Wild orchids: A framework for identifying and improving sustainable harvest

Abstract

Worldwide, thousands of orchid species are harvested from the wild. Widespread legal and illegal unsustainable trade has contributed to the decline of many species. However, there is also evidence of long-term, sustainable wild harvest of some orchid species that contribute to local livelihoods and cultural traditions. There is a clear need to help guide harvesters and resource managers towards sustainability. However, there is currently no appropriate framework to guide local harvest decisions, which is especially problematic given huge data limitations, variations in on-the-ground capacity to monitor and manage resources, and considering that the potential for sustainable harvest is context-specific. We reviewed the literature on orchid harvest, ecology and demography; assessed information on the life history of 27 harvested species; and drew on our experience with diverse orchid taxa to identify characteristics expected to influence harvest sustainability. We identified 23 characteristics within four themes: abundance and distribution; species traits related to growth and reproduction; local management practices; and demand. We selected 12 characteristics for which information was available for many species, and observable in the field, and used an iterative process to develop a decision-making dichotomous key. The key identifies if and how the harvest of a given population at a given time can be conducted more sustainably, offering sets of considerations that harvesters and managers can use and adapt to local contexts. Critical research gaps include techniques for partial plant harvest and for augmentation; and investigation into the traits and protocols that have permitted long-term persistence and that can increase current sustainability.

Keywords: conservation, dichotomous key, Orchidaceae, sustainable use, wildlife trade

1. Introduction

Millions of orchids from thousands of different species are harvested from the wild globally for their flowers, pseudobulbs, tubers, roots and fruits (reviewed in Hinsley et al., 2018). Orchids represent one of the largest and most widely distributed families of flowering plants, numbering more than 28,000 species (Givnish et al., 2015; Royal Botanic Gardens, Kew 2021), and orchid harvest and trade is equally diverse. It includes thousands of species harvested as ornamentals for backyard gardens and specialist hobbyist collections (e.g., Flores-Palacios and Valencia-Díaz, 2007; Phelps and Webb, 2015), and for cultural or religious celebrations (e.g., Emeterio-Lara et al., 2016; Ticktin et al., 2020). It also includes edible species harvested for products such as *chikanda* cake (Veldman et al., 2018), *salep* beverage, *dondurma/kaimaki* ice-cream (Hossain, 2011; Tamer et al., 2006), and vanilla ice-cream (Ecott, 2004). Many species with medicinal properties are also harvested, such as *Dactylorhiza hatagirea*, whose tubers are used in Ayurveda, Siddha, Unani, and Himalayan folk medicinal traditions (Wani et al., 2020), and *Dendrobium* spp. used in traditional Chinese Medicine (Liu et al., 2014). Trade volumes and spatial and temporal dynamics remain poorly documented for all these products, but available evidence points to the prevalence of large-scale, commercial trade of many wild-collected orchids (Table 1).

There is a widespread assumption reflected in the literature and policy, that the harvest of wild orchids cannot be sustainable (see Hinsley et al., 2018). However, there is little empirical data on the effects of harvest on the persistence of orchid populations, or on the conditions under which harvest could be sustainable (Hinsley et al., 2018; but see Mondragón, 2009; Ticktin et al., 2020). The literature on orchid conservation largely focuses on the population dynamics of species and populations that are not harvested (e.g., Acevedo et al., 2020; Ackerman et al., 2020, Shefferson et al., 2020); on variables important to *ex situ* and *in situ* conservation (e.g., Swarts et al., 2017), and on stopping unregulated or illegal trade of wild plants (e.g., Gale et al., 2019; Phelps and Webb, 2015; Wong and Liu, 2019). However, while there are many examples of unsustainable harvest, there are also compelling examples of long-term harvest of some orchid species that have persisted, suggesting sustainability (Table 2). There is a clear need for a framework to help distinguish between such opposite scenarios.

We reviewed the literature on orchid harvest, ecology and demography; assessed the available information on the life history of 27 heavily-harvested species, and drew on the authors' diverse experience—to identify characteristics and conditions expected to influence harvest sustainability. We used these to develop a decision-making dichotomous key to identify the species and population-level contexts under which the *existing* harvest of wild orchids could be made more sustainable. This is aimed specifically at those who make harvest decisions at the local level, both harvesters and local managers (e.g., local forest department officials, park managers, private landowners, community forest user groups, CITES Authorities). This does not seek to promote wild orchid harvest, but rather respond to the on-the-ground realities of widespread orchid trade, little data on the effects of harvest, and the pragmatic need to attempt to improve harvest regimes. We also identify knowledge gaps that need to be considered to better identify conditions for sustainable harvest.

