

1 **Abstract**

2 Fruiting phenology, assessed by seed fall, in five warm- and cool-temperate
3 forests on Yakushima, an island in southern Japan, were studied for 2 years in
4 one plot of 50 m*50 m and 4 years in four plots of 100 m* 50 m. The elevations
5 of the plots ranged 170-1200 m a.s.l. Seed fall phenology showed annual
6 periodicity in all of the plots. This was clear when assessed by the number of
7 species but became less clear when assessed by the biomass of seed fall.
8 Community-level annual periodicity was based on the prevalence of
9 population-level annual periodicity and interspecific synchronization of the
10 fruiting peak from autumn to winter. Fleshy fruits had peaks of seed fall in a
11 wider range of months than non-fleshy fruits, since it is sometimes beneficial to
12 bear fruit out of community-level fruiting peaks in order to avoid interspecific
13 competition for animal dispersers. No consistent effect of climatic factors on
14 seed fall phenology was detected.
15 Key words: fleshy fruits; fruit; frugivore; phenology; temperate forest

16 **Introduction**

17 Fruit abundance and its seasonality are crucial factors in understanding the
18 biomass and community structure of frugivores (Stevenson, 2001; Kissling et al.,
19 2007). Studies on fruiting phenology have progressed in tropical forests, based
20 on long-term monitoring of the entire tree community (Chapman et al., 1999;
21 Anderson et al., 2005; Brearley et al., 2007). It has been found that various
22 factors, such as temperature, rain fall and solar irradiance, affect patterns in
23 fruiting phenology (Anderson et al., 2005; Zimmerman et al., 2007). These
24 climatic factors show different seasonal patterns from region to region, and thus
25 it is difficult to predict even the calendar month in which the fruiting peak will
26 occur. On the contrary, fruiting patterns in temperate forests, as opposed to
27 tropical rain forests, are referred to as 'clearly defined seasonal patterns'
28 (Chapman et al., 1999). It is believed that the very regular, predictable changes
29 in day length and coldness in winter force all of the plant species to follow an
30 annual pattern of phenology (Newstrom et al., 1994). Data on multiple years
31 are indispensable to examine whether annual periodicity is the norm in
32 temperate forests. However, long-term data are surprisingly too scarce to
33 conduct quantitative comparisons with tropical forests.

34 Animals respond to seasonal changes in food availability by various
35 means, such as migration, hibernation, dietary switch (van Schaik et al., 1993),
36 and food-storing behavior and/or physiology, such as scatter-hoarding and fat
37 deposition (Jönsson, 1997). Annual periodicity in fruiting phenology, if it does
38 exist, offers foods for frugivores in a predictable manner, in particular regarding
39 the timing, and thus enables frugivores to adapt to seasonality easily. For
40 example, in the case of fat deposition, if there were no annual periodicity,

41 animals would not be able to predict when to start depositing fat and how long
42 the food shortage will last, and thus how much fat needs to be deposited.
43 Therefore, annual periodicity is a crucial factor in fruiting phenology for the
44 survival of frugivores.

45 Several questions need to be answered with regard to annual
46 periodicity, assuming that annual periodicity is the norm in temperate forest. It
47 remains an open question whether other climatic factors (e.g. rain fall,
48 temperature and solar irradiance) also contribute to seasonality, such as in
49 tropical forests (Anderson et al., 2005). Community-level phenology is the sum
50 of various population-level phenology which reflects the adaptive strategy of an
51 individual species, so analysis of population-level phenology is needed to
52 explain community-level annual periodicity. We expect that community-level
53 phenology becomes annually periodic when (1) population-level phenology is
54 annually periodic, (2) population-level phenology synchronizes among species,
55 and (3) duration of fruiting by individual species is short.

56 Temperate forests are also not uniform with respect to species
57 composition, primary production and biomass. For example, coniferous forests
58 in high elevation have comparatively larger basal area than broad-leaved forest
59 (Aiba et al., 2007). Warm-temperate forests have similar characteristics with
60 tropical forests when the warmth index is the same, such as species diversity,
61 basal area, tree height, stem density and above ground biomass (Takyu et al.,
62 2005). Considering these variations within temperate forest, it is necessary to
63 cover both warm- and cool- (or coniferous) forests to clarify the general pattern
64 in fruiting phenology in temperate forests.

65 In this paper, we present data on fruiting phenology of two-four years

66 using seed fall data in five temperate forests on Yakushima Island, southern
67 Japan, at different altitudes. The elevational gradient of this island covers both
68 warm- and cool-temperate forests, and thus it is an ideal place to assess the
69 degree of variability in fruiting phenology for temperate regions in general. First,
70 we examined whether annual periodicity can be detected at the community level.
71 Fleshy and non-fleshy species were examined separately because they have
72 different meanings for frugivores and their phenology must have evolved under
73 different selection pressures. Second, in order to assess the relative
74 importance of annual periodicity compared with climate, the effects of both
75 factors on fruiting phenology were examined. Third, in order to understand why
76 community-level annual periodicity exists, we examine the annual periodicity at
77 the population level of the main species. We explore the synchronization of
78 fruiting peak among species and the duration of fruiting, which may enhance or
79 disturb annual periodicity.

