I. SPECIES	*Heteromeles arbutifolia* (Lindl.) M. Roemer
NRCS CODE: (HEAR5)  Fruits (pomes) in late fall and winter.	Subfamily: **Maloideae** Family: **Rosaceae** Order: **Rosales** Subclass: **Rosidae** Class: **Magnoliopsida** photos: A. Montalvo  
A. Subspecific taxa	None recognized by Phipps (2012, 2016) in Jepson Manual or Jepson e-Flora.
B. Synonyms	*Photinia arbutifolia* (Ait.) Lindl.; *Crataegus arbutifolia* Ait. (McMinn 1939) *Heteromeles* (Lindl.) M. Roemer *arbutifolia* var. *arbutifolia*; *H. a.* var. *cerina* (Jeps.) E. Murray; *H. a.* var. *macrocarpa* (Munz) Munz; *H. salicifolia* (C. Presl) Abrams (Phipps 2016) (but see I. F. Taxonomic issues).
C. Common name	toyon, California Christmas berry, California-holly (Painter 2016); Christmas berry (CalFlora 2016).
D. Taxonomic relationships	Phylogenetic analyses based on molecular and morphological data confirm that *Photinia* is the most closely related genus (Guo et al. 2011). *Photinia* differs in having 20 stamens, fused carpels, and stone cells in the testa as well as occurring in summer-wet environments (Phipps 1992).
E. Related taxa in region	None. There is only one species of *Heteromeles.* The closely related *Photinia* is primarily tropical (Meyer 2008) and not in California. Toyon's taxonomic stability may be in part related to its reproductive mode (Wells 1969).
F. Taxonomic issues	The three varieties of *H. arbutifolia* listed above in cell I. B. are currently recognized in the USDA PLANTS (2016) database.
G. Other	One of the most widely distributed California shrubs. Also widely planted and well-known for its bright red fruits in winter. McMinn (1939) noted it had been planted widely in parks and gardens since about 1914. From the Greek words 'heter' for different and 'malus' for apple (Munz 1974). Hollywood California is said to have been named for this plant (Bornstein et al. 2005). The great dispersal ability of this taxon (see VI. F) and ability to escape cultivation suggest the distribution of toyon has increased with the help of humans. However, the distribution of herbarium records prior to 1940 is very similar to after 1950 (examined in CCH 2016).

II. ECOLOGICAL & EVOLUTIONARY CONSIDERATIONS FOR RESTORATION

A. Attribute summary list (based on referenced responses in full table)	Taxonomic stability - high Longevity - long-lived Parity - polycarpic Flowering age - 5+ yr Stress tolerance - moderate to high Environmental tolerance - broad Reproduction after fire - obligate sprouter Fragmentation history - historical and recent Habitat fragmentation - high at low elevations Distribution - widespread, rocky slopes & alluvium, riparian banks at warmer, lower elevations Seeds - short lived Seed dispersal distance - far Pollen dispersal - intermediate to far Breeding system - outcrossed Population structure - likely low Adaptive trait variation - unknown Chromosome number - no data Genetic marker polymorphism - no data Average total heterozygosity - no data Hybridization potential - none reported SDM projected midcentury suitable habitat - 69–100% stable SDM projected midcentury habitat gain - gain > loss under four of five future climate scenarios (assuming unlimited dispersal)

B. Implications for seed transfer (summary)

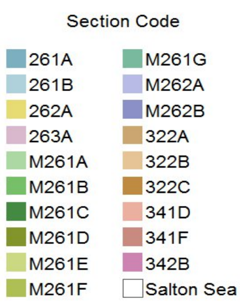
Toyon is an obligate outcrossing plant with potentially high levels of gene dispersal by both pollen and seeds. Taxonomists have periodically recognized morphological variation at the level of taxonomic variety, primarily within the Channel Islands, and there is variation among populations in fruit, seed and leaf traits that appears to correlate with environmental parameters (see VIII. C, E, F), but the commonness and great dispersal ability of this species is likely to have resulted in little genetic differentiation over small spatial scales (such as within ecological sections); however, this taxon's north to south distribution spans a range of ecological sections, elevation, temperature, and precipitation gradients (see III. A. Geographic range & B. Distribution map; IV. B D), providing ample opportunity for the development of adaptive genetic differences at larger spatial scales or widely separated positions along environmental gradients. In central and southern California, extreme habitat fragmentation in coastal areas and at low elevations may interrupt migration of seeds and pollen and reduce genetic variation over time. Under severe fragmentation, problems arising from inbreeding when populations become small or isolated is likely to be more detrimental than mixing populations from adjacent ecological sections and subsections. The species is predicted to have low exposure (little loss of suitable habitat) to future climate change projected to mid-century, but more information is needed to understand the combined effects of additional stressors such as fragmentation and shortened fire-return intervals. Toyon would likely benefit from expansion of wildlife corridors to mitigate effects of fragmentation at lower elevations and by ensuring high genetic diversity of seeds from local ecological regions are used in restoration.

III. GENERAL

A. Geographic range

Widespread and common. Occurs throughout much of cismontane California and Baja California in canyons, foothills and lower mountain slopes from Humboldt Co. southward through Baja California, and from Shasta and Tehama Counties southward through the foothills of the Sierra Nevadas; also on San Clemente and Santa Catalina Islands (McMinn 1939, Sawyer et al. 2009, Phipps 2016).