1.2 Challenges of governing orchid trade

Orchid overharvest has led to decline, local extirpation and extinction in the wild of multiple orchid species (see review by Hinsley et al., 2018; Kull, 1999; Liu et al., 2014; Table 2). Resulting concerns, and the challenges of species-level identification, have made the orchid family among the most heavily regulated plant groups, with all orchid species regulated under the Convention on International Trade of Endangered Species of Fauna and Flora (CITES)- comprising the vast majority of species listed on the Convention. The Convention bans commercial international trade for a small number of species listed on CITES Appendix I, notably the ornamental lady slipper orchids (e.g., *Paphiopedilum* spp.). Domestic regulations on orchid harvest are also very common, and in many countries wild harvest is banned or restricted (e.g., Lao PDR, Mexico, Myanmar, Thailand, USA; see Hinsley et al., 2018; Phelps and Webb, 2015). However, illegal collection and trade remain prevalent in many parts of the world (see Hinsley et al., 2018; Jiménez-López et al., 2019), and there is widespread evidence that CITES orchid regulations are regularly flaunted (e.g., Phelps et al., 2010).

Notwithstanding, there is also evidence of long-term, sustainable wild harvest of some orchid species from across genera, products and geographies (Table 2). This includes some of the terrestrial orchids that have been harvested for salep for hundreds of years (Kreziou et al., 2015), such as those in the genera *Dactylorhiza*, *Orchis* and *Anacamptis*, which remain abundant and for which local harvesters reported no observed declines (Charitonidou et al., 2019; Molnár et al. 2017b). Similarly, some species of Chinese medicinal orchids have been harvested and sold in local markets for centuries, but remain abundant (Liu et al., 2020; National Compilation Board, 1975). Various species of epiphytic orchids in Mexico have been harvested for ornamental and ceremonial uses since pre-colonial times (Emerterio-Lara et al., 2016; Halbinger and Soto, 1997). Traditional harvest methods that involve removal of a limited number of pseudobulbs or flowers, as opposed to whole plant, appear to have allowed for population persistence over centuries (e.g., Beltrán-Rodríguez et al., 2012; Orozco-Ibarrola et al., 2021). In addition, recent modeling work on the demography of Mexican species highlights the potential for sustainable wild-harvest (Ticktin et al., 2020).

Indeed, many non-timber forest products (NTFPs) are harvested legally and sustainably around the world (e.g., Schmidt et al., 2011; Shackleton et al., 2015; Stanley et al., 2012). The harvest of NTFPs has been widely promoted as part of strategies to jointly support livelihood and conservation over the past several decades (e.g., Martinez de Arano et al., 2021; Nepstad and Schwartzman, 1992; Shackleton et al., 2011). There are often benefits of sustainable wild harvest of plants, including species and habitat conservation through economic and cultural incentives, local livelihoods, biocultural heritage and human health contributions (e.g., Cocks et al., 2011; Shackleton et al., 2018).

The wild harvest and trade of orchids remains legal in many contexts: The vast majority of the family is listed on CITES Appendix II, which allows legal regulated trade based on Non-Detriment Findings (NDFs) to demonstrate sustainability. Multiple countries have regulations governing the legal harvest of wild orchids, including Mexico (SEMARNAT, 2013), Nepal (R.Bashyal, personal communication), China (Liu, 2021) and Turkey (Official Gazette, 2022). However, there are few, if any, examples of NDFs assessments being conducted to allow for legal CITES trade (Hinsley et al., 2018). Where protocols for sustainable harvest exist, the science to justify them is often lacking (Hinsley et al., 2018); there are no decision-making tools available to guide practitioners (R.Bashyal, personal communication; D.Mondragon, M. Hernández-Apolinar personal observations), and procedures to obtain permits are often unrealistic (Martínez-Hernández, 2017). Across the world–regardless of its (il)legality–the general trend is that wild orchid harvest continues with limited oversight and with limited understanding of the life history parameters that allow species to persist over time.

1.3 Need for realistic evaluations of potential for sustainable harvest

There is a pragmatic need to explore whether and how existing wild orchid harvest can be made more sustainable. This is important to operationalising existing domestic and CITES regulations and NDFs, and to addressing the on-the-ground reality of widespread illegal or unregulated trade. A more systematic approach could help grade existing harvest practices to highlight their relative sustainability and so highlight key areas of conservation concern. However, we lack an appropriate framework to evaluate if the harvest of a given orchid species and population might be managed more sustainably.