80

81 **Methods**

82 Study site

83 Yakushima is an island located in the southwestern part of Japan (30°N, 131°E)
84 that occupies an area of 503 km², with the highest peak being 1936 m a.s.l.
85 The mean annual precipitation ranges from 2500 mm to 4700 mm along the
86 coast and exceeds 8600 mm in the higher area (Eguchi, 1984). The mean
87 annual temperature is 20°C in the lowland area (Tagawa, 1980) and 12.4°C at
88 1050 m a.s.l. (Hanya, 2004). Geological substrates are sedimentary in lowland
89 areas, except in the western part, and granite in other parts. The vegetation of
90 Yakushima is roughly classified as warm- and cool-temperate forests, having a

91 border at 1000 m a.s.l. Warm-temperate forests are dominated by evergreen
92 broad-leaved trees (e.g., *Castanopsis cuspidata*, *Quercus salicina*, and
93 *Distylium racemosum*), including some subtropical species, such as strangler
94 figs (*Ficus superba* and *F. microcarpa*) in the lowland. Cool-temperate forests
95 are coniferous forests, dominated by *Cryptomeria japonica*, *Abies firma*, and
96 *Tsuga sieboldii* mixed with broad-leaved trees such as *Quercus acuta*, *Q.*
97 *salicina*, and *D. racemosum*.

98

99 Study plots and seed litter collection

100 The following five vegetation plots were set in the primary forests of Yakushima.
101 Plots were named according to the location (eastern or western side) and
102 altitude, such as E170, W280, E570, W1050, and E1200. The area was 0.25
103 ha (50 m*50 m) for W1050 and 0.5 ha (100 m*50 m) for others. Geological
104 substrates are granite for W280, E570, W1050, and E1200 and sedimentary for
105 E170. With regard to species composition, total litter fall and basal area, these
106 plots can be regarded as representatives of each altitude/geological substrate
107 (Aiba et al., 2007). All of the trees with a diameter at breast height (DBH) of
108 more than 5 cm were recorded. Details of the plots are described in Aiba et al.
109 (2007) and Table 1. The plots corresponded to Aiba et al.'s (2007) Y02Sa
110 (E170), Y02Ga (W280), Y06Gb (E570), Y12Ga (W1050) and Y12Gc (E1200).

111 Since fruit fall phenology often differs from the ripe fruit availability in
112 the canopy (Chapman et al., 1994), we analyze the seasonal pattern of seeds
113 fallen separately from pulp (or other fruit part), which is presumably dispersed by
114 animals, the wind, or other dispersal agents. In this way, we can remove the
115 effect of fallen unripe fruits or old dehiscent fruits whose seeds have already

116 been dispersed long ago. In this paper, we refer 'seed' to only the seeds fallen
117 separated from the pulp or other fruit parts, including broken seeds. For
118 Fagaceae species, we regarded one acorn as a 'seed', because each acorn is a
119 unit of dispersal. Acorns of *Quercus salicina* and *Q. acuta* could not be
120 discriminated, so they were regarded as a single species. Except for acorns,
121 most of the seeds were mature. Immature seeds were found mostly in a form
122 surrounded by pulp and other fruit parts, and thus not included in this analysis.

123 We set 25 (W1050) or 20 (other four plots) fruit traps, each with an area
124 of 0.58 m², 1-1.5 m above the ground. Each trap consisted of a polyester cloth
125 cone supported by a circular fiberglass frame. Each plot was divided into 25
126 (W1050) or 20 subplots and the traps were set in the center of the subplots.
127 The collection period was August 1999-August 2001 in W1050 and July
128 1998-August 2002 in the other four plots. During that period, we collected seed
129 litter once each month, usually in the latter half of that month. We oven-dried,
130 sorted, and weighed the seeds for each species.

131

132 Climate

133 Climatic data were taken at Yakushima Meteorological Station
134 (<http://www.jma.go.jp/jma/menu/report.html>), which is in an eastern coastal
135 village of Yakushima at 37 m a.s.l. Monthly averages of ambient temperature,
136 daily minimum temperature, daily maximum temperature and monthly total
137 rainfall and solar irradiance time were used for analysis. There is heterogeneity
138 in climate throughout Yakushima; however, the inter-site differences in absolute
139 values are not important in our analysis. The monthly or supra-annual variation
140 patterns are expected to be more or less similar within the area of Yakushima.

141 Therefore, we used the record at Yakushima Meteorological Station as a proxy
142 of seasonal changes in climatic variables for all five study sites (see below). In
143 fact, monthly average temperature and precipitation in 2000 and 2001
144 significantly correlated between the station and near the W1050 plot (Hanya,
145 unpublished data) (temperature: $r=0.984$, $p<0.0001$; precipitation: $r=0.539$,
146 $p=0.0038$).

147

148 Data analysis

149 For the analysis of phenology, we analyzed the number of species and
150 the dry biomass of seed litter (kg/ha) in each month in each plot. Since the
151 collection was not conducted on the last day of each month, the biomass of seed
152 litter in that month was estimated assuming that the falling rate was constant
153 between the two collections. For the number of species of seeds, we used for
154 analysis the number of species found in the litter collected that month. In winter,
155 we sometimes failed to collect seed litter at E570 and E1200 because the traps
156 were filled with snow. If we failed to collect litter in month X due to heavy snow,
157 we removed the data of month X and X+1 for the analysis of phenology. Seed
158 litter samples in E170 in February 2001 were lost by a postal accident. For the
159 analysis of seed fall phenology, the data of E170 in February 2001 was excluded
160 from the analysis.