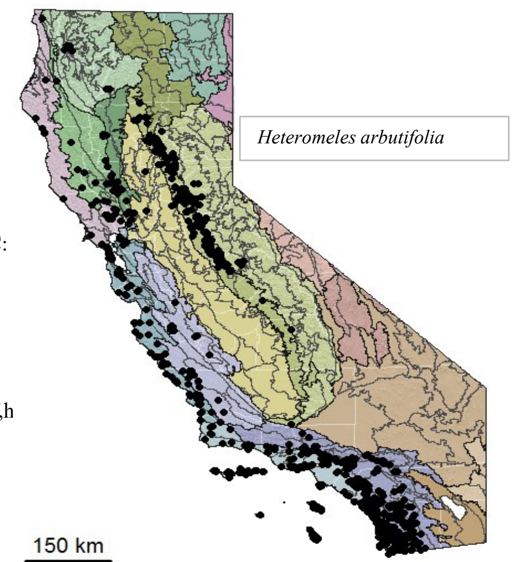
B. Distribution in California; ecological section and subsection
(sensu Goudey & Smith 1994; Cleland et al. 2007)



Map includes validated herbarium records (CCH 2016) as well as occurrence data from CalFlora (2016) and field surveys (Riordan et al. 2018).

Legend has Ecological Sections;
black lines are subsections.

Ecological Section/subsection :
Ecological Section/subsection:
Northern California Coast 263A: e,f,g,j,l,m
Klamath Mountains M261A: a,b,c,f,i,p
Northern California Coast Ranges M261B: a,b,d,f
Northern California Interior Coast Ranges M261C:
Southern Cascades M261D: l
Sierra Nevada M261E: e,f,g,m
Sierra Nevada Foothills M261F: a,b,c,e
Great Valley 262A: c,g,h
Central California Coast 261A: a,b,c,e-h,j,k,l
Central California Coast Ranges M262A: a,b,c,e,f,h
Southern California Coast 261B: a-j
Southern California Mountains and Valleys M262B: a-g,j-o



C. Life history, life form

Polycarpic, tall, evergreen shrub to small tree. Long-lived, to over 100 years (possibly 200) (Sawyer et al 2009).

D. Distinguishing traits

Tall, evergreen woody shrub to small tree 2 –7 m high (occasionally to 10 m), often very wide, with grey bark leaves alternate, petiolate (1–2 cm), elliptical to sometimes oblong, 5–10 cm long; apex and base acute; margins toothed; blades flat, dark green above, lighter below, usually glabrous. Many small (~5 mm wide) flowers with 5 green triangular sepals, 5 white petals, 10 stamens and an inferior ovary in branched inflorescences produced at tips of branches; clusters of ~1cm diameter red, berry-like pomes containing two to three brown, ovoid seeds (McMinn 1939; Munz & Keck 1968; FNA 2016).

E. Root system, rhizomes, stolons, etc.

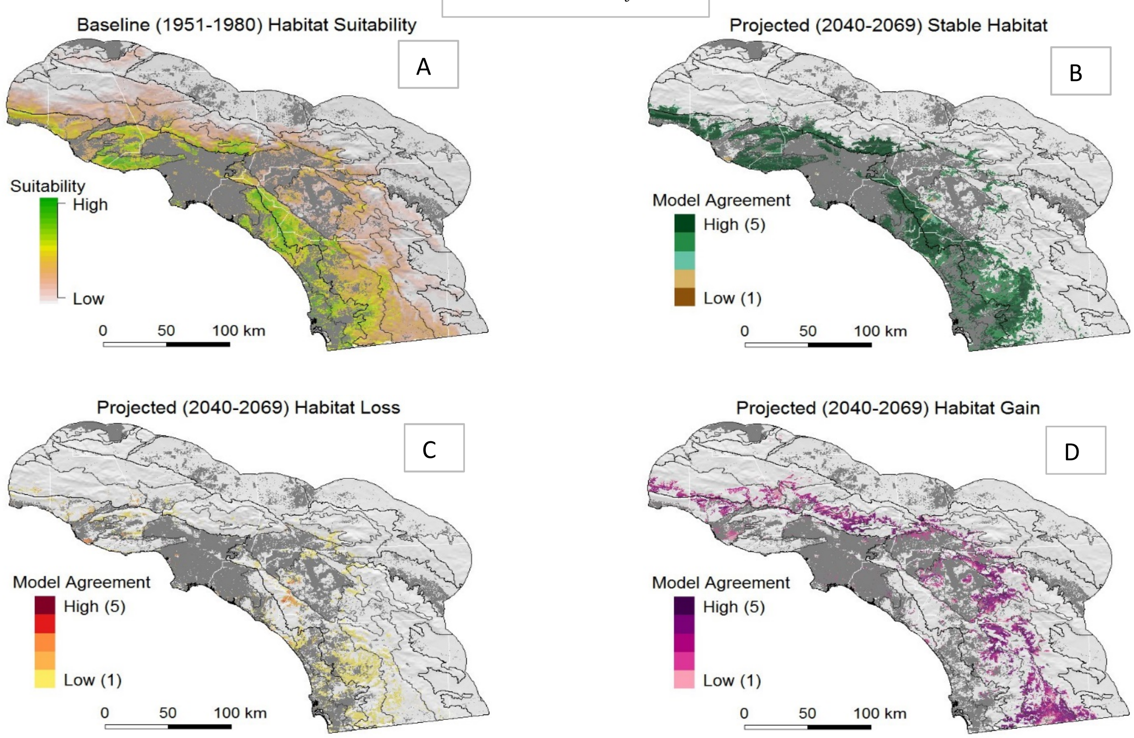
Taproot, branched, woody. Fine roots (feeder roots) are abundant in the humus layer under plants (Hellmers et al. 1955). Can develop an enlarged root crown after repeated burning (Keeley 1981). No vegetative spread.

