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BERRIES IN WINTER: A NATURAL HISTORY OF FRUIT RETENTION IN FOUR SPECIES ACROSS ALASKA

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ABSTRACT

Plants with persistent fleshy fruits that last throughout fall and into winter and spring are an important source of nutrition for animals and people in boreal, subarctic, and arctic regions, but little information on fruit retention or loss is available for these regions. We evaluated fruit loss for four species across Alaska using data from our Winterberry community science network. Plants of *Rosa acicularis* Lindl., *Viburnum edule* (Michx.) Raf., *Vaccinium vitis-idaea* L., and *Empetrum nigrum* L. were monitored on a weekly basis throughout fall until snow cover and again after snow melt in 24 communities in six ecoregions in 2016–2020. Observers counted fruits and classified them into "unhealthy" (dried, rotten, or damaged) or "healthy". Number of fruits lost per day (absolute loss rate) decreased over the course of the fall, but percent of fruits lost per day (relative loss rate) was constant for all species except *E. nigrum*, where it declined throughout the fall. Rates of loss were similar across ecoregions and climatic gradients, although for *V. vitis-idaea* the two most southern sites had the lowest relative loss rates and for *E. nigrum* the sites warmest in summer had the lowest loss rates. Fruit loss pulse events (>15% fruits lost in one week) were uncommon (<5% of weekly observations). At the time of persistent winter snow cover, plants retained 25–50% of fruits, with higher retention in more southern ecoregions. During winter, both relative fruit loss and absolute fruit loss rates dropped compared to fall, but in spring they rebounded to fall levels. Low proportions of unhealthy fruits in *E. nigrum* and *V. vitis-idaea* were in part due to rapid abscission of unhealthy fruits, while the other two species tended to retain unhealthy fruits. We estimate that vertebrate frugivores obtain 6–45 × as many fruits in fall as do decomposers / invertebrates. The higher loss rates during the snow-free seasons and constant rates of fruit loss for most of the focal species and locations suggest that longer falls and earlier fruit ripening will lead to lower fruit availability to animals in winter and spring.

Key Words: arctic, boreal, citizen science, *Empetrum nigrum*, frugivory, *Rosa acicularis*, *Vaccinium vitis-idaea*, *Viburnum edule*.

In temperate zones, most plants that use vertebrates as seed dispersers lose a high proportion of their fruits over a short time period following ripening (e.g., Thompson and Willson 1978; Stiles 1980; Sargent 1990), while a smaller number of species retain their fruits throughout the fall and winter (e.g., Stiles 1980; Borowicz and Stephenson 1985; Jones and Wheelwright 1987; Sallabanks 1992; Gervais and Wheelwright 1994). In boreal, subarctic and arctic regions, plants with persistent fruits are well represented in the woody shrub flora: they include species in the Ericaceae (e.g., *Vaccinium vitis-idaea* L., *V. oxycoccos* L., *Arctostaphylos uva-ursi* (L.) Spreng.), Empetraceae (*Empetrum nigrum* L.), Caprifoliaceae (*Viburnum edule* (Michx.) Raf.), and Rosaceae (e.g., *Rosa acicularis* Lindl.) (West 1982; Pullainen and Tunkkari 1991; Aiken et al. 2007; Krebs et al. 2010; Hupp et al. 2013; Mulder unpublished data). A few herbaceous species also retain their fruits for extended periods of time (e.g., *Cornus canadensis* L. (Cornaceae; West 1982), *Actaea rubra* Bigelow (Ranunculaceae); B. Spellman, Natural Resources Conservation Service Alaska, personal communication), and Convallariaceae (e.g., *Maianthemum racemosusm* Link.; M. Goff, personal communication). Persistent fleshy fruits constitute an important component of the late fall, winter, and early spring diet for many animals at times when other food is scarce, including microtine rodents (e.g., northern red-backed voles, *Myodes rutilus*, West 1982; Krebs et al. 2010), foxes (e.g., Dell'Arte et al. 2007; Needham et al. 2014), bears (McLellan and Hovey 1995; Munro et al. 2006), migrating waterfowl (Hupp et al. 2013), and birds that overwinter in the north like ptarmigan and grouse (Pullainen and Tunkkari 1991; Wegge and Kastdalen 2008). Fruits may also be an important source of water in springtime to birds such as grouse and geese (Pullainen and Tunkkari 1991; Hupp et al. 2013). Fleshy fruits are of high nutritional and cultural importance to Indigenous and rural communities throughout Alaska and Canada (Kari 1987; Bellew et

FIG. 1. States of fruits of the four focal species. A. Fruits of *Viburnum edule* (Highbush Cranberry) in ripe (bottom 3), infected (top left) and shriveled (top center) stage. B–D. Fruits of *Rosa acicularis* (Prickly Rose) in ripe and infected (B), dry (C) and damaged (D) state. E–F. Fruits of *Empetrum nigrum* (Crowberry) in ripe (top 2 in E and top in F), damaged (bottom left in E) and shriveled (bottom right in E, bottom in F) stages. G–H. Fruits of *Vaccinium vitis-idaea* (Lingonberry) in ripe (top in both), shriveled (bottom in G) and infected (left 3 in H) state. All images courtesy of A. Ruggles, except for D (C. Mulder).

al. 2006; Hupp et al. 2015), and people often collect species like *Vaccinium vitis-idaea* and *V. oxycoccos* in springtime (Kari 1987; Aiken et al. 2007), as reflected in the Denai'na name for *V. vitis-idaea*: "Hey Gek'a" or "Winter Berry" (Kari 1987).

A common explanation for why some species retain their fruits is that competition with other species for seed dispersers is reduced during the colder months (Stiles 1980; Jones and Wheelwright 1987). However, plants with persistent fruits also face a challenge: fruit retention over many months may result in high damage by microbes and invertebrates (Thompson and Willson 1978; Herrera 1982). To counter this, plants invest in compounds, such as the organic acids found in *Vaccinium* species (Cipollini and Stiles 1992; Aiken et al. 2007; Ermis et al. 2015; Stobnicka and Gniewosz 2017), *Arctostaphylos uva-ursi* (L.) Spreng. (Cipollini and Stiles 1992), and *Viburnum opulus* L. (Jones and Wheelwright 1987); such compounds may make fruits less palatable to vertebrate seed dispersers, resulting in slower dispersal overall (Stiles 1980; Jones and Wheelwright 1987; Cipollini and Stiles 1993). Some species may also contain non-pathogenic microbes that reduce the growth of pathogenic microbes (Cipollini and Stiles 1993). At high latitudes (>50°N), several factors may further select for persistent fruits. First, the role of ground thaw in triggering flower development combined with the short growth season results in highly synchronous flowering and ripening of fruits across species in early fall (Barr et al. 2009; Wolkovich and Cleland 2011; Mulder and Spellman 2019). This likely exacerbates competition for seed dispersers in early fall but results in fewer choices for frugivores later in the season. Second, fruit loss to microbes during extended periods on the plant may be lower than at more southern latitudes because of cool fall temperatures and, in areas with a strongly continental climate, low humidity.

Despite the demonstrated importance of fruit retention to animal populations and the potential importance to the plants themselves, very few studies have directly measured fruit retention or loss through fall and winter in high latitude wild plants. Numerous studies have attempted to indirectly evaluate the abundance of overwintering fruits in the guts, crops, and fecal matter of animals (see examples above). This information, however, does not provide an accurate measure of fruit removal over time, as it does not take into account changes in consumer population size or behavior, or availability of other foods. Furthermore, these data do not provide clear insights into the costs and benefits for plants of retaining fruits, such as how seed dispersal is distributed over time, and when and to what extent fruits are lost to decomposers. Although in some species a high proportion of fruits remain in a "healthy" state, others appear infected or shriveled, even while retained on the plant (Fig. 1). Thus, a portion of the carbon and nutrients in the fruits are likely obtained by decomposers rather than frugivores even before the fruits are lost from the plant, and a shift in the proportion of fruits in different states (e.g., due to changes in environmental conditions) would affect food web structure. The one study we were able to find in a high latitude ecosystem that addressed losses to consumers vs. decomposers documented the fate of *Cornus canadensis* fruits from peak crop to snowfall over 3 yr and found that the majority of the berries each year were removed or damaged by consumers, while decomposers infected an average of 18% of the remaining fruits (Burger 1987). The study pointed to a need for further documentation of the fate of berries in the fall and winter season within the high latitudes, where the abundance and condition of overwintering fruits may play a heightened role in winter food webs relative to other systems where other foods are more available.

Historical datasets and surveys of longtime berry pickers suggest timing of berry production is becoming more variable (Hupp et al. 2015; Spellman and Mulder 2016). Year to year variation in the timing of fruit loss and condition of the fruit is likely influenced by long term increases in high-latitude temperatures (Wolken et al. 2011) and growing season length (Mulder and Spellman 2019). Decreased precipitation as snow fall may result in an even earlier start to the growing season (Littell et al. 2018), further lengthening the growing season. In the far North, the timing of berry ripening is driven primarily by the timing of flowering, which in turn is driven by spring conditions (time of snow melt and temperature) (Mulder and Spellman 2019). As a result, berries may be exposed to consumption during late summer and early fall (above-freezing conditions) for a longer period. Will this result in a greater loss of fruit in late summer and fall, leaving fewer resources for consumers in late fall, winter, and spring? Will it result in greater carbon and nutrient flow to decomposers? We need a basic understanding of the natural history of fruit retention to start to answer these questions.

In this study, we tracked fruit retention in four plant species with very wide distributions across northern North America. We developed a youth-centered, state-wide community science network called "Winterberry" to collect direct observations of fruit retention from the time of ripening until snow cover, and again from snow melt into the spring. Our data span 46 sites in 24 communities across 6 ecoregions of Alaska and were collected during a 4-yr period (2016–2020). We asked the following questions for each species at the site level:

1. How does rate of fruit loss (number of fruits and percent of fruits) and the proportion of fruits in a "healthy" state (defined as fruits that are not rotted or shriveled and have no obvious invertebrate damage) differ between seasons (fall, winter, and spring)? We predicted lower absolute loss rates in winter than in fall or spring due to lower animal and microbial activity. Rates of fruit loss in tall (above-snow) or short (below-snow) species may depend on the relative importance as frugivores of birds and above-snow mammals, such as foxes, compared to subnivean animals such as microtine rodents.
2. How do fruit loss rates (absolute and relative) and proportion of healthy fruits change over the course of the fall? These are the result of opposing effects of number of frugivores and competition for frugivores, both of which are expected to be greater in early fall, as well as by loss rates due to abscission (expected to be greater for unhealthy fruits).
3. Do fruit loss rates and the proportions healthy fruits differ between ecoregions of Alaska? We do not have *a priori* predictions for rates of removal, as they will depend on both the total availability of frugivores and competition with other species for seed dispersal. We expected greater proportions of healthy (non-diseased) fruits in dry ecoregions, such as the Intermontane Boreal Zone, and higher rates of loss in wetter locations, such as the Coastal Rainforest and Aleutian Meadows ecoregions (Fig. 2).
4. What proportion of fruits transition from healthy to unhealthy (rotten, shriveled, or damaged by invertebrates), and at what rates are healthy and unhealthy fruits lost from the plant? Does this differ by season or by ecoregion? High losses of healthy fruits suggest a large role of vertebrate frugivores compared to decomposers and invertebrate frugivores, while high rates of transition from healthy to infected fruits suggest decomposers play a dominant role in fruit loss.

We asked an additional set of questions at the individual plant level: Do more fruits on a plant affect: a) the probability of at least one fruit being lost through either removal or abscission, or b) the proportion of fruits lost?

METHODS

Four focal species were selected: *Rosa acicularis* (Prickly Rose), *Viburnum edule* (Highbush Cranberry), *Vaccinium vitis-idaea* (Lowbush Cranberry or Lingonberry), and *Empetrum nigrum* (Crowberry). Species selection was based on the following traits: 1) a wide distribution across Alaska (Fig. 2A) and high latitudes in North America or Eurasia (Hultén 1968); 2) retention of fruits throughout fall and winter, 3) high local abundance in the communities involved in our community science program, and 4) high importance to people in Alaska and the circumpolar North (Hupp et al. 2015). *Rosa acicularis* and *V. edule* are generally >0.5 m tall in most locations and are therefore only partially covered by snow during winter, while *V. vitis-idaea* and *E. nigrum* are < 0.3 m tall and are completely covered by snow during most of the winter in most locations.