Existing resource management and policy guides are often coarse. CITES and some national legislations regulate the whole orchid family, with few distinctions for the huge diversity of life histories therein. Similarly, some national policies regulate harvest based on species identity: for example, prohibitions on harvest, or specific quotas, are applied to all populations of a given species. This is problematic because the sustainability of harvesting NTFPs can vary greatly with environmental conditions (e.g., Gaoue and Ticktin, 2010; Ghimire et al., 2008), habitat management (e.g., Hart-Fredeluces et al., 2021; Mandle et al., 2015), harvest practices (e.g., Nantel et al., 1996; Ticktin and Johns, 2002), which can vary with religious beliefs and sociocultural characteristics (e.g., Molnár et al., 2017a), and local abundances and life history characteristics, among other factors. Thus harvest of the same species may be highly sustainable in one location but unsustainable at another. National-level policies that fail to make such distinctions can potentially lead to negative outcomes for local livelihoods and conservation. This is akin to the critiques of national and global IUCN Red Listing that, despite their high value, can be problematic when downscaled to make local decisions (Sterling et al., 2019).

Existing global assessments or indices designed to guide sustainable harvest tend to focus on plants in general and do not account for some of the life history characteristics common to orchids. For example, available tools for evaluating risk of harvest for NTFP species emphasize life span, plant part harvested, population size and distribution, and reproductive output (Castle et al., 2014; Dzerefos and Witkowski, 2001; Peters, 1994; Wolf et al., 2016). The perennial nature of most orchids, the harvest of their vegetative parts, and the limited distributions of many species, automatically place most orchids in a 'high risk/no harvest' category within these assessments. This ignores the fact that local harvest techniques and habitat management practices can often override these life history characteristics in other plant species, allowing harvest to be sustainable (Shackleton et al., 2015). In addition, instead of increasing resilience, as is expected with other taxa, the high fecundity of orchids, offset by the high seed mortality and combined with extreme variation in recruitment, may actually cause them to be more vulnerable to extinction (Charitonidou and Halley, 2020), making these criteria inappropriate in orchid risk assessment. An additional complicating factor is that many terrestrial orchids go through dormant (latency) periods, making the prediction of true population size challenging (e.g., Hutchings, 2010; Shefferson et al., 2018; Tremblay et al., 2009). Although theoretically, the life history characteristics that should or could be included in decision making for conservation (Shefferson et al., 2020) and harvesting have been studied in many systems, the most basic ecological information are often lacking in orchids (e.g., evaluation of orchid lifespan, see Tremblay, 2000).

In reality, there is a continuum between unsustainable and sustainable harvest (Table 2), and the potential for sustainable harvest for any given species and population can change with changing climatic, environmental, market and management conditions (Ticktin, 2015). As such, there is a need for a dynamic framework that goes beyond evaluations of high versus low- risk species, and that provides recommendations for increasing the probability of sustainable harvest of specific populations in any given time and context.

2. Methods

We conducted a broad review of the literature on orchid harvest, ecology, demography and conservation to identify the suite of characteristics likely to affect the sustainability of orchid harvest, considering epiphytic, lithophytic and terrestrial orchid species. We built directly on a previous extensive literature review that had identified existing research on the demography of epiphytic orchids (Ticktin et al., 2020). We combined this review with our collective experience and observations on orchid ecology and harvest, which spans a broad range of taxa and geography (Appendix Table 1), to create a list of 23 characteristics (Table 3).

We then developed a process to select a subset of the most relevant, consistent and usable characteristics that could be useful to discern if the harvest of a given orchid population might be sustainable. First, we attempted to populate the list of characteristics using 27 orchid species that are currently in trade, for which we had first-hand experience and for which there is also at least some life history data available. These species reflect diverse geographies; types of trade (ornamental, medicinal, edible) and life histories (e.g., epiphytic/terrestrial/lithophytic species, species with long/short generation times) (Appendix Table 2). They also include both cases where trade is unsustainable and where it may be sustainable. Based on this exercise, and given our focus on informing decisions by local harvesters and managers and keeping the framework to a manageable size, we then identified three criteria to select a subset of usable characteristics. Specifically, characteristics needed to be (i) easily-observed in the field and/or information needed to be available and easily accessible; (ii) consistent in their potential to identify resilience to harvest pressure (e.g., we removed characteristics such as length of rhizome that did not turn out to be consistent in their effects; see Table 4); and (iii) relevant to multiple genera (e.g., given very few monocarpic or effectively monocarpic species in the family, we did not select this characteristic) We then conducted a further literature review on the selected subset of usable characteristics to identify the state of knowledge on how they likely affect sustainability.