F. Rooting depth	Toyon is among the chaparral species believed to develop deep, branched, penetrating roots. In one study, roots to were found to only penetrate 6.5 ft deep with a radial spread to 5 ft, but roots were observed penetrating deep into cracks in unweathered rock (Hellmers et al. 1955). Davis and Mooney (1986a, b) considered toyon to have intermediate rooting depth, based on water potential, conductance, and deep soil moisture measurements. Water status measurements made by Ackerly (2004) support a similar conclusion.
IV. HABITAT	
A. Vegetation alliances, associations (sensu Sawyer et al. 2009) 	Occurs as a dominant or co-dominant in many chaparral and woodland alliances as well as transitional communities between coast sage scrub and other communities (McMurray 1990, Sawyer et al. 2009): often dominant to codominant within the following shrubland alliances and listed associations: *Heteromeles arbutifolia* alliance (noted as mesic north slope chaparral (Holland 1986), in the *Heteromeles arbutifolia–Artemisia californica* association, *Heteromeles arbutifolia–Malosma laurina* association, and *Heteromeles arbutifolia–Quercus berberidifolia–Cercocarpus betuloides–Fraxinus dipetala* association. Also in the *Arctostaphylos viscida* alliance in the *Arctostaphylos viscida–Heteromeles arbutifolia–Toxicodendron diversilobum* association; the *Baccharis pilularis* alliance in the *Baccharis pilularis–Heteromeles arbutifolia–Artemisia californica* association; the *Prunus ilicifolia* ssp. *ilicifolia* alliance especially in the *Prunus ilicifolia* ssp. *ilicifolia–Heteromeles arbutifolia* association; the *Quercus berberidifolia* alliance in the *Quercus berberidifolia–Heteromeles arbutifolia* association, and *Quercus berberidifolia–Fraxinus dipetala–Heteromeles arbutifolia* association; and the *Sambucus nigra* alliance in the *Sambucus nigra–Heteromeles arbutifolia* association. A common co-dominant or sub-dominant within many more shrubland alliances including: *Adenostoma fasciculatum* alliance, *Adenostoma fasciculatum-Xylococcus bicolor* alliance, and *Adenostoma sparsifolium* alliance, *Arctostaphylos glandulosa* alliance, *Arctostaphylos glauca* alliance, *Ceanothus crassifolius* alliance; *Ceanothus cuneatus* alliance, *Ceanothus leucodermis* alliance, *Ceanothus megacarpus* alliance; *Ceanothus spinosus* alliance, *Ceanothus thyrsiflorus* alliance, *Cercocarpus betuloides* alliance, *Diplacus aurantiacus* alliance, *Eriogonum fasciculatum–Salvia apiana* alliance, *Malocothamnus fasciculatus* alliance, *Malosma laurina* alliance, *Quercus berberidifolia–Adenostoma fasciculatum* alliance, *Quercus durata* alliance, *Quercus pacifica* alliance, *Quercus wizlizeni* alliance, *Rhus integrifolia* alliance, *Venegasia carpesioides* alliance. A significant component of the shrub layer within numerous woodland alliances, including: the *Aesculus californica* woodland alliance; the *Juglans californica* alliance in the *Juglans californica/Heteromeles arbutifolia* association; the *Lyonothamnus floribundus* alliance; the *Pinus sabiniana* alliance in the *Pinus sabiniana/Artemisia californica–Ceanothus ferrisiae–Heteromeles association,* and *Pinus sabiniana /Ceanothus cuneatus–Heteromeles arbutifolia* association; the *Quercus agrifolia* alliance in the *Quercus agrifolia/Frangula californica–Heteromeles arbutifolia* association, *Quercus agrifolia/Heteromeles arbutifolia* association, *Quercus agrifolia/Heteromeles arbutifolia–Toxicodendron diversilobum* association, and *Quercus agrifolia–Umbellularia californica /Heteromeles arbutifolia–Quercus berberidifolia* association; and in the *Umbellularia californica* alliance.
B. Habitat affinity and breadth of habitat	In chaparral scrub and woodlands on semi-dry rocky slopes to valley bottoms and along alluvial terraces of streams in well drained soils (McMinn 1939, Munz & Keck 1968). In southern California, toyon occupies the more mesic microsites and mostly on north-facing, west by northwest, and east by northeast facing slopes (Hanes & Jones 1967, Borchert et al. 2004).
C. Elevation range	Sea level to 1300 m (Phipps 2016).
D. Soil: texture, chemicals, depth	Horticulturists report toyon is adaptable to a wide range of soils (Lens & Dourley 1981), with the exception of highly alkaline soils (Everett 2012). In the wild, plants occur in shallow to very deep, well-drained to excessively-drained soils including soft and hard sandstones and often gravelly sandy loams and sandy loams (Borchert et al. 2004). Toyon also grows on serpentine soils (Harrison 1997, Wolf 2001).
E. Precipitation	Occurs primarily in Mediterranean climate zone with cool to cold moist winters and warm to hot dry summers. Plants grow within a large precipitation range, but usually in areas with > 15 inches. For ecological sections occupied by toyon, annual normal precipitation ranges from 10 to 40 in (250 to 1,020 mm) in the Southern California Mountains and Valleys (M262B), from 10 to 25 in (250 to 640 mm) in the Southern California Coast (261B), and from 20 to 40 in (510 to 1,020 mm) in the Northern California Coast Ranges (M261B) and Sierra Nevada Foothills (M261F).