161 To detect annual periodicity in seed fall, we performed a series of (12)
162 generalized linear models (GLM) using cosine wave functions (Anderson et al.,
163 2005) with periodicities of 12 months having maximum values in either of the 12
164 months. For the number of species, we assumed Poisson distribution. For
165 the biomass of seed fall, we assumed normal distribution. The model having

166 the least AIC was selected, and if the model was significant ($p < 0.05$), we
167 considered that there was a statistically significant annual periodicity.

168 For the community-level phenology, we tested the effects of both the
169 annual periodicity and climatic factors. We used the cosine wave function,
170 rainfall, average temperature, maximum temperature, minimum temperature and
171 solar irradiance time as independent factors in the GLM. We examined the
172 climatic data of not only the current month X but also the average of the block of
173 the past three months, namely, the average of the months of $\{(X-1) \text{ to } (X-3)\}$,
174 $\{(X-4) \text{ to } (X-5)\}$, ..., and $\{(X-16) \text{ to } (X-18)\}$. We made three months block
175 because (1) in order to make analysis simple, it is better to make the block length
176 longer and (2) if the length of the block is longer than 3 months, each block
177 would include very different two seasons (e.g. middle of summer and late
178 autumn). We analyzed up to 18 months before because it was suggested that
179 the fruit crop in autumn was affected by the temperature in summer of the
180 preceding year, thus up to approximately 18 months before the fruiting peak in
181 autumn to winter (Noma, 1997). We start from the simplest model using only
182 one factor, such as the cosine wave function or a climatic factor, and we
183 employed the model having the smallest AIC. Then, we added other factors
184 and searched for the factor which decreased AIC the most. This procedure
185 was repeated until the AIC did not further decrease by adding other factors.

186 We used R 2.6.1. (© The R Foundation for Statistical Computing) for
187 statistical analysis. We employed the Durbin-Watson statistic to test for
188 temporal autocorrelation. If significant autocorrelation ($p < 0.05$) was found, an
189 autoregressive order 1 covariance structure was incorporated in the model
190 (Anderson et al., 2005). Although there was collinearity (correlations between

191 independent factors) among the independent variables, it was not a severe
192 problem in this procedure because we examined only a few variables in a single
193 model at any one time. In the models in which multiple independent variables
194 were adopted, maximum variance inflation factors (VIF) were smaller (1.02-2.17)
195 than the cut-off value (5) recommended in Neter et al. (2004).

196

197 **Results**

198 Seed fall phenology in Yakushima

199 Community-level seed fall showed annual periodicity, and seed fall peak tended
200 to occur from December to January. Statistically significant annual periodicity
201 was detected for the number of species in all plots and for both fleshy and
202 non-fleshy fruits (Fig. 1). The peak of seed fall occurred in December and
203 January for fleshy fruited species and in November, December and January for
204 non-fleshy fruited species (Table 3a). The same tendency was apparent but
205 became less clear when we analyzed the biomass of seed litter (Fig. 2).

206 Annual periodicity was not significant for fleshy fruits in E170. The peak
207 months of the biomass of seed litter occurred in more variable months from
208 September to February (Table 3b). The R^2 value in the GLM was significantly
209 higher for the number of species than for the seed biomass (fleshy fruits: $t=4.14$,
210 $p=0.014$; non-fleshy fruits: $t=4.39$, $p=0.012$), indicating that annual periodicity
211 was stronger for the number of species than for the seed biomass. Annual
212 periodicity tended to be clearer for non-fleshy fruits than fleshy fruits at least for
213 seed biomass, although the difference in R^2 value was not significant ($t=2.23$,
214 $p=0.089$). Peak months were one or two months earlier in highland plots
215 (W1050 and E1200) than others for fleshy fruits, but there was no such tendency

216 for non-fleshy fruits (Table 3).

217 Annual periodicity had a more consistent effect on seed fall phenology
218 than climatic factors. We examined 20 GLMs ((5 plots) * (fleshy or non-fleshy) *
219 (#species or biomass of seeds)) on the effect of climate factors, annual
220 periodicity and temporal autocorrelation on seed fall phenology. Among them,
221 annual periodicity was adopted as a determining factor of seed fall phenology for
222 17 GLMs (Table 2). Among them, annual periodicity was the only factor (except
223 for temporal autocorrelation) for 8 GLMs. Various climatic factors were adopted
224 in each model; however, no factor consistently affected in the same direction.
225 The maximum number of times that the same climatic factor was adopted in the
226 same direction in different models was only two times.

227 At population level, annual periodicity was a prevailing pattern of seed
228 fall. We examined annual periodicity for 49 populations of plants (Appendix).
229 These populations constituted at least 1% of the seed fall biomass in each plot,
230 and seed fall was observed twice (W1050) or four times (other plots). These
231 populations belonged to 28 different species. Except for one species in one
232 plot (*Illicium anisatum*, E1200), all showed statistically significant annual
233 periodicity, and *Illicium anisatum* also showed significant annual periodicity in the
234 two other plots (E570 and W1050). Fruiting peak occurred only from
235 September to February for non-fleshy fruits, but fleshy fruits had peaks in a wider
236 variety of months (Fig. 3): in March (*Schefflera heptaphylla* and *Myrsine seguinii*),
237 May (*Litsea acuminata*), June (*Machilus thunbergii* and *Myrica rubra*) and
238 August (*Cornus macrophylla*), to give some examples.