Plants were monitored at 46 sites in 24 communities by $\approx$ 1500 volunteers. All volunteers participated with free, informed, and prior consent under our University of Alaska Fairbanks IRB plan submitted and approved for our program (UAF IRB #1062412-5), which also included human subjects data for our education research (for more information on the education research see Spellman et al. 2019).

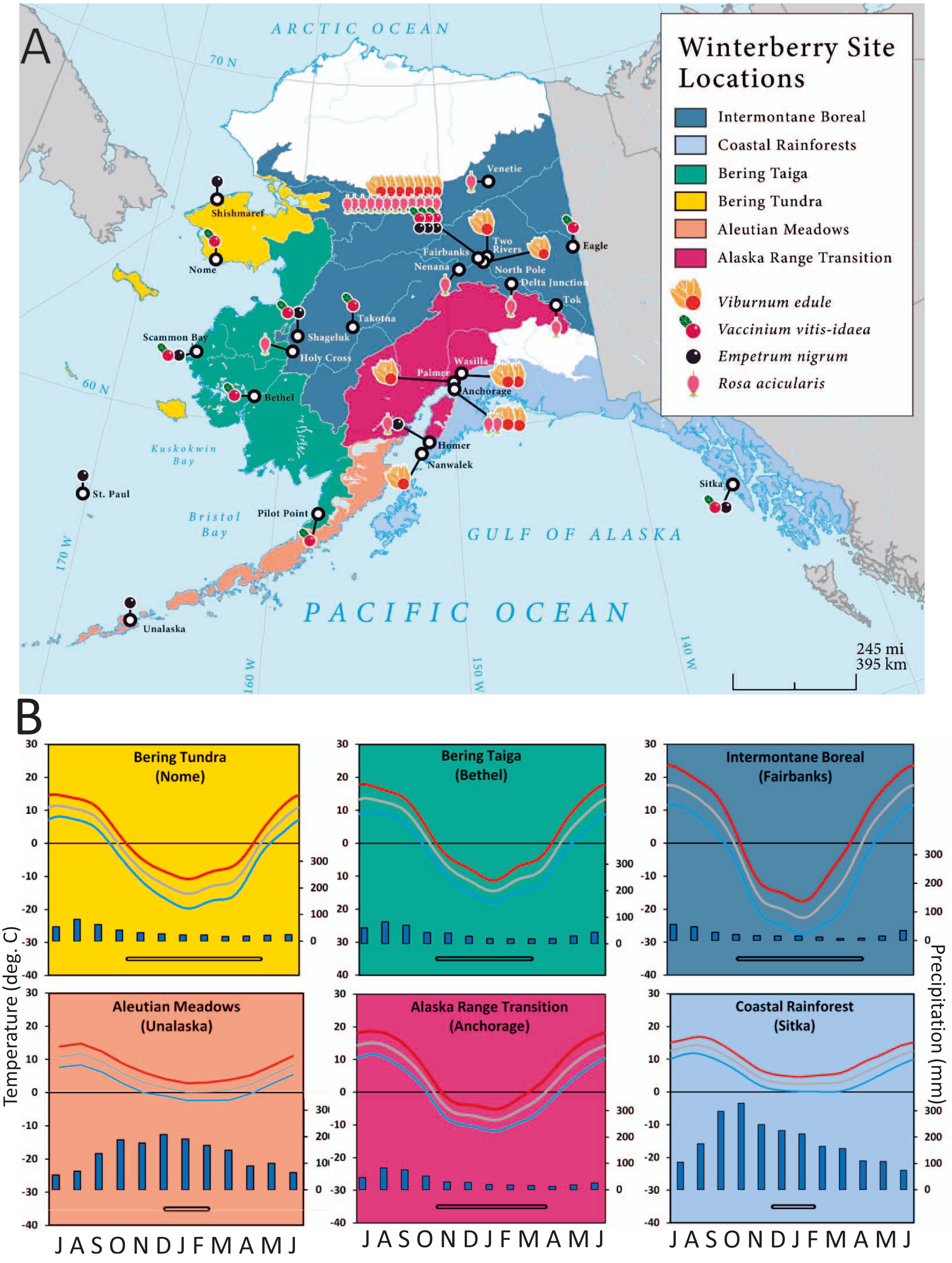

FIG. 2. Ecoregions and their climates. A. Collection site locations across the six ecoregions based on Nowacki et al. (2001). The number of symbols corresponds to the number of sites at that location. B. Temperature and precipitation profiles for a representative town in each ecoregion based on 1981–2010 means (U.S. Climate Data, 2020). Note that profiles are centered on mid-winter. The bar across the bottom of each graph represents time during which the ground is covered in snow, for most regions defined as from >50 mm of snowfall after the minimum daily temperature < 0°C until the mean daily temperature > 0°C. In the Coastal Rainforest and Aleutian Meadows habitats there is no season-long snow cover, but most snow fall occurs in December, January, and February.

Individuals, families, youth groups and educators tracked the abundance and condition of the fruits on a minimum of 20 marked individual plants with a minimum of 100 fruits across the plants. Individual plants were added and marked as needed to meet the minimum 100 fruits for the start of the monitoring season. Each individual plant was observed each week at all of the sites, and the total number of fruits remaining on the plant was recorded in five condition categories: "unripe" (defined as having green color still visible on the fruit), "ripe" (fully red or black in color), "rotten" (discolored and squishy or moldy), "dried" (berry is dehydrated, shriveled and hard to the touch), and "damaged" (fruit skin is ripped or has holes in it) (Fig. 1). Since observers reported having difficulty distinguishing between rotten and dried, especially later in the season for *R. acicularis*, after the first year we added a "rotten or dried" category. In some instances, volunteers tracked multiple species within their site, each with a minimum of 20 individual plants. All volunteers received training setting up their site and in the classification of these berry conditions. Weekly monitoring began as soon as the fruit began to ripen or at the start of the school year for the youth groups in mid-August, ceased when the snow fell and remained at the site so as not to disturb the subnivean environment, and resumed in the spring when the snow had melted until the berries had all been removed, or the first flowers appeared. Observers were encouraged to report sightings of animals or animal sign. Data quality was assured through a rigorous quality review process that included consultation with each group of volunteers in a "data jam" session. Mean data quality issue rates were very low (only 2.7% of all observations). The full protocol for citizen scientists is available in Appendix S1. Total number of plant observations were 3559 for *R. acicularis*, 3676 for *V. edule*, 2754 for *V. vitis-idaea*, and 1507 for *E. nigrum* (grand total = 11,496 observations).

Sites spanned six of the eight "unified ecoregions" of Alaska: Bering Tundra, Bering Taiga, Intermontane Boreal, Alaska Range Transition, Coastal Rainforest, and Aleutian Meadows ecoregions (Nowacki et al. 2001) (Fig. 2, Table 1; see Appendix 1 for details of data collection). These ecoregions are described according to broad similarities in climate, vegetation and disturbance regime, and represent polar, boreal, and maritime-like systems. Annual temperature and precipitation means for representative locations within each ecoregion are shown in Figure 2B. Bering Tundra sites are characterized by a mix of maritime and polar climates, with sea ice and dry winds in winter, and cool, moist conditions after spring break up. Soils are underlain by continuous permafrost, and vegetation is treeless tundra. Bering Taiga has a moist polar climate, with shrub tundra and wetlands dominating the discontinuous permafrost landscape. Intermontane Boreal sites are characterized by a strong continental climate with very cold winters and warm summers. The permafrost is discontinuous and vegetation is dominated by White Spruce (*Picea glauca* (Moench) Voss, Pinaceae), Birch (*Betula neoalaskana* Sarg., Betulaceae), and Aspen (*Populus tremuloides* Michx., Salicaceae) trees on south facing slopes, and Black Spruce (*Picea mariana* Britton, Sterns & Poggenb., Pinaceae) and scrub tussock on north facing slopes and valley bottoms. Alaska Range Transition is a mix of maritime and continental climates, with an abundance of precipitation; soils are generally free of permafrost. Coastal Rainforest has a cool, hypermaritime climate with only minor seasonal variation and long periods of cloudy, rainy weather. Permafrost is absent, and vegetation is dominated by rainforests of Sitka Spruce (*Picea sitchensis* (Bong) Carrière, Pinaceae) and Hemlock (*Tsuga heterophylla* Sarg., Pinaceae). Aleutian Meadows have a cool maritime climate, with cold ocean winds and persistent clouds and fog; the soil is permafrost-free and vegetation is dominated by low shrubs and ericaceous heath and grass. The town of Shageluk is in the transition zone between Intermontane Boreal and Bering Taiga and was assigned to Bering Taiga based on the greater similarity to sites in this ecoregion. If the sample size for an ecoregion was very low for a given species (one or two site-year combinations) and the location was on the edge of an ecoregion, it was combined with the most similar ecoregion for that species only; this occurred once for each species (Appendix 1).

Because our ecoregions are very large and some sites are near the border with another ecoregion, analyzing by ecoregion might miss changes across space driven by continuous variables such as temperature and precipitation. To classify communities by climate gradients, we obtained long term means (1961–1990) for temperature (mean daily averages for January, April, July and October) and precipitation (total precipitation as rain and as snow, number of months with only rain, only snow, or mixed) for each community (see Appendix 2 for details). Since we were interested in spatial variation rather than the effect of individual climate variables, we combined these nine variables in a principal components analyses (function *prcomp* in R version 3.5.2, R Foundation for Statistical Computing, Vienna, Austria) to generate climate axes. The first two axes explained 81% of variation (Appendix 2). The first axis, PC1, represented fall and winter conditions: in communities with high values winter came earlier (lower mean temperature in October), was colder (lower meant temperature in January), and lasted longer (more months of snow only) than in communities with lower values. The second axis, PC2, represented spring and summer conditions: in communities with high values the growth season started late (lower mean temperature in April) and was cool (lower July temperature) and there were more months of rain only than in communities with lower values (Appendix 2). We will refer to sites with

TABLE 1. SITE LOCATIONS AND DESCRIPTIONS. S = School. Species abbreviations: Empnig = *Empetrum nigrum*, Rosaci = *Rosa acicularis*, Vacvit = *Vaccinium vitis-idaea*, Vibedu = *Viburnum edule*.