F. Drought tolerance	Drought tolerant in gardens (Bornstein et al. 2005, Perry 2010), but plants tend to grow in the more mesic microsites and exposures in chaparral and sage scrub habitats. Tolerating drought is in part tied to its fairly deep roots (Gigon 1979) and the anatomical structure of the leaves (Balsamo et al. 2003). Jarbeau et al (1995) found toyon to be somewhat resistant to drought-induced embolism. It has small pores in its pit membranes and narrow vessels that provide the ability to withstand low water potentials, but the deep roots are important for avoiding catastrophically low water potentials. In a study of post-fire resprouting during drought, 100% of toyon resprouted but only 73% survived the drought, less than some other more drought tolerant species such as *Malosma laurina* (Pratt et al. 2014). The inability of plants to rebuild carbohydrate reserves due to an extreme drought may have contributed to root death and subsequent shoot loss (Pratt et al. 2014). After successive, extreme heat waves where temperatures exceeded 35°C, recovery of carbon assimilation in the leaves was much slower than after earlier heat waves and may be one of the reasons for such shoot death (A. Pivovaroff and others, 2016 Abstract for American Geophysical Union).
G. Flooding or high water tolerance	Not tolerant of standing water but withstands episodic flooding of sloping alluvial terraces along streams (A. Montalvo pers. obs.).
H. Wetland indicator status for California	None.
I. Shade tolerance	Full sun to partial shade. Seedlings establish in shade. Plants can grow under the canopies of shrubs that require full sun and eventually overtop them (Hanes & Jones 1967).

V. CLIMATE CHANGE AND PROJECTED FUTURE SUITABLE HABITAT

Heteromeles arbutifolia



A. Species Distribution Models (SDM forecasts, Riordan et al. 2018) Map descriptions	Modeled habitat suitability under (A) baseline (1951–1980) and (B–D) projected midcentury (2040–2069) climate conditions. Projected future habitat suitability maps show agreement across five different climate model scenarios: (B) stable = suitable under both baseline and future conditions; (C) loss = suitable under baseline but unsuitable under future conditions; (D) gain = unsuitable under baseline and becoming suitable under future conditions. In all maps, land area that has already been converted to urban and agriculture land uses is masked in dark gray (FRAP 2015 Assessment; https://map.dfg.ca.gov/metadata/ds1327.html). High resolution maps are available for download (see Riordan et al. 2018).

B. SDM summary	Species distribution model predictions of future suitable habitat for toyon under 21st century climate change are variable. Assuming a future of continued high greenhouse gas emissions, Riordan et al. (2018) predicted 69–100% of baseline habitat for toyon in southern California would remain suitable (stable) under mid-century conditions across future climate scenarios from five different general circulation models (GCMs) (V. A. Fig. B). The high predicted stable suitable habitat was accompanied by moderate gains in suitable habitat (42–56%) which exceeded loss under four of five climate scenarios (V. A. Figs. C-D). Only under the wettest future climate scenario did predicted loss in suitable habitat (31%) exceed gain (3%). Principe et al. (2013) also predicted high stability in suitable habitat for toyon under mid-century conditions, but lower habitat gain. In contrast, Riordan and Rundel (2014) predicted widespread loss in suitable habitat for the species in southern California by the end of the century (2100). The combined effects of land use, altered fire regimes, and climate change could negatively affect toyon, even if the projected loss in habitat from climate change alone is relatively low. In southern California human activity is the primary driver of fire (Keeley & Syphard 2016), with fire ignitions and fire frequency increasing with increasing human population density (Syphard et al. 2007, 2009). Toyon is an obligate sprouter that tolerates a range of fire return intervals (10–100 yrs), but extremely frequent fires can be detrimental (see VI. D. Regeneration after fire or other disturbance) and postfire drought conditions can decrease resprout survival (Pratt et al. 2014). The high level of habitat conversion and fragmentation at lower elevations of the species' range creates a considerable barrier to dispersal and gene flow that could negatively affect the adaptive capacity and ability of the species to respond to changing conditions. Riordan and Rundel (2014) caution that human land use may compound projected climate-driven losses in suitable habitat in southern California shrublands.
C. SDM caveat	The five GCMs used to predict future habitat suitability assume a 'business-as-usual' scenario of high greenhouse gas emissions that tracks our current trajectory (IPCC scenario RCP 8.5). They show how climate may change in southern California and highlight some of the uncertainty in these changes. The true conditions at mid-21st century, however, may not be encompassed in these five models. Predictions of current and future habitat suitability should be interpreted with caution and are best applied in concert with knowledge about the biology, ecology, and population dynamics/demographics of the species. They are best interpreted as estimates of exposure to projected climate change. Our models characterize habitat suitability with respect to climate and parent geology but do not include other factors, such as biotic interactions or disturbance regimes, that may also influence species distributions. Additionally, they do not include the adaptive capacity of a species, which will impact its sensitivity to changes in climate. See Riordan et al. (2018) for more information on SDM caveats.

VI. GROWTH, REPRODUCTION, AND DISPERSAL

A. Seedling emergence relevant to general ecology Seedlings with two nearly round cotyledons below serrated true leaves. Photo: A. Montalvo.	 After dispersal, seeds are stratified by winter temperatures and seedlings emerge in moist litter (Gordon & White 1994, Sawyer et al. 2009). Seedling recruitment appears restricted to mesic sites in well developed litter beneath mature shrubs (McMurray 1990) with success associated with high rainfall years (Sawyer et al. 2009). Meyer (2008) reports seedlings emerge in winter but mortality tends to be high. Keeley (1990) noted that toyon seeds germinate soon after dispersal and that seedlings tend to survive best in woodlands and very old chaparral. Many seedlings were observed within old chaparral in deep litter (Keeley 1992).
B. Growth pattern (phenology)	In studies in northern California, leaf flush began in early spring, reaching maximum size quickly; plants flowered in late summer with fruits maturing in late fall to early winter (Dement & Mooney 1974). Mature fruits are most often found in late fall to early winter in southern California too, but flowering varies with rainfall patterns and location. Based on herbarium collections, most have been collected May through July suggesting peak flowering within that period (CCH 2016). In southern California, we have observed plants flowering primarily late spring into early summer (May–July). Minnich (1985) found that plants responded quickly to rainfall, producing flowers while plants still bore green fruits, then maturing the new fruits within a month. He also found flowering April to July in northern Baja California and in March to May and December in southern Baja California.
C. Vegetative propagation	Plants resprout readily after fire or cutting, but plants do not spread vegetatively.