239 Duration of seed fall tended to be shorter for fleshy fruits than for
240 non-fleshy fruits. Seed fall lasted only for five months per year at maximum for

241 fleshy fruits, but it lasted for more than six months for some non-fleshy fruited
242 species such as *Stewartia monadelphica* (E170: 10 mo), *Tsuga sieboldii* (W1050:
243 10 mo; E1200: 7 mo), *Abies firma* (W1050: 9 mo), *Cryptomeria japonica*
244 (W1050: 8 mo), *Quercus salicina/acuta* (E170: 7 mo; W280: 9 mo; and E570: 9
245 mo), and *Illicium anisatum* (W1050: 6 mo). When all of the plots were
246 combined, mean+SD of the months in which seed fall was observed per year
247 was 3.6+1.1 months for fleshy fruits and 5.2+2.6 months for non-fleshy fruits
248 ($t=2.4$, $p=0.019$). This difference was also nearly significant when Fagaceae
249 were excluded ($t=2.0$, $p=0.058$; non-fleshy fruits: 4.8+2.5 months). Therefore,
250 the longer seed-fall duration of non-fleshy fruits than fleshy fruits could not be
251 explained only by the fact that the seed-fall duration of Fagaceae was prolonged
252 by the inclusion of unripe acorns.

253

254 Discussion

255 We showed that there was a clear annual periodicity in the seed fall phenology in
256 all five forests of Yakushima. As we expected, the robust population-level
257 annual periodicity was the basis for community-level annual periodicity. For the
258 fruits that constituted at least 1% of the fruit fall, almost all of them showed
259 statistically significant annual periodicity. Although annual periodicity is the
260 norm in Yakushima, there are species which show non-annual patterns of
261 fruiting. For example, *Ficus superba* and *F. erecta* populations continuously
262 bear fruits throughout the year in the lowland forest in Yakushima (Agetsuma,
263 1995). However, no other species are known to show the same fruiting pattern
264 and fruit production of these species is small and does not affect
265 community-level fruiting phenology. For fleshy-fruited species, seed fall tended

266 to be earlier in highland plots than lowland plots, but there was no such tendency
267 for non-fleshy fruited species. In highland plots, late fruiting of fleshy fruits may
268 be disadvantageous due to damages by coldness or absence of frugivores
269 (Hanya, 2005).

270 We also expected that community-level phenology would become
271 annually periodic when population-level phenology synchronizes among species,
272 and this expectation was also supported. Both fleshy and non-fleshy species
273 tend to have their peak from autumn to winter, which is the same as the general
274 pattern in temperate forest (Ting et al., 2008). The fact that non-fleshy species
275 had stronger community-level annual periodicity than fleshy species may
276 support our expectation, since non-fleshy species synchronized seed fall more
277 strongly than did fleshy species. All of the species in temperate forests are
278 under a common physical stress, such as low temperature and frostbite in winter
279 (Debussche and Isenmann, 1992), and thus it is reasonable to synchronize the
280 timing of fruiting among species. In addition, migrant frugivores migrate from
281 high to low latitude and switch their diet from insectivory to frugivory, making it
282 beneficial to bear fleshy fruits from autumn to winter (Thompson and Willson,
283 1979; Fuentes, 1992; Noma and Yumoto, 1997). However, the degree of
284 synchrony was smaller for fleshy fruits, because some species have their peak
285 in spring or summer. For non-fleshy fruits, there is no competition over
286 dispersal agents, and thus they do not need to avoid overlapping fruiting. For
287 fleshy fruits, it may sometimes be beneficial to bear fruits out of the
288 community-wide fruiting peak to avoid inter-species competition for frugivores
289 (Eriksson and Ehrlen, 1998). The species which bear fruits out of the autumn
290 and winter are only a minority among the community, so community-level annual

291 periodicity is not affected so much if assessed by the number of species.
292 However, when assessed by the seed biomass, community-level annual
293 periodicity can be disturbed by the heavy fruiting of these few species (e.g. E170,
294 fleshy fruits).

295 We expected that the annual periodicity would become evident when
296 the duration of fruiting by individual species becomes shorter. This expectation
297 was not supported because non-fleshy species having a longer duration showed
298 a stronger annual periodicity than fleshy species having a shorter duration. As
299 long as the peak is synchronized among species, community-level seed fall
300 phenology seems to become annually periodic even if individual species drop
301 seeds for a long time. Some non-fleshy fruits dropped seeds for a prolonged
302 period, such as for 10 months a year; however, all of these were wind-dispersed
303 species or acorns. For acorns, unripe and ripe seeds were mixed in the results.
304 For wind- and gravity-dispersed species, a small portion of seeds may have
305 stayed in the canopy even after they became mature.

306 We could not find any climatic factor which consistently affected the
307 timing and intensity of seed fall. However, these results do not negate the
308 possibility that climate affects seed fall. At the coarse scale used in this study
309 (month), the effects of annual periodicity in day length or temperature seem to be
310 much stronger than other factors on the timing of seed fall. When assessed by
311 a finer scale, such as day, however, climate is known to affect phenology in
312 temperate forests (Lechowicz, 1995). In addition, annual periodicity, as a rule,
313 can only affect the timing and cannot affect the intensity of supra-annual
314 variations, which actually existed in Yakushima (Noma, 1997). Based on the
315 seven-year data in the W280 plot, Noma (1997) suggested that summer

316 temperature positively affected the intensity of fruiting in the next year, although
 317 the effect was also not statistically significant in his analysis. Consequently,
 318 four years might be too short to show the effect of climate statistically.