Eco-region	Site name	Nearest town	Lat. (°N)	Long. (°W)	Elev. (m)	Habitat type	Species
Bering Tundra	Shismaref S.	Shishmaref	66.257	166.072	5	grasses, forbs	Empnig
	Anvil City Science Academy	Nome	64.541	165.411	30	tundra	Vacvit
	Kamenista	St. Paul	57.160	170.270	10	tundra	Empnig
Bering Taiga	Innoko River S.	Shageluk	62.654	159.532	42	boreal forest / tundra	Empnig Vacvit
	Holy Cross Elementary	Holy Cross	62.202	159.766	23	grasses, forbs	Rosaci
	Scammon Bay S.	Scammon Bay	61.842	165.582	5	tundra	Empnig Vacvit
	Bethel Regional High S.	Bethel	60.803	161.767	7	tundra	Vacvit
	Pilot Point Secondary Classes	Pilot Point	57.59	157.59	8	tundra	Vacvit
Inter-montane Boreal	John Fredson S.	Venetie	67.016	146.412	175	coniferous forest	Rosaci
	Denali Elementary School 3rd and 5th grades	Fairbanks	64.839	147.753	134	deciduous forest	Rosaci
	Tanana Middle S.	Fairbanks	64.846	147.665	138	coniferous forest	Rosaci Vibedu
	Randy Smith Middle S.	Fairbanks	64.857	147.754	134	deciduous forest	Vibedu
	Parkinson Yard	Fairbanks	64.862	147.918	200	coniferous forest	Empnig Vacvit Rosaci
	Parkinson #2	Fairbanks	64.803	147.997	277	mixed boreal forest	Vibedu Rosaci
	Smith Lake	Fairbanks	64.864	147.864	165	mixed boreal forest	Empnig Vacvit Vibedu
	Murie Trail	Fairbanks	64.860	147.845	180	Deciduous forest	Empnig Vacvit
	UAF satellite dish	Fairbanks	64.859	147.856	180	Deciduous forest	Rosaci Vibedu
	Mulder Yard	Fairbanks	64.896	147.813	227	Deciduous forest	Rosaci Vibedu
	Weller Elementary	Fairbanks	64.887	147.592	281	Deciduous forest	Vibedu
	Two Rivers Elementary	Two Rivers	64.877	147.039	228	Deciduous forest	Vibedu
	Anne Wien Elementary	Fairbanks	64.858	147.746	133	Deciduous forest	Rosaci
	Hunter Afterschool Club	Fairbanks	64.833	147.730	135	Deciduous forest	Rosaci
	Watershed Elementary - KG	Fairbanks	64.827	147.868	134	Tall shrubs	Rosaci
	Watershed Elementary - Powerline Trail	Fairbanks	64.823	147.874	135	Tall shrubs	Rosaci
	Watershed Sit Spots	Fairbanks	64.820	147.878	136	Deciduous forest	Rosaci
	Boreal Sun S.	Fairbanks	64.825	147.735	134	Deciduous forest	Rosaci
	Arctic Light Elementary	North Pole	64.826	147.692	138	Tall shrubs	Rosaci
	North Pole Middle S.	North Pole	64.746	147.342	153	Coniferous forest	Vibedu
	Eagle Community S.	Eagle	64.787	141.205	272	Deciduous forest	Vacvit
	Nenana S.	Nenana	64.564	149.080	110	Tall shrubs	Rosaci
	Delta Future Farmers of America	Delta Junction	64.03	145.698	364	Deciduous forest	Rosaci
	Tok School	Tok	63.326	142.98	502	Deciduous forest	Rosaci
	Takotna Community S.	Takotna	62.989	156.043	121	Moss / lichen	Vacvit
Alaska Range Transition	Mat-Su Career & Technical High	Wasilla	61.607	149.363	138	Deciduous forest	Vibedu
	Palmer Girl Scout Troop 849	Palmer	61.579	149.291	64	Deciduous forest	Vibedu
	Anchorage Botanical Garden	Anchorage	61.334	149.751	175	Mixed boreal forest	Vibedu
	Birch Hill	Anchorage	61.250	149.702	92	Mixed boreal forest	Vibedu
	East High Environmental Club	Anchorage	61.200	149.804	53	Deciduous forest	Vibdu
	Campbell Creek Bridge	Anchorage	61.165	149.768	84	Deciduous forest	Rosaci
	Polaris K–12 S.	Anchorage	61.163	149.853	40	Deciduous forest	Rosaci
	Wynn Nature Center	Homer	59.686	151.481	404	muskeg	Empnig
	Center for Alaska Coastal Studies HQ	Homer	59.646	151.524	28	herbaceous	Rosaci
Coastal Rainforest	Nanwalek S.	Nanwalek	59.354	151.921	11	Tall shrub	Vibedu
	Sitka Raptor Center	Sitka	57.052	135.314	16	muskeg	Empnig Vacvit
Aleutian Meadows	Unalaska City High S.	Unalaska	53.874	166.520	27	Shrub tundra	Empnig
	Eagles View Elementary	Unalaska	53.870	166.520	23	Shrub tundra	Empnig

high PC1 values as "winter cold" and ones with high PC2 values as "summer cold". When plotted by PC1 and PC2, most communities clustered by ecoregion, but there was a cluster of five winter warm / summer cold communities that included one community from every ecoregion except Intermontane Boreal (Appendix 2); we therefore analyzed data both by ecoregion and by climate variables (PC axes).

Data Analysis

Because of large differences in data collection efforts in fall, winter, and spring, data were analyzed by season. "Fall" was defined as the period prior to season-long snow on the ground; data were usually collected weekly during this time period. "Winter" was the period when the ground and / or plants were covered with snow or ice; data were not collected during this period because of the potential for disturbance of the vegetation. "Spring" was defined as the period from re-initiation of data collection once the snow had melted until data collection ceased (either because the group disbanded or because the plants came into flower); at many sites data were collected only once or a few times in spring. These were good operational definitions for Bering Tundra, Bering Taiga, Intermontane Boreal, and Alaska Range Transition ecoregions, where snow melt events in winter are rare and short lived. In the two southern-most ecoregions, Coastal Rainforest and Aleutian Meadows, there was no season-long snow cover and data were collected continuously (though less frequently in winter). However, these ecoregions did have a 3-mo period (Dec–Feb) during which snowfall was considerable, so we defined this as "winter".

We expected a lack of independence for plants within a site because a given consumer or decomposer could affect multiple plants, and for some species (e.g., *V. vitis-idaea*) multiple ramets might constitute a single genet. Therefore, we used the means per site for a given date for all analyses except those at the plant-level (the effect of number of fruits on probability of fruit loss), which used individual plants as the experimental unit.

Ideally, data collection would have started as most fruits were ripening, all plants would have been monitored weekly until snowfall, and weekly once the snow melted until no fruit remained. However, at many sites observations were not initiated until after all fruits had ripened, leaving the initial size of the cohort unknown. Many groups only recorded data once in the springtime (because the school year was ending or because very few fruits remained) and some groups recorded only in the fall (e.g., one-semester college or high school courses). As a result, the dataset for fall is much more extensive than for winter or spring. We therefore perform simple comparisons of patterns of fruit loss for the three seasons, followed by in-depth analyses of changes over the course of the fall season.

Comparisons between seasons. We first calculated the percentage of fruit lost in each season based on the change in fruit number at each site from start to end of the season. The number of year-site combinations decreased from fall to winter to spring; sites for which no data were recorded were excluded from the following season unless it was known that no fruits remained at the start of that season, in which case it was recorded as zero. We then expressed the change from the start to the end of the season as number of fruits lost per plant per day (including zeroes for sites where no fruits were present at the start of the season) and percent of fruits lost per plant per day (excluding sites where no fruits were present at the start of the season). Absolute rate of fruit loss is indicative of supply rates to animals, while relative rate of fruit loss, the complement of retention rate, represents the risk of loss from the plant for an individual fruit.

A third variable, proportion of fruits in a "healthy" state, was calculated as: prophealthy = (# unripe fruits + # ripe fruits) / total number of fruits. Unripe or ripe fruits were considered healthy while shriveled (dry), infected (rotten), or damaged fruits were considered unhealthy. We combined these three "unhealthy" categories because of difficulties distinguishing between the first two, and because damaged fruits, which were uncommon (<3.2% of all observations except for *R. acicularis* [8.3% of observations]), were usually also shriveled or infected.

For each of the three response variables (absolute and relative fruit loss and proportion of healthy fruits) we ran maximum-likelihood based mixed models with season as the fixed variables and the year-site combination as a random variable using the *lmer* function in the *lme4* package in R. Only sites for which data for both seasons being compared were available were included in these analyses. The number and percent of fruits lost per day were $\log_{10}$-transformed and prophealthy was arcsine-square root transformed to improve adherence to model assumptions. We controlled the family-wise error rate by comparing the P-values from the set of 36 tests to values generated using a Benjamini-Hochberg procedure (Benjamini and Hochberg 1995).

Changes over the course of the fall season. Intervals between monitoring were not consistent, and not every plant was monitored on every occasion. We therefore focused our analyses on changes between consecutive observations, rather than comparisons to the initial cohort. The absolute rate of fruit loss was calculated as:

$$numlost = \frac{(fruits_{t-1} - fruits_t)}{days}$$

Where fruits_{t-1} is the number of fruits at the previous observation, fruits_t is the number of fruits at the current observation, and days is the number of days between the two observations. Similarly, the relative rate of fruit loss was calculated as:

$$perlost = \frac{(fruits_{t-1} - fruits_t) / fruits_{t-1}}{days} * 100$$

We evaluated changes in the absolute and relative loss rates as well as in proportion healthy fruits (prophealthy) over the course of the fall season, and tested for differences between ecoregions in these rates, restricting the dataset to the period for which data were available for at least 2 ecoregions. As for the season comparisons, numlost and perlost were $\log_{10}$-transformed and prophealthy was arcsine-square root transformed to improve adherence to model assumptions. We ran maximum-likelihood based mixed models that included Julian date and ecoregion as fixed variables and year and site as random variables using the *lmer* function in the *lme4* package in R. We started with the full model (including Julian date, ecoregion, and their interaction) and evaluated the impact of each term by dropping it from the model and comparing the simplified model to the more complex one using a chi-square value from a likelihood ratio test. If the variable removed explained a significant amount of the variation it was replaced before the next variable was dropped. We again controlled the family-wide error rate using a Benjamini-Hochberg procedure (Benjamini and Hochberg 1995).

To evaluate whether climate variables measured on a continuous basis explained variation not captured by the ecoregion classifications, we used the same approach to test for effects of PC1 (winter conditions) and PC2 (summer conditions) on numlost, perlost, and prophealthy. The full model included Julian date, PC1, PC2, and all 2-way interactions (plus year and site as random variables).

Transitions between states. We counted the number of fruits (healthy, unhealthy, or lost) on each plant during each observation period to determine whether healthy or unhealthy fruits are more likely to be lost by plants and whether this differs by season or ecoregion. There were three possible transitions: healthy to unhealthy, healthy to lost, and unhealthy to lost (we assumed that unhealthy fruits could not revert to healthy). Because we did not track individual fruits within plants, we were not always able to unambiguously determine the fate of each fruit. Ambiguity arose when a plant started with both healthy and unhealthy fruits and ended with fewer healthy fruits and at least some unhealthy fruits. For example, a plant with five healthy fruits and two unhealthy fruits (seven total) at the time of the first observation and with two healthy fruits and three unhealthy fruits (five total) during the next observation may have A) lost two healthy fruits and had one transition from healthy to unhealthy, or it may have B) lost two unhealthy fruits and had two transitions from healthy to unhealthy, or it may have C) lost one healthy and one unhealthy fruit and had no other transitions. We calculated the proportion of fruits in each transition under two extreme scenarios. In Scenario 1, ambiguous losses are attributed to healthy fruits; this is expected if most losses are due to consumers and consumers are more likely to remove healthy fruits than unhealthy fruits. In the example above, this is option A. In Scenario 2, ambiguous losses are attributed to unhealthy fruits; this is expected if unhealthy fruits are more likely to be abscised than healthy fruits. In the example above this is option B. These two extreme scenarios bracket the range of possibilities for each of the three transitions. For example, the proportion transitioning from healthy to lost in option C ($1/5 = 0.2$) is intermediate between that of option A ($2/5 = 0.4$) and option B ($0/5 = 0$). Because we were comparing ranges rather than single values and because we do not know which of the two extreme scenarios is closer to reality for each species, we were not able to conduct statistical tests comparing ecoregions or seasons.

We estimated the proportion of healthy fruits lost per week to decomposers in fall and spring as:

$$decomposer\_loss = \frac{propfruits_{HtoU} * propfruits_{UtoL}}{2}$$

Where $propfruits_{HtoU}$ is the proportion of fruits that transitioned from healthy to unhealthy and $propfruits_{UtoL}$ is the proportion of fruits that transitioned from unhealthy to lost.

In other words, we assumed this was a two-step process: first fruits partially decomposed (healthy to unhealthy), and then they dropped from the plant (we divided by 2 to produce a weekly rather than biweekly estimate).

We also calculated an index of the relative importance of vertebrate frugivory as:

$$propfruits_{HtoL} / decomposer\_loss$$

where $propfruits_{HtoL}$ is the proportion of fruits that transitioned from healthy to lost.

For this calculation we again used means from the two extreme scenarios. This index assumes that: 1) healthy fruits do not abscise in the absence of frugivores, 2) infections by decomposers severe enough to result in loss were visible in the previous week, and 3) frugivores do not consume unhealthy fruit.

Plant-level analyses. We evaluated whether the number of fruits on the plant affected the rate of removal of individual fruits by using plant level data and running an ANOVA that included site-year combination and Julian date in the model. To evaluate whether the probability of any losses increased with fruit number we ran logistic regressions with some loss or no loss as the response variable and site-year combination, Julian date, and number of fruits as the predictors.

