM	0.1989	<0.001
AMT	AP	-0.1464	<0.001

298 †The trunk circumference analysis considered the plant species of each giant tree as a random  
 299 effect.

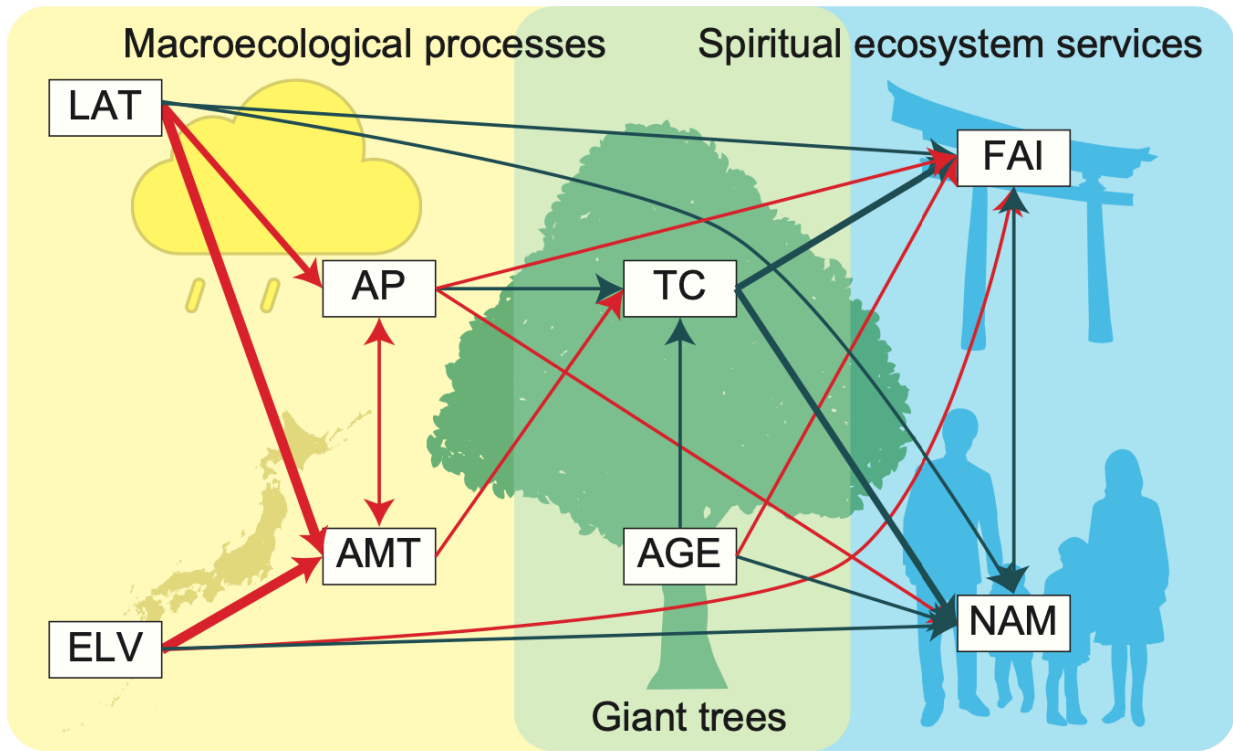
300

### 301 **Figure legend**

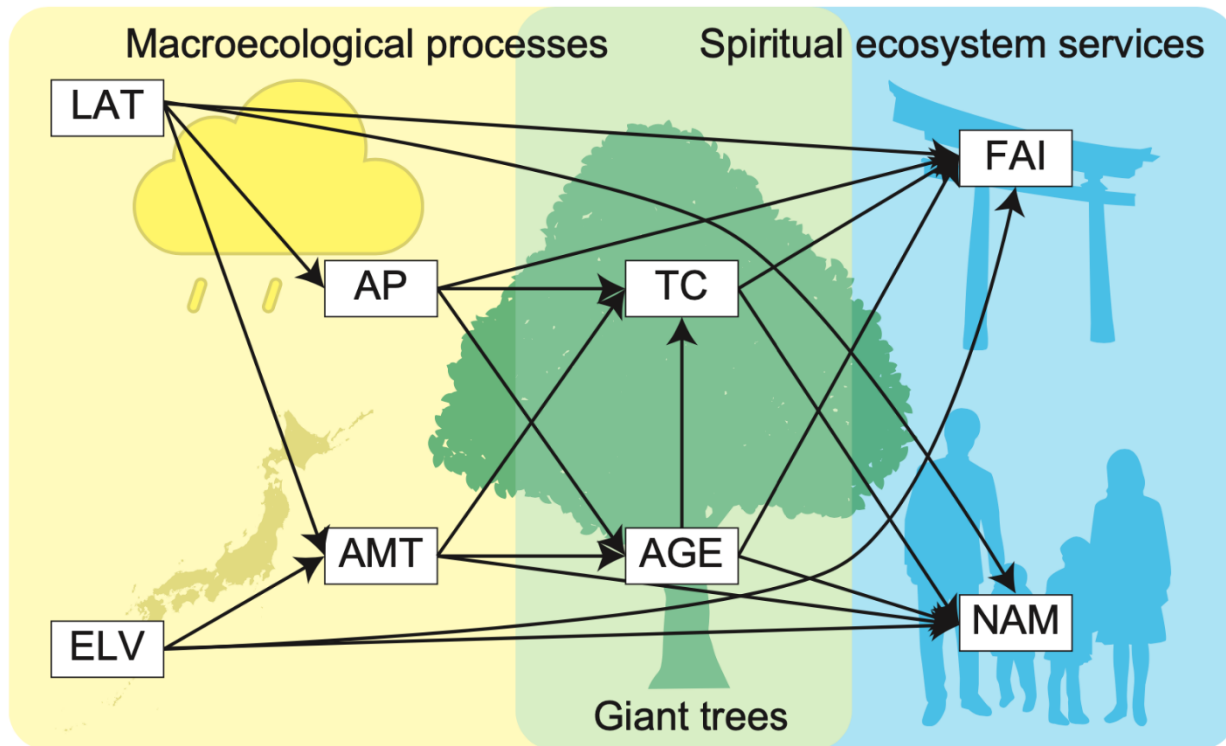
302 **Fig. 1.** Relationship diagram of piecewise structural equation modeling (SEM) explaining links  
 303 among macroecological processes, giant trees, and spiritual ecosystem services. Green and red  
 304 arrows indicate significant positive and negative correlations, respectively. Path thickness  
 305 indicates the strength (absolute value) of the standardized coefficients at three levels:  $\leq 0.3$ ,  $>$   
 306  $0.3$ , and  $> 0.6$ . Abbreviations: LAT, latitude; ELV, elevation; AMT, annual mean temperature;  
 307 AP, annual precipitation; TC, trunk circumference; AGE, tree age; FAI, probability of being an  
 308 object of faith; NAM, probability of receiving a unique name.

309

310 **Figure 1**



311

312 **Extended data**313 **Figure 1.** Initial model structure for piecewise SEM analysis.

314