319

320 In conclusion, community-level seed fall phenology in Yakushima clearly showed
 321 annual periodicity, and this was based on the species-level annual periodicity
 322 and synchronization of fruiting among species from autumn to winter.

323 Fleshy-fruited species tended to have peaks of seed fall in more various months
 324 than non-fleshy fruited species, presumably because to reduce inter-species
 325 competition for frugivores.

326

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Table 1. Number of tree species, stems and total basal area in the five plots in Yakushima

Plot	Altitude (m)	Area (ha)	Overall		
			#Species*	#Stems	Basal area (m ² /ha)
E170	170	0.5	33(29,29)	771	50.5
W280	280	0.5	36(31,30)	1290	53.1
E570	570	0.5	32(30,25)	1360	65.8
W1050	1050	0.25	21	447	100
E1200	1200	0.5	26(22,20)	801	84.2

*: Numbers in the parentheses indicate the value when the plot was divided into two 0.25 ha subplots.

399

400

Table 2. Independent factors adopted in the best-fit generalized linear models on seed fall phenology

#Species/ Seed amount	Fleshy/ Non-fleshy	Plot	Adopted factors			
#Species	Fleshy	E170	+AN		+SI16-18	+AR
#Species	Fleshy	W280	+AN			
#Species	Fleshy	E570	+AN		-SI16-18	
#Species	Fleshy	W1050	+AN	+RA4-6		
#Species	Fleshy	E1200	+AN	-RA13-15,-RA16-18		
#Species	Non-fleshy	E170	+AN			
#Species	Non-fleshy	W280	+AN			
#Species	Non-fleshy	E570	+AN	-RA0	-SI10-12	
#Species	Non-fleshy	W1050	+AN			
#Species	Non-fleshy	E1200	+AN			
Seed amount	Fleshy	E170			-AT10-12	
Seed amount	Fleshy	W280	+AN	-RA4-6		+AR
Seed amount	Fleshy	E570	+AN			+AR
Seed amount	Fleshy	W1050	+AN	-RA16-18	-SI4-6	
Seed amount	Fleshy	E1200		+RA4-6		
Seed amount	Non-fleshy	E170	+AN			+AR
Seed amount	Non-fleshy	W280	+AN	+RA,-RA13-15	-SI10-12	+AR
Seed amount	Non-fleshy	E570	+AN			+AR
Seed amount	Non-fleshy	W1050		+RA4-6		
Seed amount	Non-fleshy	E1200	+AN	-RA0	AT0	-SI4-6

AN: annual periodicity (cosine wave function having peak in the month indicated in Fig. 1 and Fig. 2), RA: rainfall, AT: average temperature, MX: maximum temperature, MN: minimum temperature, SI: solar irradiance time, AR: autoregressive factor

Figures after the factors indicate the three months block. RA0 denotes the rainfall of the current month, and RA1-3 denotes the rainfall 1-3 months before the current months.

Bold: significant factors ($p < 0.05$)

+/- before the factor indicates the direction of the regression.

401

402

Table 3. Peak months of seed fall

a. Number of species

Site	Fleshy fruited species	Non-fleshy fruited species
E170	January	November
W280	January	November
E570	December	January
W1050	December	December
E1200	December	January

b. Biomass of seed fall

Site	Fleshy fruited species	Non-fleshy fruited
E170	January*	December
W280	February	September
E570	January	December
W1050	November	December
E1200	November	February