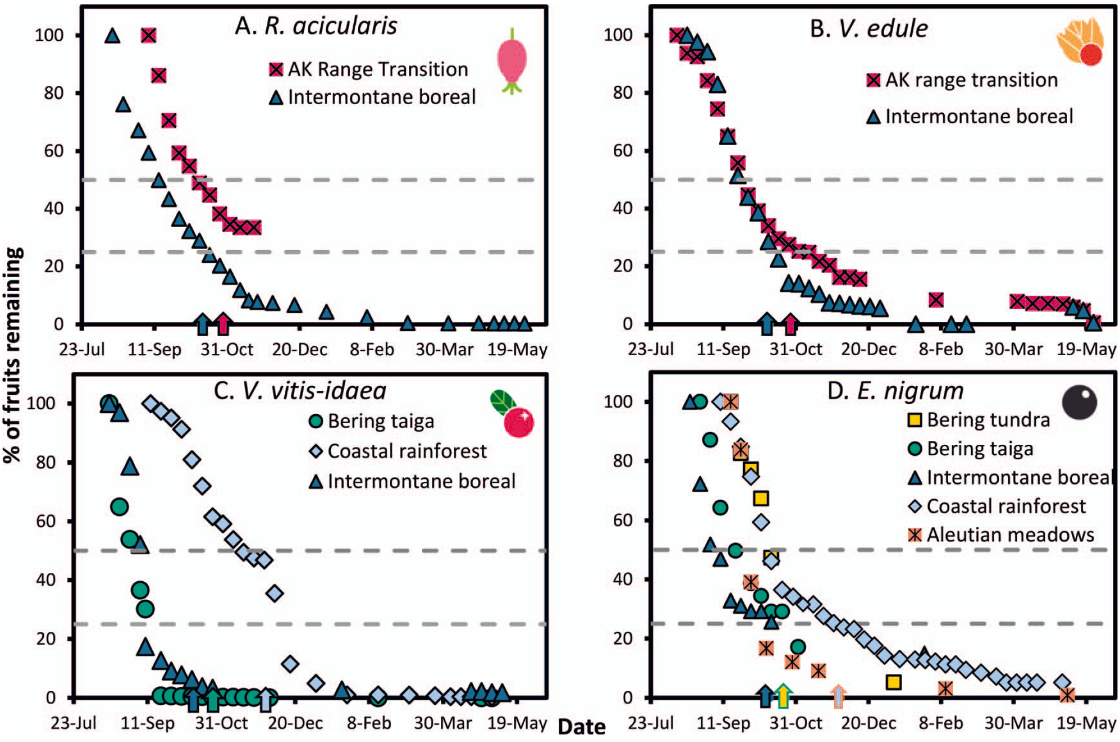

FIG. 3. Fruit loss over time for each species. Each data point is at the midpoint of the time period (a week in fall and spring, 2–4 wk in winter). The earliest date of collection was set to 100%, and each subsequent data point was calculated based on the mean percent fruit loss per day during the period for all site-year combinations in that ecoregion. This method was used because fruit collection was initiated on different dates across years and sites, so the actual percentage of the cohort remaining could not be compared across sites or years. Arrows along the x-axis indicate the long-term average time of snowfall, for most regions defined as from >50 mm of snowfall after the minimum daily temperature < 0°C until the mean daily temperature > 0°C but as December 1 for the Coastal Rainforest and Aleutian Meadows habitats.

RESULTS

General Patterns Across the Year

Numbers of fruits on the plants dropped steadily over the fall period for all four species, and most species in most ecoregions retained 25–50% of fruits by the date of season-long snow fall based on long-term averages (Fig. 3). For *V. vitis-idaea,* however, less than 25% of fruit was retained by start of snowfall in Bering Taiga and Intermontane Boreal ecoregions (Fig. 3C). In general, data collection was initiated earlier in northern ecoregions (Bering Taiga, Intermontane Boreal) than in southern ecoregions (Coastal Rainforest, Aleutian Meadows) (Fig. 3).

Comparisons Between Seasons

Collection periods for all three seasons varied widely by location and collecting group (Table 2), and number of sites for which data were available declined with each progressive season. For all four species, percent fruit lost was lower in spring than in the other two seasons (Fig. 4A–D). However, because the winter period was much longer than the other two periods, the absolute loss rate (fruits lost per day per plant) was significantly lower in winter than in fall for all four species (Fig. 4E–H, Table 2). The only other seasonal differences were a higher absolute loss rate in fall than in spring for *E. nigrum* and in spring than in winter for *V. edule* (Table 2). The relative loss rate (% fruits lost per plant per day) was also higher in fall than in winter for all species except *R. acicularis*, but similar between fall and spring (and higher in spring for *V. edule*) (Fig. 4I–L, Table 2). In other words, for most species the relative rates of loss decreased during the period of snow cover, but returned in the spring to rates similar to or higher than those in fall.

The percent of fruits in a "healthy" state at the end of the fall varied by species (Fig. 4M–P). For *R. acicularis* only a small portion of the fruits remaining on the plants were still healthy at the time of snow fall (<30% for most sites; Fig. 4M) and this declined to almost zero in winter and spring. When comparing sites where both values were available, in fall plants had a higher percentage of healthy fruits than either winter or spring (Table 2). In sharp contrast, the vast majority of fruits of *V. vitis-idaea* and *E. nigrum* were in a healthy state at the time of snowfall (Fig. 4O, P),

TABLE 2. COMPARISON OF SEASONS. "Season" and "Season length" include all sites, while season comparisons include only sites with data for the two seasons being compared. Positive effect sizes indicate higher values for the first season listed. Rosaci = *Rosa acicularis*, Vibedu = *Viburnum edule*, Vacvit = *Vaccinium vitis-idaea*, Empnig = *Empetrum nigrum*. Values in bold indicate significant differences following a Benjamini-Hochberg procedure with a false discovery rate of 0.05.

			Season Comparisons												
				# fruits lost plant^{-1} day^{-1}				% fruit lost plant^{-1} day^{-1}				% fruit in healthy state			
Species	Season (# site-year combos)	Season length in days (range)	Comparison	Effect size	n	χ^2	P	Effect size	n	χ^2	P	Effect size	n	χ^2	P
Rosaci	Fall (33)	45 (12–92)	Fall vs winter	0.22	24	5.73	**0.017**	0.22	20	2.62	0.106	0.31	32	13.61	**<0.001**
	Winter (12)	190 (148–228)	Winter vs. spring	<0.01	12	<0.01	0.999	−0.52	8	15.37	**<0.001**	−0.01	26	1.06	0.30
	Spring (6)	24 (14–44)	Fall vs. spring	0.89	12	4.59	0.032	0.62	8	0.970	0.325	0.31	30	12.13	**0.005**
Vibedu	Fall (30)	49.0 (15–92)	Fall vs. winter	0.30	28	11.67	**<0.001**	0.81	28	36.70	**<0.001**	0.19	36	8.88	**0.003**
	Winter (15)	166.7 (42–203)	Winter vs. spring	−0.44	16	5.41	**0.020**	−0.51	16	6.11	**0.013**	−0.13	28	6.85	0.032
	Spring (9)	24.1 (6–46)	Fall vs. spring	−0.14	16	1.19	0.276	0.35	16	4.27	0.039	0.38	26	9.57	**0.002**
Vacvit	Fall (16)	45.6 (20–79)	Fall vs. winter	0.73	18	16.89	**<0.001**	0.48	18	15.74	**<0.001**	0.40	18	3.21	0.073
	Winter (9)	152.4 (76–212)	Winter vs. spring	0.10	10	0.06	0.800	−0.11	10	0.10	0.752	0.26	14	1.47	0.226
	Spring (5)	32.2 (5–80)	Fall vs spring	0.66	10	2.51	0.112	0.29	10	0.83	0.364	0.69	14	6.28	**0.012**
Empnig	Fall (14)	51.9 (13–114)	Fall vs Winter	0.88	14	16.73	**<0.001**	0.32	14	8.22	**0.004**	0.58	14	6.69	**0.010**
	Winter (7)	145.7 (76–241)	Winter vs. spring	−0.20	8	0.895	0.344	−0.35	8	1.253	0.263	0.18	10	2.74	0.10
	Spring (4)	34.8 (4–80)	Fall vs. spring	0.40	8	14.50	**<0.001**	0.63	8	0.31	0.578	0.99	10	33.65	**<0.001**

and by the end of winter the variance was very high: many sites had no healthy fruits but at other sites, even within the same ecoregion, all or almost all fruits were in a healthy state. *Viburnum edule* showed an intermediate pattern, with a small, but significant, decline in percentage of healthy from fall to winter (Fig. 4N, Table 2).

Changes over the Fall Season

All species showed a drop in the number of fruits lost per day (numlost) over the course of the fall (Table 3, Fig. 5; statistically significant for all species after applying the Benjamini-Hochberg correction except *V. edule*). For *R. acicularis* there was an interaction between Julian date and ecoregion: there was a rapid decrease in fruits lost per day in the Alaska Range Transition sites but no change in the Intermontane Boreal sites (Fig. 5A, Table 3). Summer-cold sites (high PC2 sites) showed a steeper decline in fruits lost per day than summer-warm sites (low PC2 scores; Fig 6A). For *V. vitis-idaea*, winter-warm sites (low PC1 scores) had lower values than winter-cold sites (high PC2 scores); this pattern was driven by the communities of Pilot Point and Sitka (Fig. 6B). For *E. nigrum*, summer-cold sites (low PC2 scores) had higher rates of loss than winter-cold sites (high PC2 scores; Fig. 6C).

Across all sites, the relative loss rate (perlost) was constant over the course of the fall for all species except *E. nigrum,* where it declined over time (Table 3, Fig. 7). However, for some species there were opposing patterns by ecoregion (a significant interaction between Julian date and ecoregion). In *R. acicularis* the relative loss rate declined throughout fall in Alaska Range Transition sites but showed no change for the Intermontane Boreal sites (Fig. 7A). Winter-warm sites showed steeper declines than winter-cold sites, with positive slopes (higher perlost as the season progressed) for the coldest sites (Fig. 6D). *Vaccinium vitis-idaea* also showed significant differences in perlost between ecoregions, with lower relative loss rates in Coastal Rainforest than in the Bering Taiga and Intermontane Boreal ecoregions (Fig. 7C, and, consistent with this, lower loss rates in winter-warm (low PC2) sites, driven by Pilot Point and Sitka (Fig. 6E). *Empetrum nigrum* showed no differences between ecoregions (Fig. 7D), but summer-warm sites had lower loss rates than summer-cold sites (Fig. 6F).

Despite these general patterns of consistent loss throughout the fall, observers reported pulses in fruit loss at individual sites. Sharp declines in the number of healthy fruits between observation periods were paired with observations of animal activity: a 23% drop in one week for *V. edule* site in Two Rivers (Intermontane Boreal) in 2017 and a 15% drop in one week in *V. vitis-idaea* in Shageluk (Bering Taiga) attributed to grouse, a 20% drop in one week in *R. acicularis* in Venetie (Intermontane Boreal) in 2016 attributed to snowshoe hares and a damage rate of

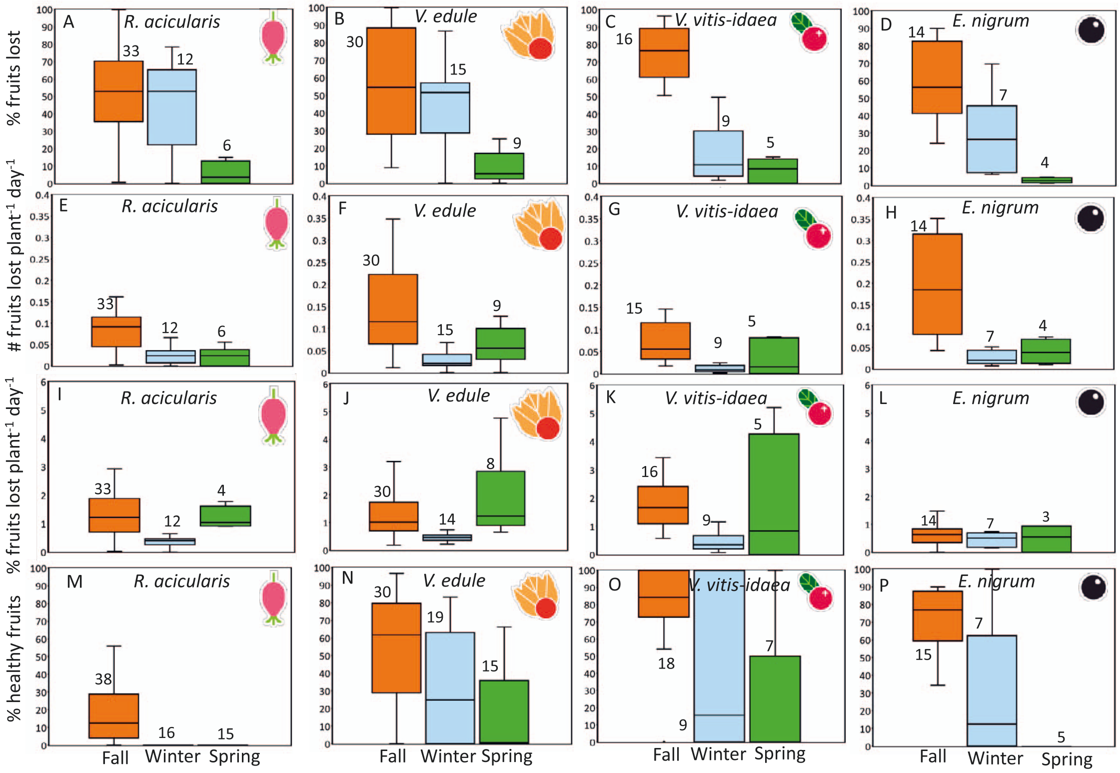

FIG. 4. Seasonal differences. A–D. Percent fruits lost during the season. Because sample size varied by season, values do not sum to 100. E–H. Number of fruits lost per plant and per day. I–L. Percent of fruits lost per plant and per day. M–P. Percent of the fruits remaining at the end of the season that are healthy. Samples sizes are number of year-site combinations. Graphs do not match results in Table 2 exactly because they show averages for all sites, whereas in Table 2 comparisons are limited to sites where data for both years were available.