D. Regeneration after fire or other disturbance	Toyon is an obligate sprouter (Keeley 1991). Postfire recovery is by resprouting from the root crown (Sawyer et al. 2009); seeds are non-refractory and generally killed by fire (Keeley 1991). Heating seeds to 120°C killed most seeds, and heating to 70°C for one hour resulted in a large drop in viability (Keeley 1987). As such, seedlings are rarely observed in the first season after fire and pesistence in fire-prone communities is tied to resprouting. Recruitment from seed and expansion of populations occurs between fires with the largest expansions in stands of vegetation that have not burned for a long time (McMurray 1990, Keeley 1991, Keeley 1992). Toyon occurs within a variety of fire regimes of 10 to 100 years (McMurray 1990). Although it has been considered resilient to short or longer interval fires (Gordon & White 1994), repeated short interval fires are likely to exhaust reserves and kill plants.
E. Pollination	 Flowers are visited and likely pollinated by a variety of native bees. Kremen et al. (2002) reported visits from 30 different species of native bees at a site in northern California. Jha et al. (2013) found *Bombus vosnesenskii* showed a significant preference for toyon during the period of their study in central California. Moldenke (1976) reported several genera of native bees, beetles, wasps, syrphid flies, and butterflies as flower visitors and probable pollinators. Also visited by non-native honey bees (Goltz 1987). *Apis mellifera* (European honey bee) visiting toyon flowers. A. Montalvo.
F. Seed dispersal  American robin eating fruits in late December. A. Montalvo.	The fruits are dispersed by a variety of birds and mammals (McMurray 1990). Coyotes also eat the berries and disperse viable seeds. Seeds recovered from coyote scat were found to germinate (Silverstein 2005). Some seeds are expected to fall close to the parent plant while birds are feeding, but dispersal distances of seeds swallowed by birds and coyotes can be large because the animals can cover large distances in a single day. In a study in northern California, 10 different avian species removed over 90% of toyon fruits (Aslan 2011). The foragers were classified "pulse feeders" which feed in large, transient flocks that move quickly among plants and sites, or "background feeders" which are resident, territorial feeders. In toyon, 48.6% of fruits were removed by pulse feeders which can move seeds long distances. Two handling guides were also recognized; those that swallowed fruits whole, defecate whole seeds, vs. "seed predators" that destroy the consumed seeds. Over 94% of the fruits were taken by dispersers.
G. Breeding system, mating system	No studies found for toyon. In the Rosaceae, subfamily Maloideae, diploid taxa are generally self-incompatible and polyploids tend to be self-compatible (Dickinson et al. 2007). Toyon is considered diploid.
H. Hybridization potential	There are no related species with which toyon can hybridize within its natural range. No studies were found on the ability to mate with genetically distant populations.
I. Inbreeding and outbreeding effects	No studies found.

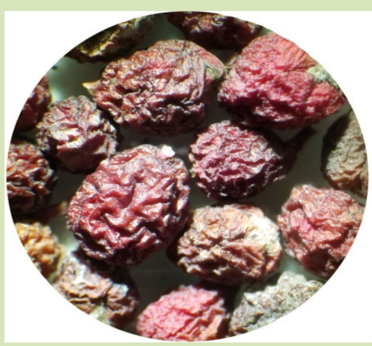
VII. BIOLOGICAL INTERACTIONS

A. Competitiveness	Seedlings are able to emerge and grow under the canopy of other woody plants (V1. A. Seedling emergence). Their shade tolerance may confer an advantage to seedling establishment within mature stands of vegetation where other shrubs may act as nurse plants (Sawyer et al. 2009).
B. Herbivory, seed predation, disease	**Herbivory:** Fruits are eaten by a variety of animals and a proportion of the seeds are expected to be destroyed when the fruits are consumed (see VI. F. Seed dispersal). The seeds are reported to contain cyanogenic glycosides that may have toxic effects on some consumers (Fuller & McClintock 1986, Dement & Mooney 1974). The young, flushing foliage and green fruits appear to be protected from herbivory by high tannin and cyanogenic glucoside content (Dement & Mooney 1974). The glucosides are shifted from fruit pulp to seeds at fruit maturity. Tannins increase with leaf maturity while glucoside content decreases. Most herbivore damage to leaves occurs in April to May, and in September (Swan in Dement & Mooney 1974) .