403 *: Annual periodicity not significant

404 Legends to the figures

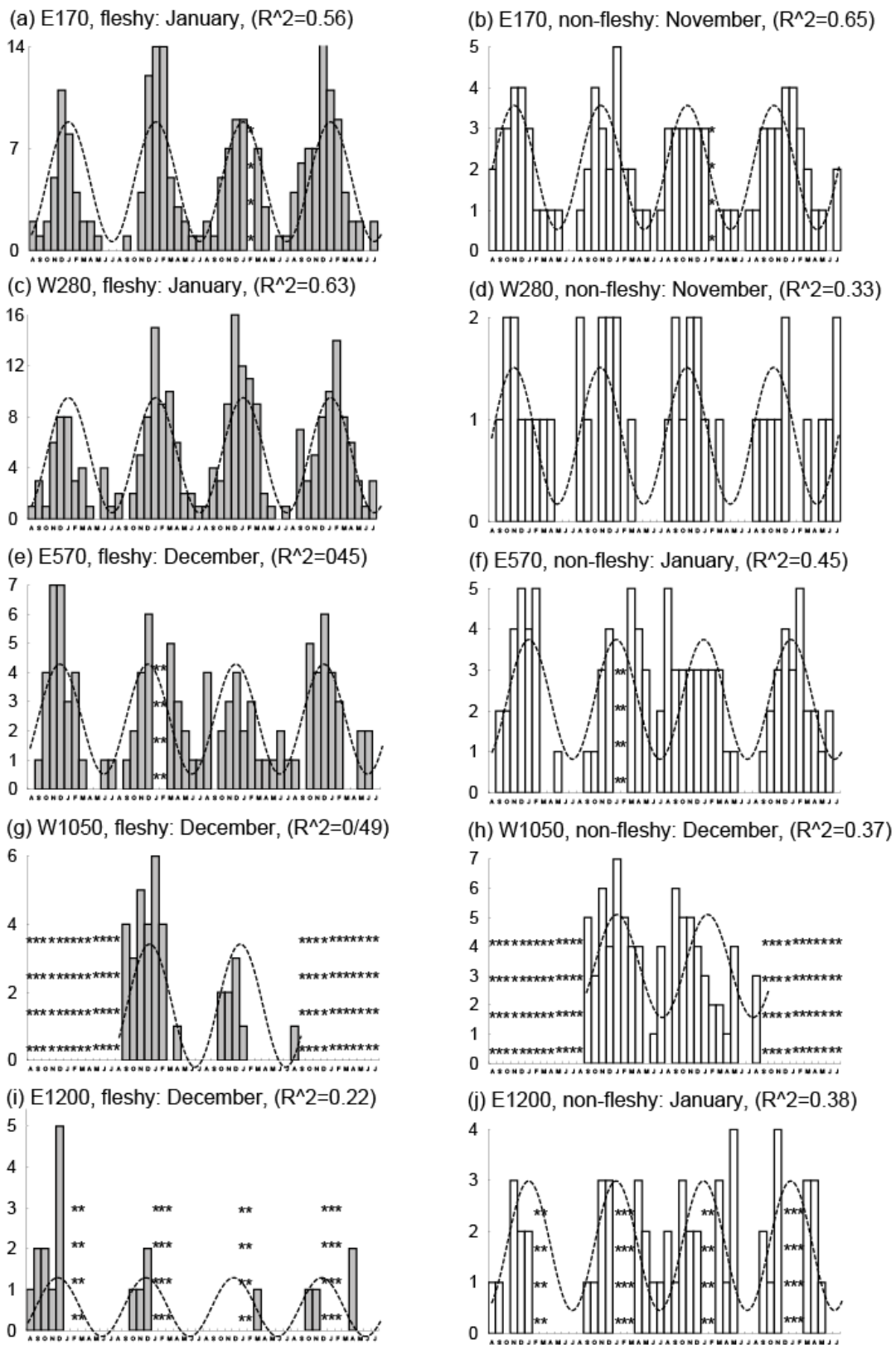
405 Fig. 1. Seasonal variations in the number of species of seed fall. Best-fit
406 cosine curve was drawn and the peak months were indicated in the headers.
407 Y-axis is the number of species. Note that the scale is different among
408 graphs. Data were not available for the months indicated as asterisks. R^2
409 values indicate the proportion that the seasonal variation in seed fall
410 phenology is explained by the annual periodicity (cosine wave function).
411 Left (filled bars): fleshy fruits, right (open bars): non-fleshy fruits.

412 Fig. 2. Seasonal variations in the biomass of seed fall. Y-axis is kg/ha. See
413 legends for Fig. 1.

414 Fig. 3. Number of species whose seed fall peak occurred in each calendar
415 months. Filled bars: fleshy fruits, open bars: non-fleshy fruits. Height of
416 the bars is the number of species.