75% of *V. edule* in one week by an unknown invertebrate in Palmer (Alaska Range Transition) in 2018. Smaller losses (5–10% in one week) were also associated with observed high levels of activity of bear for *R. acicularis* in Holy Cross (Bering Taiga) in 2018, and migratory waterfowl for *E. nigrum* in Scammon Bay (Bering Taiga) in 2018. However, in general pulse events were rare: >15% loss in one week were observed once for *V. vitis-idaea* and *V. edule* (out of 148 and 250 weekly observations resp.)

TABLE 3. EFFECT OF JULIAN DATE, ECOREGION, AND THEIR INTERACTION ON NUMBER OF FRUITS LOST PER DAY (NUMLOST), PERCENT OF FRUIT LOST PER DAY (PERLOST), AND PERCENT OF FRUIT THAT ARE HEALTHY (PERHEALTHY) IN FALL. Values in bold indicate significant differences following a Benjamini-Hochberg procedure with a false discovery rate of 0.05.

		numlost				perlost				perhealthy			
Species	Explanatory variable	χ^2	df	P	N	χ^2	df	P	N	χ^2	df	P	N
R. accularis	Julian date	21.31	1	**<0.001**	190	2.81	1	0.09	199	126.2	1	**<0.001**	268
	Ecoregion	1.15	1	0.563		<0.01	1	0.95		6.77	1	**0.009**	
	Interaction	8.46	1	**0.003**		7.62	1	**0.006**		4.38	1	0.036	
V. edule	Julian date	4.30	1	0.038	182	0.15	1	0.698	181	50.14	1	**<0.001**	218
	Ecoregion	<0.01	1	0.991		0.23	1	0.635		0.35	1	0.553	
	Interaction	0.76	1	0.383		1.04	1	0.308		4.54	1	0.033	
V. vitis-idaea	Julian date	7.71	1	**0.005**	97	0.04	1	0.844	102	22.08	1	**<0.001**	123
	Ecoregion	5.50	2	0.063		10.68	2	**0.005**		1.31	2	0.517	
	Interaction	1.33	2	0.515		1.54	2	0.463		2.56	2	0.278	
E. nigrum	Julian date	12.11	1	**<0.001**	74	6.09	1	**0.014**	76	34.70	1	**<0.001**	92
	Ecoregion	7.58	4	0.108		3.08	4	0.544		12.09	4	**0.017**	
	Interaction	4.40	4	0.354		1.46	4	0.834		9.63	4	0.047	

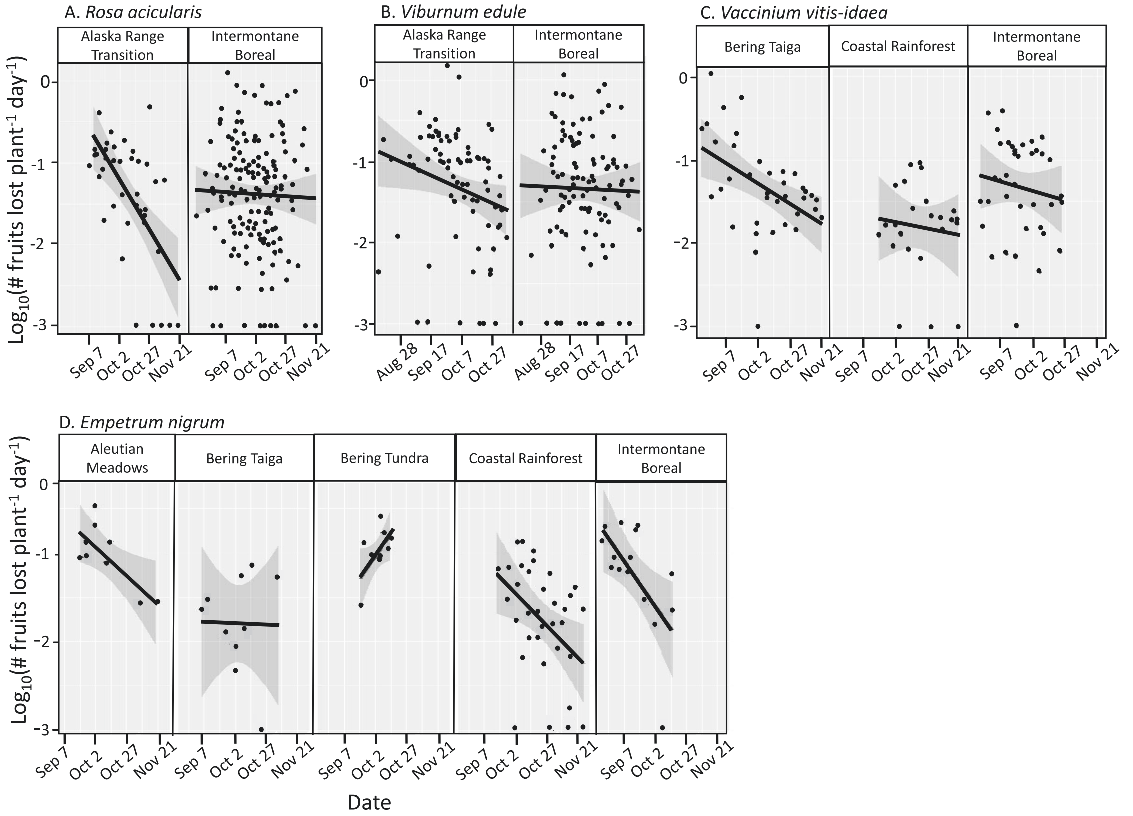

FIG. 5. Number of fruits lost per plant and per day by region and by Julian date. Data points are site means. Shaded area indicates the 95% confidence interval around the regression line. Results of the analyses can be found in Table 3.

and twice for *R. acicularis* (out of 201 observations); there were none for the 119 *E. nigrum* observations.

The proportion of berries on the plant that were healthy declined over the course of the fall for all four species (Table 3. Fig. 8). For *R. acicularis* there was a significant difference between ecoregions, with a lower percentage of healthy in the Intermontane Boreal ecoregion than in the Alaska Range Transition (Table 3, Fig. 8A). However, winter-warm sites had steeper declines than winter-cold sites over the course of the fall (Fig. 6G). For *V. vitis-idaea* and *V. edule* there were no differences between ecoregions (Fig. 8C) and climate variables did not explain significant amounts of variation in this trait ($P > 0.1$ for all). For *E. nigrum*, there were differences in means, with the lowest percentage of healthy fruits in the Aleutian Meadows ecoregion (Fig. 8D), but no differences in slopes (Table 3). Winter-warm sites (Sitka, Homer, and Unalaska) had lower percentage of healthy fruits than winter-cold sites (Fig. 6H).

Transitions Between States

Comparisons of species. When we evaluated transitions of individual fruits between states (healthy, unhealthy, or lost), the proportion of healthy fruits lost per interval (usually a week) was smaller than the proportion of unhealthy fruits lost in both fall and spring for all four species (Table 4). In fall, *R. acicularis* had the highest rate of transition from healthy to unhealthy, but a low rate of unhealthy fruit loss; multiplying these two rates resulted in the highest rate of healthy fruits that were lost following infection / dehydration (1.8% per wk; Table 4). *Empetrum nigrum* had a similar rate of healthy fruits lost following infection / dehydration (1.8% per wk) but this was driven primarily by high loss rates of unhealthy fruits rather than high rates of transition from unhealthy to healthy. *Viburnum edule* was intermediate in both rates of transition from healthy to unhealthy and loss rates of healthy fruits, resulting in intermediate loss rates of healthy fruits following infection / dehydration (0.7% per wk). *Vaccinium vitis-idaea* had the highest loss rates of unhealthy fruits, but the rates of transition from healthy to unhealthy were very low so the rate of loss of healthy fruits following infection / dehydration was also very low (0.4% per wk). Our index of the relative importance of vertebrate frugivory (the ratio of direct loss of healthy fruits to indirect losses via the unhealthy state) was >6 for all species, lowest for *R. acicularis* and highest for *V. vitis-idaea* in both fall and winter (Table 4).

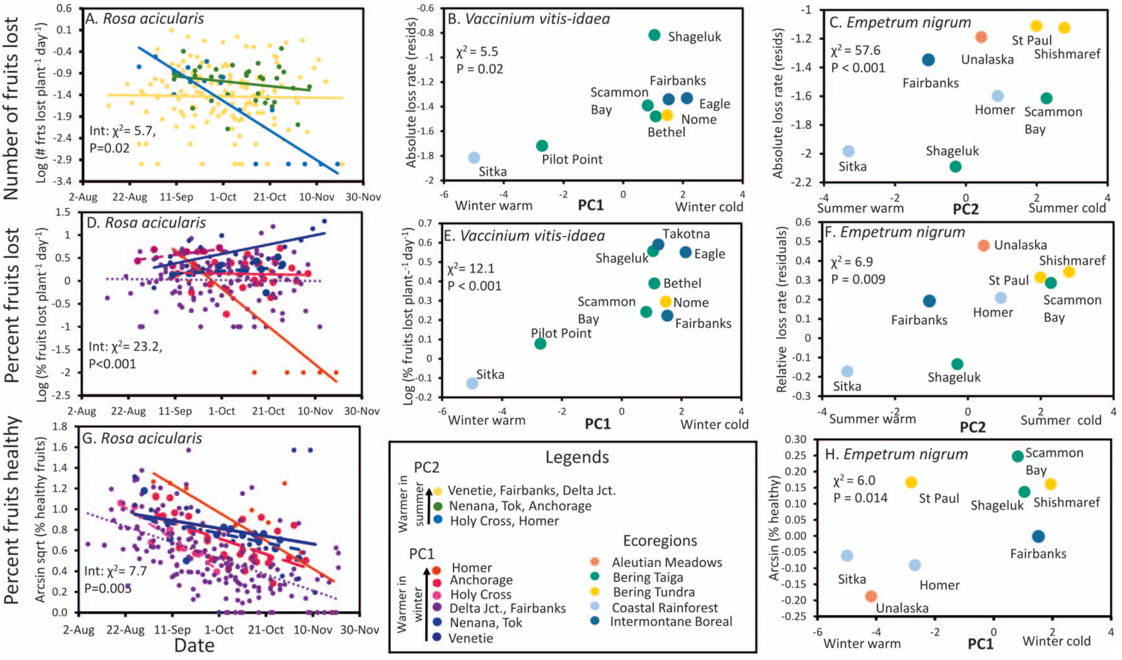

FIG. 6. Changes in fruit loss and percent healthy fruits by climate gradient. Only variables that showed a relationship between a response variable and PC1 or PC2 (panels B,C,E,F and H) or significant interactions between Julian date and PC1 or PC2 (panels A,D,G) are shown. For *R. acicularis* (A,D, and G) there were no significant main effects of PC1 and PC2. For absolute loss rates (panels B and C) and relative loss rates in *E. nigrum* (panel F), values are residuals after including Julian date in the model (for effects of Julian date, see Table 3).