B. Herbivory, seed predation, disease… continued	**Disease:** Toyon is a proven host for the pathogen, *Phytophthora ramorum* which causes leaf blight and dieback of leaves and branches (Cave et al 2008- USDA Risk Analysis). However, risk assessments and mapping of the pathogen suggest it is unlikely to be problematic in southern California (Meetemeyer et al. 2004). However, plants are also susceptible to *Phytophthora* root rot (Filmer et al 1986), and *Phytophthora tentaculata*, a particularly virulent water mold, was detected in toyon in native plant nurseries and at restoration sites indicating a need for improved best management practices at restoration nurseries (Rooney-Latham et al. 2015). Die off of whole branches during drought sometimes occurs and may also be caused by endophytic fungi similar to those found in *Malosma laurina* (Stephen Davis pers. com.). Such infections have been found to cause extensive damage during extended drought. Plants are also susceptible to a bacterial fireblight disease (see X. C. Horticulture).
C. Palatability, attractiveness to animals, response to grazing	The leathery leaves are considered useless to horses and cattle, poor to useless for sheep, and good to fair for goats and deer, with most browsing of the tender resprouts after fire. (Sampson & Jespersen 1963). Tegzes et al (2003), however, found that a herd of goats died after being fed clippings of toyon. The leaves contain non-toxic glycosides which after ingestion can be transformed into hydrogen cyanide in the rumen, causing respiratory failure. The highest concentrations of glycosides are found in the young leaves (also see VII. B. Herbivory).
D. Mycorrhizal? Nitrogen fixing nodules?	Plants form symbiotic associations with arbuscular mycorrhizal fungi (AM). In a greenhouse experiment, seedlings were planted in pots inoculated with 25 g whole soil (collected from natural site), or without whole soil, and 64.4% of inoculated roots became colonized with AM compared to 1.7% of controls (L. Egerton-Warburton, A. Montalvo, & E. Allen, unpublished data). Seedlings were grown in autoclaved soil, 1:1:1 native soil, coarse sand, fine sand. The plants were found to be 64.3% mycorrhizal dependent. They achieved significantly greater height, volume, and dry weight than uninoculated control plants. Toyon also forms symbiotic associations in root nodules with nitrogen-fixing strains of *Frankia* (Battenberg et al. 2017).
E. Insect pollinators	Several genera of toyon pollinators (see VI. C. Pollination) are known to forage over large distances, which may facilitate intermediate to long-distance pollen flow. *Apis mellifera* and several species of *Bombus* were found to fly distances of 1,000 to 10,000 m (Zurbuchen et al. 2010). However, the way different species of bees travel across fragmented habitat or respond to the spatial scale of urbanization varies. For example, Schochet et al. (2017) found the three most common species of *Bombus* in southern California respond differently to habitat variables at a range of spatial scales (variables such as amount of floral resource, impervious surfaces, distances to major roads, and distance to coast for habitat reserves, fragments, and urban areas). In particular, the three species responded to the scale of impervious surfaces associated with urbanization differently. One of the species studied, *B. vosnesenskii*, is a pollinator of toyon (see VI. C). It was found to cross developed areas and forage in urban and non-urban landscapes. Declines in native bee and honey bee populations are of great concern (Murray et al. 2009). Habitat fragmentation from agriculture and urbanization have resulted in declines in pollinator populations and decreases in pollination services (e.g., Kremen et al 2002). Habitat corridors and hedgerows within agricultural lands (see X. C. Horticulture and agriculture) are used by bees and can help maintain bee and plant populations (Kreman et al. 2002, Townsend & Levey 2005).

VIII. ECOLOGICAL GENETICS

A. Ploidy	No chromosome count reported for toyon. Not likely to be variable. Within Rosaceae, subfamily Maloideae, all of the monotypic genera studied have 2n = 34 (or n = 17) chromosomes (Dickinson et al. 2007). Polyploidy and variation in chromosome numbers is common in family Rosaceae, but is associated with hybridization potential. Genera with multiple species have more potential for hybridization (Dickinson & Talent 2007).
B. Plasticity	Plants can respond to different environmental conditions to achieve homeostasis through physiological responses or morphological changes. For example, Gigon (1979) compared irrigated and unirrigated toyon grown from seeds in an experimental garden at Stanford, California. He found photosynthetic rates generally decreased with water stress and irrigated toyon had higher photosynthetic rates in summer and fall than unirrigated plants. Plants produce different shoot architecture in shade compared to full sun, allowing shade leaves to photosynthesize more efficiently than sun leaves in lower light (Valladares & Pearcy 1998).

C. Geographic variation (morphological and physiological traits)	**Morphology:** Yellow fruits occur occasionally throughout the species range, and a large-fruited form with sub-entire leaves occurs in the Channel Islands and has been called var. *macrocarpa* (see I. B. Synonyms, McMinn 1939, Munz 1974). Ramirez (2015) compared cavitation resistance for island and mainland plants and found essentially no difference, despite less drought stress experienced by island plants. However, island plants had significantly larger leaves and greater leaf specific area (less sclerophyllous leaves) than mainland plants. Seed weight was found to vary significantly among populations sampled along an ecological gradient in Baja California (Martijena & Bullock 1997). Seed weight increased significantly with increased elevation but not with precipitation. It is not known if these differences in seed and leaf traits are genetically controlled, a plastic response to different conditions for growth, or some combination.
D. Genetic variation and population structure	No studies found.
E. Phenotypic or genotypic variation in interactions with other organisms	There is an association between leaf traits and deterrence of large herbivores (see VIII. F, below), but we have not found any studies on the genetic control of leaf-trait variation.
F. Local adaptation	Toyon is a very widely distributed species so there are likely to be adaptive differences among populations from very environmentally different or distant locations. In many plants, including toyon, entire margins are associated with thinner leaves and have been hypothesized to be favored in less arid environments than thicker, spinose leaves (Givnish & Kriebel 2017). Furthermore, in the Channel Islands where many taxa evolved in the absence of large, introduced herbivores, Bowen & van Vuren (1997) examined the association between leaf traits in six shrub species, including toyon, and leaf consumption by sheep. The Channel Island forms of all six species had less spinose leaves than mainland forms and were eaten significantly more by sheep than the mainland forms, suggesting the differences could be, in part, influenced by a historical lack of herbivore pressure on the islands.
G. Translocation risks	No studies found on the risks of moving toyon among different environments over its range. No studies found on mating compatibility among plants from environmentally or geographically distant locations or for mating among close relatives.
IX. SEEDS	 Dried fruits (left) and seeds (right). A. Montalvo 4 mm 
A. General	Seeds are transient and do not form persistent seed banks (Keeley 1991, Meyer 2008). Seed viability shortly after cleaning can exceed 90% (Montalvo pers. obs.). The seeds lack endosperm (Meyer 2008).
B. Seed longevity	Reported to have a shelf life of less than one year when stored dry in a laboratory at room temperature and likely in the field (Keeley 1991). Seeds air dried indoors after wet processing (see IX. F. Seed processing) and stored in a refrigerator at 2–4 °C in sealed containers retained viability for 6+ years (A. Montalvo pers. obs.) suggesting seeds might be orthodox in cold dry storage (e.g., Meyer 2008). Seedling emergence and seedling vigor declined after the first few years.
C. Seed dormancy	Seeds are non-dormant at dispersal, but can become secondarily dormant (Meyer 2008). No treatment is needed if planted right after collection, but otherwise may require moist, cold stratification. Cold treatment is recommended before planting in spring (Meyer 2008).
D. Seed maturation	Fruits and seed mature in late fall to early winter. Fruits remain on the plants into January or until flocks of birds remove them.
E. Seed collecting and harvesting	Harvest soon after fruits are mature (when bright red and seed inside is brown) before they are harvested by birds. Collect by stripping clusters of ripe into sacks or buckets. Keep fruits away from heat.