315 **Table 1.** Global goodness-of-fit of the final model is an overview of piecewise structural  
 316 equation modeling (SEM)<sup>13</sup> results with *Fisher's C* = 7.834 and *P-value* = 0.898, satisfying the  
 317 criteria of adequate fit. Abbreviations: LAT, latitude; ELV, elevation; AMT, annual mean  
 318 temperature; AP, annual precipitation; TC, trunk circumference; AGE, tree ages; FAI,  
 319 probability of being an object of faith; NAM, probability of receiving a unique name.

Response	Explanatory variable	Standardized coefficient ( <i>r</i> )	P-value
Causal effect			
AMT	LAT	-0.7625	<0.001
AMT	ELE	-0.7266	<0.001
AP	LAT	-0.3491	<0.001
TC†	AMT	-0.0720	<0.001
TC†	AP	0.0914	<0.001
TC†	AGE	0.1997	<0.001

FAI	LAT	0.0727	<0.001
FAI	TC	0.3224	<0.001
FAI	AGE	-0.1141	<0.001
FAI	AP	-0.1370	<0.001
FAI	ELE	-0.0867	<0.001
NAM	LAT	0.1126	<0.001
NAM	TC	0.4110	<0.001
NAM	AGE	0.1051	<0.001
NAM	AP	-0.0689	<0.001
NAM	ELE	0.1459	<0.001
Covariance			
FAI	NAM	0.1989	<0.001
AMT	AP	-0.1464	<0.001

320 †The trunk circumference analysis considered the plant family of each giant tree as a random  
321 effect.