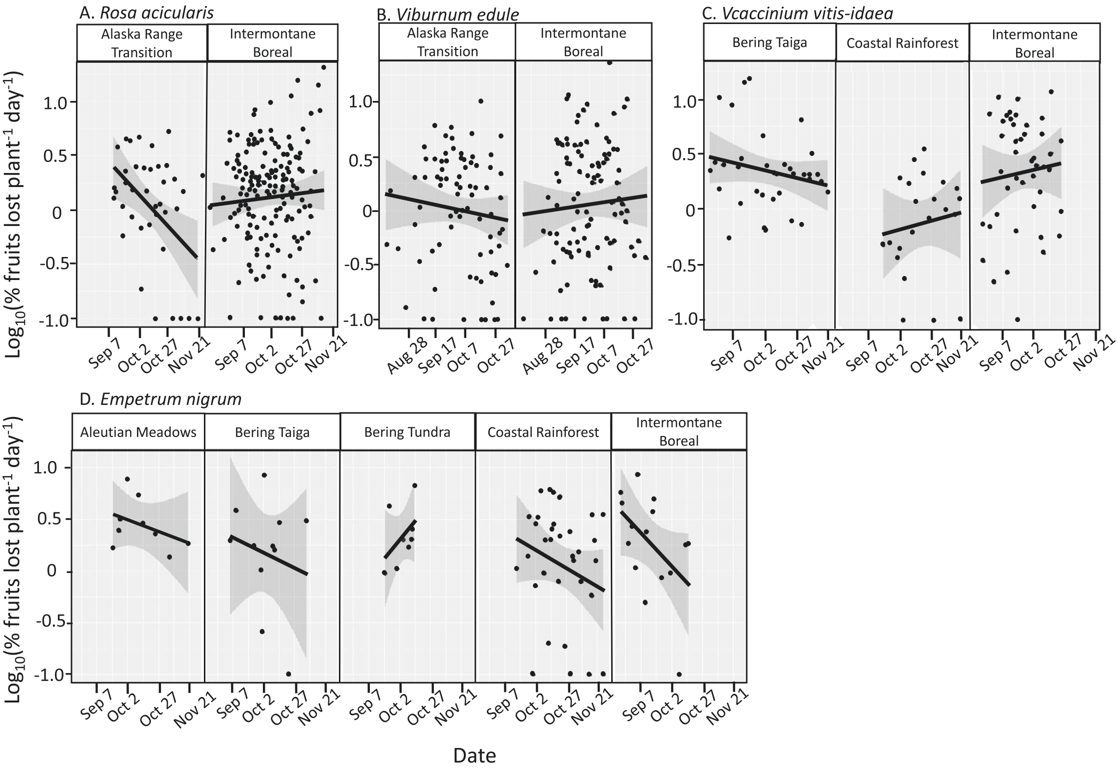

FIG. 7. Percent of fruits lost per plant per day by ecoregion and Julian date. Datapoints are site means. Shaded area indicates the 95% confidence interval around the regression line. Results of the analyses can be found in Table 3.

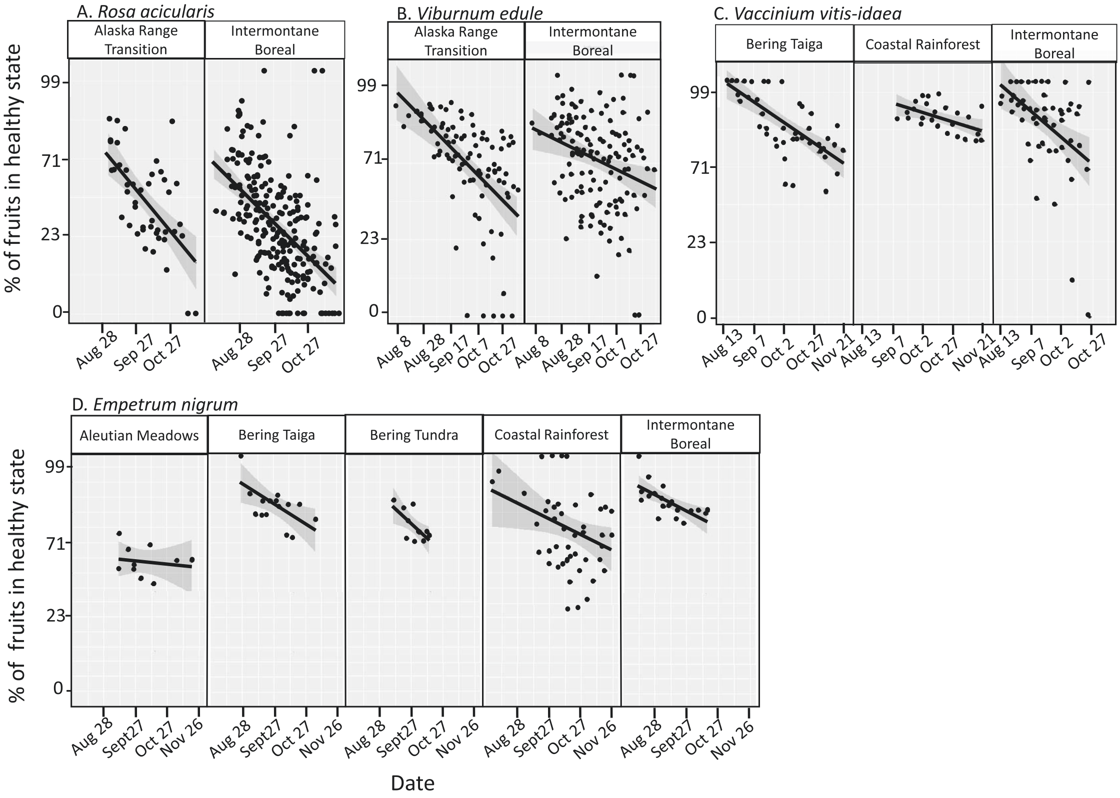

FIG. 8. Changes in percentage of fruits in a healthy state over the course of the fall period. Data points are site means. Values on the y-axis are back-transformed from an arcsin square-root transformation; the axis is not linear. Shaded area indicates the 95% confidence interval around the regression line. Results of the analyses can be found in Table 3.

Comparisons of seasons. The proportion of fruits that remained healthy from week to week was reduced between fall and spring, though this reduction was much greater for *R. acicularis* and for *E. nigrum* than for the other two species (Table 4). For three out of four species this was primarily because a higher proportion of fruits went to an unhealthy state, but for *E. nigrum* it was the result of

TABLE 4. PROPORTIONS OF FRUITS TRANSITIONING BETWEEN STATES FOR CONSECUTIVE OBSERVATIONS BY SEASON. Ranges are based on the two scenarios that differ in how they deal with ambiguous transitions (losses attributed first to healthy fruits vs. first to unhealthy fruits).

Species (# plant observations)	Season (# fruit observations)	State at start of interval	State at end of interval			Prop. healthy fruits lost via unhealthy fruits per week	Ratio of direct to indirect loss
			Healthy	Unhealthy	Lost		
Rosa acicularis (2601)	Fall (15,640)	Healthy	0.67	0.14–0.24	0.09–0.18	0.018	7.5
		Unhealthy	0	0.71–0.76	0.15–0.24		
	Spring (408)	Healthy	0.22	0.26–0.35	0.28–0.35	0.043	7.3
		Unhealthy	0	0.71–0.72	0.28–0.29		
Viburnum edule (3085)	Fall (29,691)	Healthy	0.82	0.07–0.09	0.10–0.12	0.007	15.7
		Unhealthy	0	0.79–0.86	0.14–0.21		
	Spring (713)	Healthy	0.74	0.16–0.18	0.08–0.10	0.031	2.9
		Unhealthy	0	0.64–0.64	0.36–0.36		
Vaccinium vitis-idaea (2237)	Fall (7681)	Healthy	0.80	0.02–0.02	0.18–0.18	0.004	45
		Unhealthy	0	0.60–0.66	0.34–0.40		
	Spring (84)	Healthy	0.77	0.03–0.04	0.19–0.2	0.004	48.8
		Unhealthy	0	0.74–0.77	0.23–0.26		
Empetrum nigrum (1915)	Fall (4984)	Healthy	0.77	0.06–0.08	0.15–0.18	0.018	9.2
		Unhealthy	0	0.61–0.71	0.28–0.38		
	Spring (51)	Healthy	0.18	0.18–0.18	0.64–0.64	0.023	27.8
		Unhealthy	0	0.75–0.75	0.25–0.25		

TABLE 5. PROPORTIONS OF FRUITS TRANSITIONING BETWEEN STATES FOR CONSECUTIVE OBSERVATIONS IN FALL BY ECOREGION. Ranges are based on the two scenarios that differ in how they deal with ambiguous transitions (ambiguous losses attributed to healthy fruits vs. to unhealthy fruits).

Species (# plant observations)	Ecoregion (# fruit observations)	State at start of interval	State at end of interval			Prop. healthy fruits lost via unhealthy fruits per week	Ratio of direct to indirect loss
			Healthy	Unhealthy	Lost		
Rosa acicularis (2601)	Bering Taiga (381)	Healthy	0.62	0.18–0.25	0.14–0.20	0.031	5.5
		Unhealthy	0	0.67–0.76	0.24–0.33		
	Intermontane Boreal (9590)	Healthy	0.66	0.14–0.26	0.08–0.20	0.027	37.0
		Unhealthy	0	0.75–0.84	0.16–0.25		
	AK Range Transition (3039)	Healthy	0.73	0.13–0.18	0.09–0.14	0.013	68.7
		Unhealthy	0	0.81–0.85	0.14–0.19		
Viburnum edule (3068)	Intermontane Boreal (15,001)	Healthy	0.81	0.05–0.08	0.11–0.14	0.008	15.6
		Unhealthy	0	0.79–0.86	0.14–0.21		
	AK Range Transition (14,690)	Healthy	0.84	0.07–0.09	0.08–0.10	0.007	12.9
		Unhealthy	0	0.83–0.88	0.16–0.17		
Vaccinium vitis-idaea (1913)	Bering Taiga (1623)	Healthy	0.81	0.02–0.02	0.16–0.16	0.004	40
		Unhealthy	0	0.60–0.62	0.38–0.40		
	Intermontane Boreal (2601)	Healthy	0.74	0.01–0.03	0.23–0.24	0.009	26.1
		Unhealthy	0	0.47–0.59	0.41–0.53		
	Coastal Rainforest (1662)	Healthy	0.90	0.01–0.01	0.09–0.09	0.001	90
		Unhealthy		0.86–0.86	0.14–0.14		
Empetrum nigrum (1215)	Bering Tundra (833)	Healthy	0.81	0.05–0.09	0.10–0.15	0.012	14.6
		Unhealthy	0	0.59–0.74	0.26–0.41		
	Bering Taiga (280)	Healthy	0.81	0.04–0.06	0.15–0.15	0.010	15.0
		Unhealthy	0	0.60–0.64	0.36–0.40		
	Intermontane Boreal (893)	Healthy	0.78	0.03–0.08	0.17–0.19	0.009	20.0
		Unhealthy	0	0.48–0.73	0.27–0.39		
	Aleutian Meadows (414)	Healthy	0.63	0.11–0.21	0.16–0.26	0.035	5.1
		Unhealthy	0	0.50–0.64	0.38–0.50		
	Coastal Rainforest (1084)	Healthy	0.76	0.05–0.07	0.16–0.17	0.007	23.6
		Unhealthy	0	0.75–0.78	0.21–0.25		

greater losses of healthy fruits from the plant. For *R. acicularis* and *V. edule* the proportion of unhealthy fruits that were lost in spring vs. fall was higher, for *E. nigrum* the values were similar, and for *V. vitis-idaea* they were lower. As a result, the ratio of direct losses of healthy fruits to indirect losses via unhealthy fruits was much lower in spring than in fall for *R. acicularis* and *V. edule*, similar for *V. vitis-idaea*, and higher for *E. nigrum*.

Comparisons of ecoregions. In general, the more northern ecoregions (Bering Tundra, Bering Taiga, and Intermontane Boreal) had lower rates of loss for unhealthy fruits than the more southern regions (Alaska Range Transition, Coastal Rainforest, and Aleutian Meadows), driving lower indirect losses of healthy fruits via an unhealthy state, though for *V. edule* the two ecoregions were very similar (Table 5). An exception was for *E. nigrum* in the Aleutian Meadows, which had very high rates of loss of healthy fruits. The ratio of direct to indirect losses of healthy fruits showed the expected inverse pattern (Table 5).

Plant Level Effects

For all four species plants with more fruits were more likely to have at least one fruit removed (*R. acicularis*: $Z = 7.12$, $P < 0.001$, parameter estimate [PE] $= 0.088 \pm 0.011$; *V. edule*: $Z = 8.36$, $P < 0.001$, $PE = 0.046 \pm 0.005$; *V. vitis-daea*: $Z = 6.47$, $P < 0.001$, $PE = 0.160 \pm 0.025$; *E nigrum*: $Z = 4.69$, $P < 0.001$, $PE = 0.091 \pm 0.020$). For *R. acicularis*, *V. vitis-idaea* and *E. nigrum* the proportion of fruits removed was not affected by the number of fruits on the plant ($F_{(1,232)} = 0.026$, $P = 0.96$, $F_{(1,1899)} = 3.47$, $P = 0.06$, and $F_{(1,1197)} = 2.32$, $P = 0.13$ respectively), but for *V. edule* a higher proportion of fruits were removed from plants with more fruits ($F_{(1,2442)} = 6.55$, $P = 0.01$, $PE = 0.00186 \pm 0.00072$).