417

Fruiting phenology in Yakushima

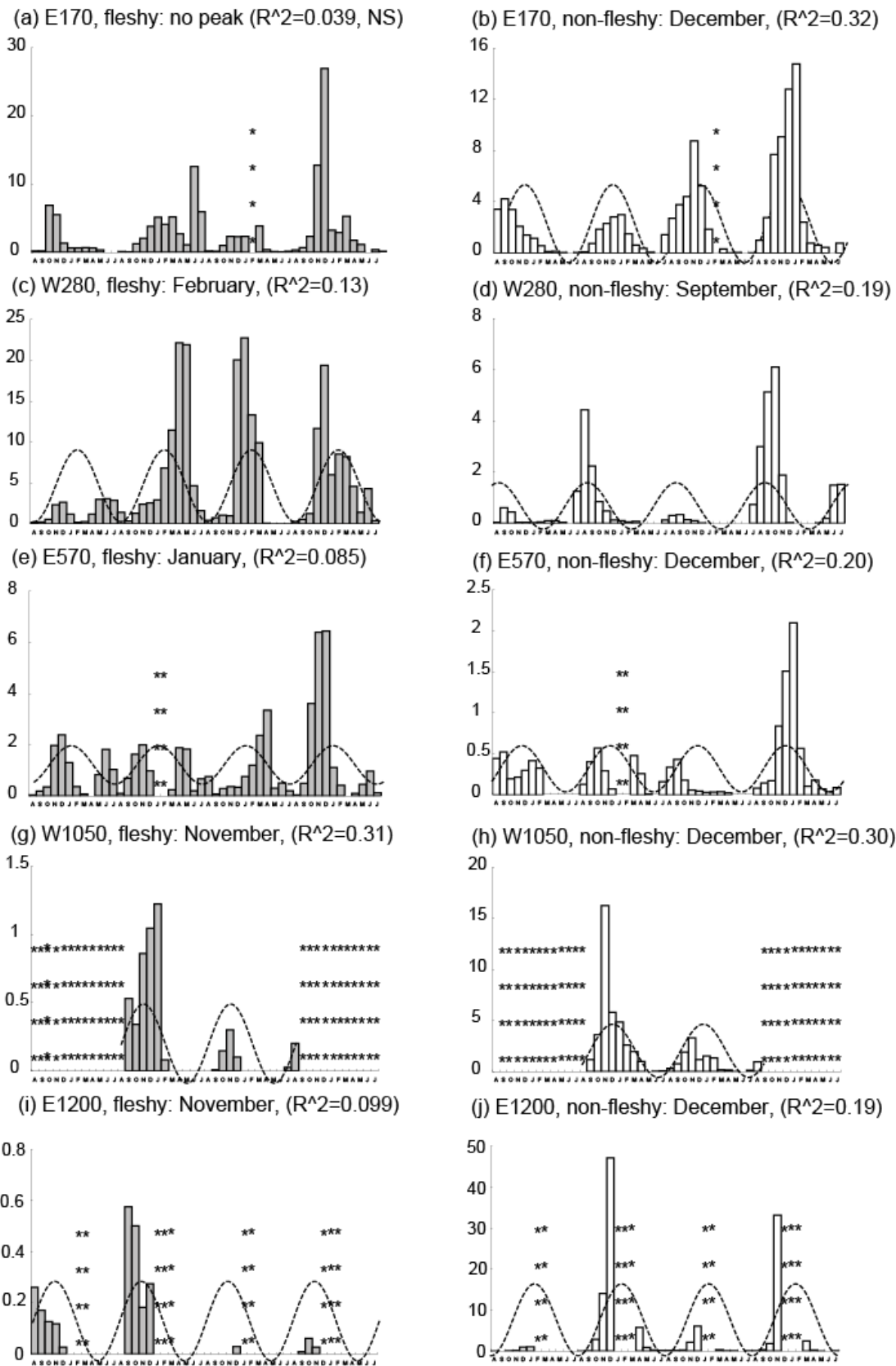


418

419 Fig. 1

420

Fruiting phenology in Yakushima

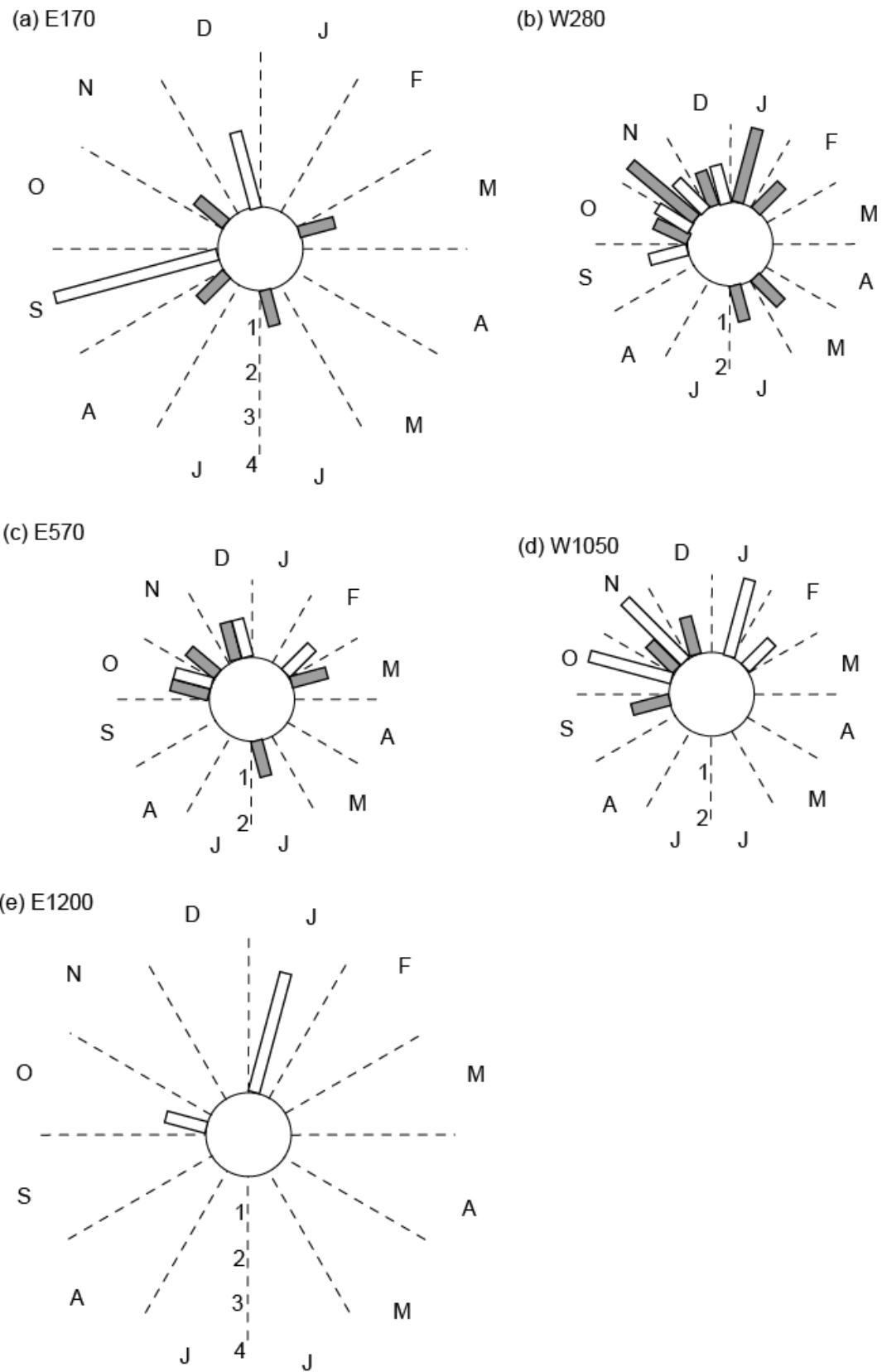


421

422 Fig. 2

423

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424

425 Fig. 3

426

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Appendix. Peak months and duration of seed fall of main species