F. Seed processing	It can be difficult to extract the seeds from the firm pomes (Meyer 2008, Montalvo pers. obs.). Fruits can be soaked until the fruit flesh softens (one to two weeks), then pushed through a 1/4 inch screen to extract seeds, taking care not to damage the seeds. Long soaking times can cause damage to the softened seeds during processing. Use of a flexible plastic screen can help reduce damage to seeds (Genny Arnold, pers. com.). Much of the pulp can be floated off after maceration. After air drying the remaining seeds and pulp, more of the pulp can be driven off by processing in a seed blower. Gordon (2014) processes fresh fruits in a blender at low to moderate speed, then rubbing fruits against a rough surface to release seeds. Greever (1979) recommended pushing crushed pomes through a 1/2 inch screen and then planting.
G. Seed storage	Store processed seeds or air-dried fruits at 2–4 °C in sealed containers (see IX. B. Seed longevity).
H. Seed germination	 Young seedling with cotyledons. Photo by Lee Gordon, CNPS Propagation Committee (Gordon 2014). The amount of time to germinate depends on freshness of seeds. Everett (2012) found fresh seeds tend to germinate in eight to 15 days. Others report 10 to 40 days for emergence from untreated seeds with success in December similar to May (Meyer 2008).
I. Seeds/lb	Seed weight varies greatly among populations. Seed weight was found to vary along an elevational gradient in Baja California (see VIII. C. Geographic variation); the average for 12 populations was 12,600 seeds/lb (range: 9,200–16,200 seeds/lb). Values of 23,900 seeds/lb and 82,500 seeds/lb have also been reported elsewhere (Meyer (2008) and pure seeds from a collection from the Santa Ana Mountains of southern California had an estimated 68,000 seeds/lb (estimated from weight of 340 pure seeds =0.0050 lb). S&S Seeds (2016) reports an average of 2,475 live seeds/bulk lb and 5,000 seeds per PLS lb for commercial seed lots.
J. Planting	To control spread of water molds and other infections, processed seeds can be placed in a 10% household bleach solution for 1 minute, then rinsed before treating or planting (see XIII. Link for NPNPP). Plant seeds in the nursery fall to spring, but cold stratify seeds if planting in spring (Greever 1979, Meyer 2008). Plant seeds at surface or to about 5 mm deep in deep flats filled with sand or a well-drained soil mix for seedlings. Deep flats or deep plugs are needed because taproots grow quickly. Alternatively, if seeds are planted at the surface, they can be shifted easily to deep pots (Gordon 2014). Seedlings or seedling mix can be successfully inoculated with arbuscular mycorrhizal fungi (see VII. D. Mycorrhizae). Greever (1979) found that by May, seedlings from seeds planted in flats in December were no larger than those planted the following March. Direct-seeding of open wild sites is not likely to be successful owing to the need for shade, litter, and moisture (Meyer 2008). On Santa Catalina Island, experimental plots were direct seeded and also planted with seedling starts (Stratton 2004). Toyon seeded into chaparral mix plots at a rate of 25 seeds/m^2 resulted in no seedling establishment (12 x 12 m plot size). Planted seedling survival was 21% in watered plots and 8% in unwatered plots after 2 years time, but individual plant cover was slightly higher in the unwatered plots (0.04 m^2) than in the watered plots (0.02 m^2).
K. Seed increase activities or potential	No seed increase activities were found. In southern California, seed yield in wild population can be low, especially in drought years. To ensure good seed yields of regionally local seeds, plantings in hedgerows or screens would double as seed orchards.
X. USES	
A. Revegetation and erosion control	Its deep roots and large evergreen canopy make it a valuable plant for erosion control on banks and slopes (Lens & Dourley 1981). It is approved for fuel modification zones in Riverside County (see http://rctlma.org/Portals/7/documents/landscaping_guidelines/comprehensive_plant_list.pdf).
B. Habitat restoration	Container plants grown from seed (1 gallon, 2 gallon or larger) have been used successfully with high survival rates when planted in late fall thorough winter and drip irrigated minimally through first dry season (A. Montalvo pers. obs.)