DISCUSSION

Through a very high quality, robust, geographically diverse dataset collected by ≈ 1500 volunteers across Alaska, this study provides baseline natural history of fruit retention and fate over time for the four focal species. Following ripening in August, all four species showed a reduction in absolute loss rates over the course of the fall; since the majority of these fruits were in a healthy state, this indicates that the supply rate to frugivores diminished over the course of the fall. For two species, *V. edule* and *V. vitis-idaea*, the relative loss rate (% fruits lost per day) did not change over time, indicating that an individual fruit is as likely to be lost in early fall as in late fall. This pattern of constant loss rate explains why plants invest in persistent fruits and is similar to that for

Ilex verticillata (L.) A.Gray and *Mitchella repens* L. in Maine (Gervais and Wheelwright 1994), but in sharp contrast to *C. canadensis*, which showed a rapid loss of the majority of fruits due to migratory birds in late fall (Burger 1987), and *V. opulus*, which lost fruit rapidly in late November, in part due to abscission by the parent plant (Gervais and Wheelwright 1994). *Rosa acicularis* showed a steep decline in proportional loss rates over time in the Alaska Range Transition sites, but no change in the Intermontane Boreal ecoregion, while *E. nigrum* showed a decline in proportional loss rates in all habitats. Observers reported five events with rapid fruit loss or damage (pulse events) associated with four different animals in four ecoregions, and our data showed high rates of loss (>15% in a week) on four occasions. While these events were dramatic (especially for the youth and adults observing them!), these occurrences represent <5% of the 106 yr-site combinations. Our sites were not randomly located across the state and were all located near towns or villages, and it is possible that this resulted in reduced frugivore populations and is partially responsible for low pulse events. However, small species like grouse, red-backed voles and snowshoe hare are common at the sites used in this study (e.g., there were many reports of sightings of voles and hares by observers), and even large vertebrates such as bears (e.g., Smith et al. 2005) and foxes (Selås et al. 2010) may become habituated to and even attracted to areas of human habitation (sign of one bear and multiple foxes were also observed). While we cannot conclude that pulse events are uncommon, out dataset provides no evidence that they are common.

During the winter period the absolute rates of fruit loss were reduced compared to spring in all species and the relative rate was reduced in all species except *R. acicularis*. The continued high percent fruit removal in *R. acicularis* is likely the result of resident winter birds and snowshoe hare, as suggested by observer sightings of these animals or their sign in or near the sites. The two short-statured ericaceous species had a smaller reduction in relative loss rates in winter than *V. edule* (Table 2); the most likely explanation is continued frugivory by subnivean species such as voles (West 1982; Krebs et al. 2010). In spring the relative rates of fruit loss returned to rates similar to those in fall (though absolute rate was higher for *E. nigrum*). However, whether the losses were driven by healthy or unhealthy fruits depended on the species; we discuss this further in the next section.

Frugivores Versus Decomposers

While we did not measure losses to frugivores vs. decomposers directly, our estimates of transitions between states (healthy, unhealthy, and lost) allow us to draw some inferences. Based on casual observations we expected the highest rates of loss to decomposers in *R. acicularis* and *V. edule* which carry high proportions of infected fruit (Fig. 1A, B), and the lowest rates for the two ericaceous species, *V. vitis-idaea* and *E. nigrum*, on which infected fruits are seldom seen. These observations were confirmed by the Winterberry data: at the end of the fall *R. acicularis* had the lowest percentage of healthy fruits while *V. vitis-idaea* and *E. nigrum* had the highest percentage of healthy fruits (>80% for both) while *V. edule* was intermediate (Fig. 4M–P). However, the data on transitions between states in fall revealed that the percentage of unhealthy fruits on the plant is not a good indication of the relative importance of decomposers because species differ in the rate at which infected fruits are lost from the plant. As expected, *R. acicularis* had the highest rates of healthy fruits lost following infection/ dehydration (≈2% per wk). At the other extreme, *V. vitis-idaea* had by far the lowest rates of fruits lost following infections (0.4% per wk), and this was driven by the very low transition of fruits from healthy to unhealthy fruits. *Vaccinium* species are protected by high levels of organic acids and phenolics and by the presence of protective nonpathogenic fungi (Cipollini and Stiles 1992, 1993; Aiken et al. 2007; Ermis et al. 2015, Stobnicka and Gniewosz 2017). However, once infected the fruits were dropped rapidly (34–40% per wk), contributing to the low conspicuousness of infected fruits. Fruits of *V. edule* and *E. nigrum* were about equally likely to become unhealthy, but there were very few unhealthy *E. nigrum* fruits on the plants because they were abscised at high rates, while unhealthy *V. edule* fruits are common because they are retained on the plant.

If we assume that losses of healthy fruits are due to vertebrate frugivores and losses of unhealthy fruits are due to decomposers and invertebrates, then in fall, frugivores removed 6–45 times as many fruits as decomposers / invertebrates, with the lowest ratio for *R. acicularis* and the highest for *V. vitis-idaea*. It is possible that a few fruits became unhealthy and dropped within an observation interval, or that healthy fruits are abscised. We consider the latter unlikely: in the pilot year we tracked fruits on the ground as well as on the plant and observed very few healthy fruits on the ground (Mulder unpublished data). It is more likely that some unhealthy fruits are consumed by vertebrate frugivores, especially as healthy fruit becomes scarce (García et al. 1999). However, we have several reasons to believe unhealthy fruits are likely unpalatable or less palatable to vertebrate frugivores. First, fruits that are in an infected or shriveled state have lower dry mass than "healthy" fruits; for "rotten" and "dry" fruits collected in September of 2020 the reduction in dry mass was 37% and 48% for *V. edule* and 19% and 38% respectively in *R. acicularis* (Mulder unpublished data). Water content was also lower in "dry" fruits than in healthy ones (20% in both species; Mulder unpublished data). Unhealthy fruits are therefore likely of lower nutritional value to herbivores than healthy fruits. Second, fruits infected by microbes or insects may be less palatable than uninfected fruits (e.g., Manzur and Courtney 1984; Burger 1987; Cipollini and Stiles 1993; Traveset et al. 1995; García et al. 1999). This begs the question: why do *R. acicularis* and *V. edule* retain unhealthy fruit for so long? Further research on the relative losses to vertebrate frugivores, invertebrate frugivores, and different groups of decomposers (e.g., fungi and bacteria) using approaches such as exclosure experiments and camera traps are needed to understand the fate of fruits and their seeds in these habitats.

Invertebrate damage. Damage by invertebrates appeared to be low in the two ericaceous species, with reports of ants on fruits in one Intermontane Boreal site for each species, and one report of a snail on *Empetrum nigrum* in the Aleutian Meadows. Damage by invertebrates may be quite high in *V. edule*, where the ≈15% of fruits classified as "dry" by observers at the end of fall frequently appeared to have intact integument and seed but no pulp. Burger (1987) observed that on *Cornus canadensis*

> "…slugs made small holes in the fruit integument and then ate out much of the inner flesh leaving the seed and skin attached to the plant". (p. 6)

We did receive reports of invertebrates on *V. edule* including the sighting of one caterpillar, reports of spider webs covering branches at three Alaska Range Transition and two Intermontane Boreal sites, and several "stink bugs" present on fruits, suggesting invertebrate frugivory a likely explanation for these flat fruits. Observers at seven sites noted "punctures" in fruits of *R. acicularis*, and there were at least six reports of damage followed by "rotting". It seems likely that in this species invertebrate damage increases the probability of infection by microbes.

Differences between fall and spring. We had expected high fruit loss rates in spring due to snowmelt providing greater access to fruits, warmer conditions increasing decomposition rates, and the reappearance of hibernating or migrating animals. While all fruits had higher relative fruit loss in spring than in fall, the main drivers differed among species. We found support for higher frugivory rates in spring for only one species: in *E. nigrum* healthy fruits were lost at almost quadruple the rate in fall, but unhealthy loss rates were unchanged, which we interpret as preferential removal by animals. We found support for higher spring decomposition rates in two species: *R. acicularis* had a tripling from fall to spring in the rate of healthy fruit transitioning to unhealthy and in *V.edule* loss rates of unhealthy fruits doubled. However, higher losses of unhealthy fruits could also be the result of increased reliance on sub-optimal fruit by frugivores as food becomes scarce (e.g., Foster 1977; Stiles 1980). The fourth species, *V. vitis- idaea*, showed very little change from fall. These identity-dependent changes between seasons suggest it is difficult to extrapolate from our results to other species with persistent fruits.

Differences Between Ecoregions

We had expected higher loss rates in the more southern ecoregions: they are warmer, wetter, and have a longer snow free period (Fig. 2B). These predictions were not supported; *V. edule* showed no differences in loss rates between ecoregions and no relationships with the climate variables. *Empetrum nigrum* showed no differences between ecoregions, no relationship with winter conditions (PC1), and the relationship with the summer conditions axis was the opposite of that expected: the warmest sites had the lowest fruit losses. *Vaccinium vitis-idaea* also showed the opposite pattern from the predicted one: it had a lower relative loss rate in the Coastal Rainforest sites than in other ecoregions, and lower absolute loss rates in winter-warm sites like Sitka and Pilot Point. *Rosa acicularis* was the only species where there was some evidence for greater loss at warmer sites: steeper absolute loss rates in summer-warm sites, and steeper relative loss rates in winter-warm sites (but no main effects of PC1 or PC2). In summary, for two species there was support for higher loss rates at colder sites, for one there was support for greater changes at warmer sites, and for one there was no support for differences by ecoregion or climate gradients. Lower loss rates in more southern or warmer regions for the two ericaceous species, which are small and have few fruits, may be the result of a greater variety of fruits available to vertebrate frugivores. Of 50 species of fleshy fruits in Hultén (1968), 43 can be found in the Coastal Rainforest, 38 in the Alaska Range transition, 27 in the Intermontane Boreal, 24 in the Aleutian Meadows, 19 in the Bering Taiga, and only 14 in the Bering Tundra. However, frugivory is also likely driven by the diversity and density of the frugivores. An investigation of competition for frugivores would help clarify the patterns we found.

There was also little evidence for higher rates of loss to decomposers in the more southern ecoregions. At time of snow fall the proportion of healthy fruits still available in southern ecoregions was either higher than (*R. acicularis*, *V. vitis-idaea*) or similar to (*V. edule*, *E. nigrum*) those in more northern ecoregions (Fig. 8). While this may be partially attributable to later ripening in the southern ecoregions than in the more northern ones, data on the fate of individual fruits also suggest a lower rate of loss to decomposers in the more southern regions. For *R. acicularis* and *V. vitis-idaea* the proportion of healthy fruits lost after transitioning to unhealthy was the lowest in the southern-most ecoregions, and for *V. edule* it did not differ. For *E. nigrum* this value was much higher in the Aleutian Meadows than in the other ecoregions (Table 5), and the three sites that were warmest in winter (Sitka, Unalaska, and Homer) had the lowest percentage of healthy fruits

(Fig. 6H). However, even those results are not clear, as for Sitka this was driven by a high retention of unhealthy fruit rather than a high rate of transition from healthy to unhealthy. These results are not easily explained and point to the need for a greater understanding of the microbiome of wild fruits.

Potential Consequences under Climate Change

Warmer temperatures will reduce the number of days with snow cover, and earlier springs are expected to lead to earlier flowering and fruiting in our focal species (Mulder and Spellman 2019). Given that for most species and most locations the probability of fruit loss was constant over the course of the fall, and that loss rates during the snow-free period was higher than during winter for all species, all else being equal we predict a lower number of fruits at time of snow fall and reduced food availability for frugivores in winter and spring in future decades. However, our study did point to the potential for some resilience: since a small proportion of fruits were still on the plant in April and May, there is the potential for southern genotypes to be transported to more northern latitudes during spring bird migration. The distance by which the average seed is transported in or on birds is unknown, but it is presumably larger than would normally occur in unaided migration. This may be important if southern genotypes are better adapted to the warmer conditions expected in northern latitudes. We are aware of only one study on genotypic variation or local adaption in our target species: Roy and Mulder (2014) conducted a common garden / reciprocal transplant experiment and found some evidence for differential survival and morphology of *V. vitis-idaea* genotypes from different origins, but little evidence for local adaptation. However, although selected to maximize differences in environmental conditions, the origin sites were located within 60 km of each other, and role of local adaptation over a larger scale is unknown.