(a) E170

Family	Species	Fleshy /Non-fleshy	Peak month	Duration of seed fall (#months/year)
Theaceae	<i>Stewartia monadelpha</i>	N	Dec	9.5
Fagaceae	<i>Quercus salicina</i>	N	Dec	7
Theaceae	<i>Camellia japonica</i>	N	Sep	4
Magnoliaceae	<i>Michelia compressa</i>	N	Sep	1.5
Hamamelidaceae	<i>Distylium racemosum</i>	N	Sep	4
Lauraceae	<i>Neolitsea sericea</i>	F	Nov	3
Lauraceae	<i>Machilus thunbergii</i>	F	Jun	1
Theaceae	<i>Camellia sasanqua</i>	N	Sep	2
Cornaceae	<i>Cornus macrophylla</i>	F	Aug	0.5
Araliaceae	<i>Schefflera heptaphylla</i>	F	Mar	2

(b) W280

Family	Species	Fleshy /Non-fleshy	Peak month	Duration of seed fall (#months/year)
Fagaceae	<i>Quercus salicina</i>	N	Nov	9.25
Lauraceae	<i>Neolitsea aciculata</i>	F	Nov	3.5
Theaceae	<i>Ternstroemia gymnanthera</i>	F	Oct	4.25
Myrsinaceae	<i>Ardisia sieboldii</i>	F	Jan	4
Lauraceae	<i>Litsea acuminata</i>	F	May	3.25
Fagaceae	<i>Lithocarpus edulis</i>	N	Oct	2.75
Theaceae	<i>Cleyera japonica</i>	F	Jan	4.25
Lauraceae	<i>Machilus thunbergii</i>	F	Jun	3.25
Lauraceae	<i>Neolitsea sericea</i>	F	Dec	3.75
Fagaceae	<i>Castanopsis sieboldii</i>	N	Sep	2
Symplocaceae	<i>Symplocos prunifolia</i>	F	Nov	5
Hamamelidaceae	<i>Distylium racemosum</i>	N	Dec	2.25
Myrsinaceae	<i>Myrsine sequinii</i>	F	Feb	4.5

(c) E570

Family	Species	Fleshy /Non-fleshy	Peak month	Duration of seed fall (#months/year)
Fagaceae	<i>Quercus salicina/acuta</i>	N	Sep	8.5
Myricaceae	<i>Myrica rubra</i>	F	Jun	3
Theaceae	<i>Stewartia monadelpha</i>	N	Dec	5
Myrsinaceae	<i>Myrsine sequinii</i>	F	Mar	4.25
Symplocaceae	<i>Symplocos prunifolia</i>	F	Dec	5.25
Pinaceae	<i>Tsuga sieboldii</i>	N	Feb	4.75
Illiciaceae	<i>Illicium anisatum</i>	N	Oct	1.5
Lauraceae	<i>Neolitsea aciculata</i>	F	Nov	1.5
Theaceae	<i>Ternstroemia gymnanthera</i>	F	Oct	2.5

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(d) W1050

Family	Species	Fleshy /Non-fleshy	Peak month	Duration of seed fall (#months/year)
Cupressaceae	<i>Cryptomeria japonica</i>	N	Jan	10
Pinaceae	<i>Abies firma</i>	N	Nov	8.5
Pinaceae	<i>Tsuga sieboldii</i>	N	Feb	5
Hamamelidaceae	<i>Distylium racemosum</i>	N	Nov	5.5
Theaceae	<i>Stewartia monadelphica</i>	N	Jan	5
Fagaceae	<i>Quercus salicina/acuta</i>	N	Oct	5.5
Symplocaceae	<i>Symplocos tanakae</i>	F	Jan	1
Illiciaceae	<i>Illicium anisatum</i>	N	Oct	7.5
Araliaceae	<i>Dendropanax trifidus</i>	F	Nov	2
Symplocaceae	<i>Symplocos myrtacea</i>	F	Sep	2
Theaceae	<i>Cleyera japonica</i>	F	Dec	4.5

(e) E1200

Family	Species	Fleshy /Non-fleshy	Peak month	Duration of seed fall (#months/year)
Pinaceae	<i>Tsuga sieboldii</i>	N	Jan	6.5
Pinaceae	<i>Abies firma</i>	N	Jan	5.5
Cupressaceae	<i>Cryptomeria japonica</i>	N	Jan	2.5
Theaceae	<i>Camellia japonica</i>	N	Oct	1.5
Fagaceae	<i>Quercus salicina/acuta</i>	N	Aug	4.5
Illiciaceae	<i>Illicium anisatum</i>	N	Nov*	4.5

F: fleshy-fruits; N: non-fleshy-fruits

*: Annual periodicity not significant