C. Horticulture or agriculture	**Horticulture:** Toyon are widely planted as screens, hedges, or specimen plants in urban landscapes, gardens and parks (Lenz & Dourley 1981, Bornstein et al. 2005, Perry 2010). The plant is valued for its evergreen leaves, attractive fruits, ability to naturalize, and its broad tolerance to different soils and climates from coastal to inland locations. These evergreen plants accumulate few dead branches (Cowan & Ackerly 2010) and the leaves are slower to ignite than those of many other shrubs (Montgomery & Cheo 1971). The lower flammability rating has resulted in acceptance of plants in fuel modification zones. This is a wide-ranging species with the potential for a number of ecotypes. Taking this into account is important, especially for moist coastal areas where pathogen infections can be problematic (Lenz & Dourley 1981). Plants tolerate occasional deep watering which may be needed in hot, inland locations with low rainfall. Available from many nurseries. Horticultural selections have been made, including*Heteromeles abutifolia* var. *cerina* 'Davis Gold' known for its bright yellow fruits (Bornstein et al. 2005). Plants can be started from cuttings (Hartmann et al. 1997, Meyer 2008, Everett 2012) but starting plants from seeds is more successful, increases genetic diversity of planting stock, and fewer issues with spread of pathogens. Seeds planted in early fall can achieve 1-gallon size by spring (Gordon 2014). Prune in winter prior to spring flush and flowering (O'Brien et al. 2006). **Pests:** Plants harbor a number of insect pests at low densities and young plants are susceptible to fungal pathogens (Bornstein et al. 2005, see VII. B. Herbivory, seed predation, disease). Growing container plants in media with air-filled porosity of > 10% (10–20%) can help to reduce infection by*Phytophora cinnamomi* (Filmer et al 1986). Plants can be infected with a bacterial disease of pome-producing plants in the Rosaceae, called "fireblight". All infected plant parts need to be cut away, tools sterilized, and parts disposed of carefully to prevent spread (Bornstein et al. 2005). For control of fireblight, see Teviotdale (2011). Care must be taken to avoid occasional damping off of seedlings (Everett 2012). **Hedgerows:** Currently used and recommended for hedgerow plantings (Kremen et al. 2002). Of the 39 species of bees visiting toyon at one location, 10 were important crop visitors. Morandin et al. (2016) examined the cost of hedgerow installation relative to the cost of insecticide use and effects of limited pollination service and found the return time to break even at about 7 yr. **Orchards:** No records of seed/cutting orchards were found, but there may be row plantings in northern California, possibly at UC Davis (mentioned in Filmore 1984). It may be possible to use hedgerows as seed orchards with sufficient source documentation and genetic diversity in planting stock.
D. Wildlife value	The fruits are eaten by a variety of birds and mammals and are an important source of food in winter (McMurray 1990). Flocks of cedar waxwings and American robins often strip plants of fruits in early winter (Lenz & Dourley 1981). Other birds such as band-tailed pigeons, sapsuckers, thrashers, and wren-tits as well as mammals such as woodrats also eat the fruits (Anderson & Roderick 2003). Aslan (2011) found 10 avian species consumed toyon fruits in one study. Coyotes also eat the fruits (see VI. F. Seed dispersal), but the plants are not normally utilized as browse (Borchert et al. 2004,). Ramirez et al. (2012) found that exotic deer ate over 80% of post-fire resprouts on Santa Catalina Island, but deer did not consume many resprouts on the mainland. Plants also provide for nesting sites and cover for foraging birds and mammals. Next to agricultural fields, hedgerows made of a mixture of native species, inlcuding toyon, supported significantly more bird species, evenness and abundance than the weedy margin alternative (Heath et al. 2017). Dusky-footed woodrats (*Neotoma fuscipes*) also feed on plants (Barrett et al 2016).
E. Plant material releases by NRCS and cooperators	None.
F. Ethnobotanical	The fruits were used raw or cooked by native people (Chumash, Cahuilla) as food in winter (Bean & Saubel 1972, Timbrook 2007, Garcia & Adams 2009); they have a powdery texture and tart apple taste and are better cooked by roasting or boiling (Garcia & Adams 2009). Timbrook (2007) reports the Chumash did not boil fruits and describes some traditional preparations. There were many medicinal uses for toyon. For example: flowers or leaves were steeped in hot water to make a tea to treat irregular menses; a tea from bark and leaves for aches and pains; and mash of leaves to bathe sores (Garcia & Adams 2009). Fruits were also used (along with elderberry fruits) to treat dementia (Alzheimer's) (Garcia & Adams 2009). A recent study examined the phytochemistry and safety of toyon fruits as a traditional treatment for Alzheimer's disease (Wang et al. 2016). Consumption of dried fruits was found to be safe. Leaves were tested (after freezing them) and no cyanogenic compounds were detected, contradicting other reports (see VII. C. Palatability, attractiveness to animals). A number of compounds isolated from toyon fruits are anti-inflammatory agents that the authors suspect may protect the blood-brain barrier by preventing inflammatory cell infiltration into the brain. Adams (2017) reviewed the mechanism by which chemicals from toyon and several other traditional medicinal plants are thought to illicit an antiflammatory response. The hard wood was used for making bowls, cups, pegs, frames, clubs, arrows, poles for buildings, and many other items (Timbrook 2007).

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XIII. LINKS TO REVIEWED DATABASES & PLANT PROFILES

Fire Effects and Information System (FEIS)	https://www.fs.fed.us/database/feis/plants/shrub/hetarb/all.html
Calflora	https://www.calflora.org//cgi-bin/species_query.cgi?where-calrecnum=4140
Calscape	https://calscape.org/Heteromeles-arbutifolia-()
Jepson Interchange	https://ucjeps.berkeley.edu/cgi-bin/get_cpn.pl?28072
Jepson eFlora (JepsonOnline, 2nd ed.)	https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=28072
USDA PLANTS	https://plants.usda.gov/core/profile?symbol=HEAR5
Native Plant Network Propagation Protocol Database (NPNPP)	https://npn.rngr.net/propagation
Native Plants Journal	http://npn.rngr.net/journal
Native Seed Network (NSN)	http://www.nativeseednetwork.org/
Native Plant Notebook (NPN)	https://www.fs.usda.gov/detail/umatilla/landmanagement/resourcemanagement/?cid=fsbdev7_016129
GRIN (provides links to many recources)	https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearch.aspx
Flora of North America (FNA) (online version)	http://www.efloras.org/florataxon.aspx?flora_id=1&taxon_id=115321
Native American Ethnobotany (NAE)	http://naeb.brit.org/
Woody Plant Seed Manual	https://rngr.net/publications/wpsm
Rancho Santa Ana Botanic Garden Seed Program, seed photos	http://www.hazmac.biz/050321/050321HeteromelesArbutifolia.html
XIV. IMAGES	

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