CONCLUSIONS

This study is a first attempt at understanding the complexities of fruit loss for four plant species with persistent fruits. While the four species shared some patterns (e.g., similar overall patterns of change between seasons), they showed very different patterns of loss for healthy vs. unhealthy fruits and unexpected differences between ecoregions. The large spatial scale and large number of sites at which we obtained data allowed us to compare ecoregions and demonstrate that events like rapid fruit loss are uncommon. This work would not have been possible without an extensive community science network of dedicated group observers who are passionate about berries and demonstrates the value of public participation in scientific research.

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DATA ACCESSIBILITY

All data are available at http://dx.doi.org/10.6073/pasta/6c5885f8f1423b274a3fea6c20e25c66

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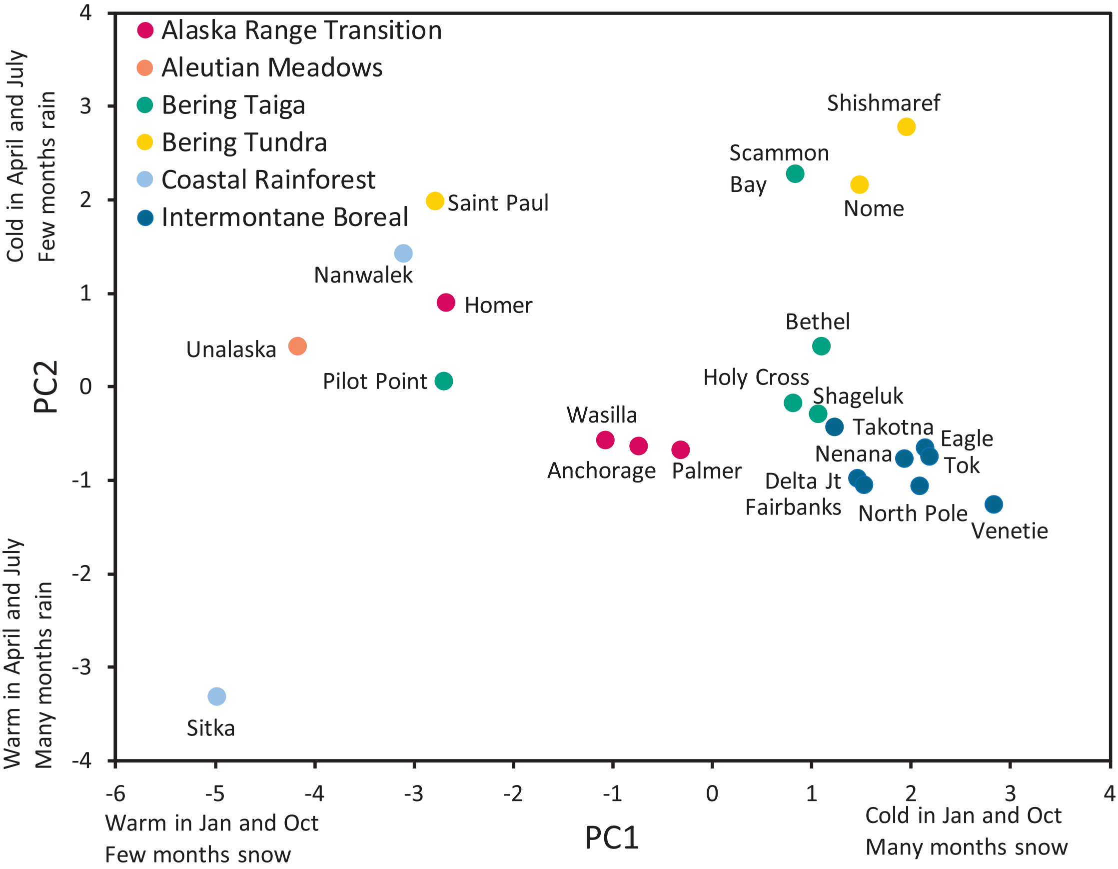
APPENDIX 1

DETAILS OF DATA COLLECTION BY SPECIES



APPENDIX FIG. A. Communities by ecoregion and climate gradients. PC1 values (x-axis) indicate conditions in fall and winter while PC2 (y-axis) indicates conditions in spring and summer.

Appendix 1 Table A. *Rosa acicularis*. An asterisk (*) signifies that a site is in the transition zone between Bering Taiga and Intermontane Boreal, but was combined with Intermontane Boreal due to low sample size.

Region	Site	Years	# Plants	# Dates
Intermontane Boreal	Holy Cross Elementary School*	2018–2019	19	7
	Anne Wien Elementary School	2018–2019	19	7
		2019–2020	30	7
	Arctic Light Elementary School	2017–2018	10	5
		2018–2019	6	3
	Boreal Sun Charter School	2019–2020	12	5
	Delta Future Farmers of America	2017–2018	20	5
		2018–2019	18	8
		2019–2020	12	8
	Denali Elementary School	2018–2019	16	11
		2019–2020	20	13
	Hunter Elementary School	2018–2019	22	2
	Mulder Yard	2016–2017	20	9
		2017–2018	20	4
		2018–2019	18	9
		2019–2020	20	8
	Murie Trail	2018–2019	14	2
	Nenana School	2018–2019	17	4
		2019–2020	15	5
	Parkinson Yard	2016–2017	20	16
	Parkinson Site 2	2016–2017	20	9
	Tanana Middle School	2016–2017	21	11
		2017–2018	18	6
	Tok School	2018–2019	20	4
	UAF Satellite Dish	2016–2017	20	5
	John Fredson School	2016–2017	21	5
		2018–2019	18	7
		2019–2020	12	12
	Watershed Kindergarten	2017–2018	11	5
		2018–2019	11	
	Watershed Powerline Trail	2017–2018	11	8
		2018–2019	8	3
		2019–2020	10	2
	Watershed Sit Spots	2017–2018	19	8
		2018–2019	8	6
		2019–2020	10	5
	Total	**36**	**586**	**234**
Alaska Range Transition	Center for Alaska Coastal Studies HQ	2019–2020	17	12
	Campbell Creek Bridge	2017–2018	20	4
	Polaris K–12 School	2017–2018	26	6
		2018–2019	18	8
		2019–2020	26	9
	Totals for Alaska Range Transition	**8**	**166**	**39**
Species total	**23 sites**	**44**	**752**	**273**

Appendix 1 Table B. *Viburnum edule*. An asterisk (*) indicates a site was on the edge of the Coastal Rainforest, but counted as Alaska Range Transition because of low sample size.

Region	Site	Years	# Plants	# Dates
Intermontane Boreal	Parkinson Site #2	2016–2017	20	10
	Mulder Yard	2016–2017	21	7
		2017–2018	20	4
		2018–2019	20	9
		2019–2020	20	8
	UAF Satellite Dish	2016–2017	20	5
		2017–2018	20	8
		2018–2019	14	8
		2019–2020	26	17
	Randy Smith Middle School	2017–2018	22	9
		2018–2019	20	9
	Smith Lake	2017–2018	21	7
	Tanana MS	2017–2018	12	13
	Two Rivers Elementary	2017–2018	20	4
		2018–2019	18	9
		2019–2020	13	5
	North Pole MS	2018–2019	17	16
	Weller Elementary	2018–2019	9	7
		2019–2020	8	10
	Total	**19**	**341**	**165**
Alaska Range Transition	Birch Hill	2017–2018	20	10
		2018–2019	31	17
		2019–2020	20	7
	East High Environmental Club	2017–2018	16	11
	Mat–Su Career & Technical High	2017–2018	20	9
		2018–2019	19	15
		2019–2020	24	10
	Anchorage Botanical Garden	2018–2019	20	13
	Palmer Girl Scout Troop 849	2018–2019	19	10
		2019–2020	19	3
	Nanwalek School*	2018–2019	20	2
	Total	**11**	**228**	**107**
Species total	**15 sites**	**30**	**569**	**272**

Appendix 1 Table C. *Vaccinium vitis-idaea*. An asterisk (*) indicates a site was counted as Bering Taiga instead of Bering Tundra due to low sample size. Two asterisks (**) indicates a site was not used in calculations of absolute loss rates because data were not recorded on a per-plant basis.

Region	Site	Years	# Plants in each year	# Dates in each year
Bering Taiga/ Tundra	Bethel Regional High School	2017–2018	21	8
		2018–2019	22	3
		2019–2020	24	6
	Scammon Bay	2018–2019	22	6
	Pilot Point	2019–2020	27	10
	Innoko School	2018–2019	14	11
	Nome Anvil City Science*	2019–2020	58	6
	Total	**7**	**188**	**50**
Intermontane Boreal	Parkinson Yard	2016–2017	20	12
		2017–2018	19	6
	Murie Trail	2017–2018	21	5
		2018–2019	6	3
	Smith Lake	2016–2017	20	5
		2017–2018	20	4
		2018–2019	21	5
	Eagle Community School	2017–2018	25	5
		2018–2019	26	12
	Takotna Community School**	2018–2019	8	6
	Total	**10**	**338**	**63**
Coastal Rainforest	Sitka Raptor Center	2017–2018	40	22
		2018–2019	38	24
		2019–2020	22	14
	Total	**3**	**100**	**60**
Species total	**11 sites**	**20**	**626**	**173**

APPENDIX 1 TABLE D. *EMPETRUM NIGRUM*. An asterisk (*) indicates a site located in transition zone and counted as Coastal Rainforest instead of as Alaska Range Transitional because of low sample size.

Region	Site	Years	# Plants	# Dates
Bering Tundra	Kamenista	2018–2019	23	4
	Shishmaref School	2017–2018	12	4
		2018–2019		
	Total	**3**	**35**	**8**
Bering Taiga	Innoko River School	2018–2019	8	7
	Scammon Bay School	2018–2019	24	6
	Total	**2**	**32**	**13**
Intermontane Boreal	Parkinson Yard	2016–2017	20	12
	Smith Lake	2016–2017	19	5
		2019–2020	11	4
	Total	**3**	**50**	**21**
Coastal Rainforest	Wynn Nature Center*	2017–2018	23	4
		2018–2019	23	11
	Sitka Raptor Center	2017–2018	31	20
		2018–2019	17	26
		2019–2020	20	15
	Total	**5**	**114**	**76**
Aleutian meadows	Unalaska City High School	2018–2019	19	3
	Unalaska Eagles View	2018–2019	22	9
	Total	**2**	**41**	**12**
Species total	**10 sites**	**15**	**272**	**130**

APPENDIX 2

PRINCIPAL COMPONENTS ANALYSES (PCA) OF CLIMATE VARIABLES

Climate data were obtained from the SNAP (Scenarios Planning for Alaska + Arctic Planning) at http://ckan.snap.uaf.edu/dataset/community-charts-temperature-and-precipitation. We used historical CRU 1961–1990 baseline climatology data for each community with the exception of Twin Rivers (since it was not available, we used nearby Fairbanks instead). All variables were centered and scaled.

The following variables were included in the PCA:

1. Mean daily temperature in January (°C)
2. Mean daily temperature in April (°C)
3. Mean daily temperature in July (°C)
4. Mean daily temperature in October (°C)
5. Number of months with precipitation as snow only (maximum temperature < 0°C)
6. Number of months with precipitation as rain only (minimum temperature > 0°C)
7. Number of months with precipitation as a mix of rain and snow (remaining months)
8. Total annual snow (mm of rainwater equivalent)
9. Total rain (mm)

APPENDIX 2 TABLE A. CHARACTERISTICS AND IMPORTANCE OF PRINCIPAL COMPONENTS.

	PC1	PC2	PC3
Standard deviation	2.3077	1.4084	0.9795
Proportion of variance	0.5917	0.2204	0.1066
Cumulative Proportion	0.5917	0.8121	0.9187

APPENDIX 2 TABLE B. LOADINGS (EIGENVECTORS) FOR THE FIRST TWO COMPONENTS (ABSOLUTE VALUES $\geq$0.40).

PC1	PC2
Months of snow (0.417)	July mean temp. (−0.535)
October mean temp. (−0.417)	April mean temp. (−0.487)
January mean temp. (−0.404)	Months of rain (−0.479)
Months of mixed precip. (−0.400)	