We used the selected characteristics and review to develop a dichotomous key to help guide population-level decisions about the harvest of specific orchid populations (rather than for an entire species across a country). This approach was chosen to help assimilate complex information from the review into a format accessible to resource managers. This was also an iterative process, involving trialing with species with diverse life histories (Appendix Table 3). Using this process, we also identified the principal knowledge gaps.

3. Results

3.1 Salient characteristics and dichotomous key

We identified 23 characteristics hypothesized to be important to population-level harvest decisions (Table 3). These can be broadly grouped into four categories: abundance and distribution; species traits related to growth and reproduction; local management practices (including cultivation practices); and demand. Of these characteristics, 12 met our three criteria for inclusion into a framework that could be usable at the local level (see Methods) for existing orchid harvest and were incorporated into a dichotomous decision key (Table 4). The rationale for including or excluding characteristics from the key is described in Table 3. We briefly review the state of knowledge on each of the 12 selected characteristics as it pertains to the sustainability of harvest, presented in the order in which they appear in the dichotomous key (Table 4), with references to the decision "Steps" in the key identified in bold.

3.2. Management of cultivated populations

The key starts by considering whether the target species is cultivated, since cultivation is a common strategy to meet demand and achieve conservation in the wild (Anderies, 2015; Challender et al., 2015; Phelps et al., 2014). For orchids, cultivation can be an important conservation approach, but it is not widely implemented for the majority of commercially traded orchids. Moreover, cultivation and wild harvest are intertwined. In particular, some orchids can be propagated vegetatively and have been cultivated using this method for decades, even centuries (Halbinger and Soto-Arenas, 1997; Liu et al., 2010); however, this technique requires periodic harvest of new mother plants from the wild, which can potentially lead to overharvest of wild populations (e.g., IUCN, 2017; Liu et al., 2019). In addition, greenhouse cultivation is sometimes used to disguise illegal wild-collected plants as greenhouse-grown (laundering, e.g., medicinal *Dendrobium* in Lao PDR, IUCN, 2017). In such cases, the sustainability of wild harvest for large-scale cultivation needs to be evaluated (**Table 4a, Steps 1**).

Orchids can be difficult to cultivate via seeds because natural seed germination requires mycorrhizal associates (Rasmussen et al., 2015). However, the development of asymbiotic germination and tissue culture technique in the 1950s has made large scale cultivation of many orchids relatively easy. More recently, great progress in orchid biology, especially regarding the isolation, identification and function of fungal associates has been made (e.g., Reiter et al., 2018), which has made symbiotic seed germination possible on a large scale. Nonetheless, progress in cultivation remains limited for many key traded species, including those used to make *salep* (Kurt, 2020), *chikanda*, and some Chinese medicines (Liu et al., 2020), and may be difficult to adopt and manage in the rural areas where wild orchid harvest often occurs (Phelps et al., 2014).

Small-scale cultivation (e.g., community greenhouse, backyard cultivation) may also depend on periodic wild harvest to sustain itself if farmers/harvesters grow wild-sourced plants in rudimentary equipped nurseries until they flower or gain enough biomass for a profitable sale (e.g., IUCN, 2014; Liu et al., 2019). When the species are propagated vegetatively, wild harvest frequency may be reduced and these operations may be more sustainable (**Table 4a, Step2**). The collection of nursery material only from fallen epiphytic orchids is also a sustainable alternative (Damon, 2017), providing that both harvesters and consumers comply with the rules.

It is often assumed that cultivation should be the solution for all wild-harvested species, but even if it were possible to cultivate all species in trade, evidence supporting this assumption is limited (Liu et al., 2019; Phelps et al., 2014). For example, for some medicinal and ornamental species, cultivation operations may be limited because some consumers continue to prefer wild-harvested plants (Phelps et al., 2014).

3.3. Distribution and Abundance

The key considers both the geographic distribution and abundance of orchids. These variables represent the availability of plants at two scales: i) regional; indicating localities in which an orchid species is present, and ii) local; indicating the number of individuals of a species present in a particular site. Orchids show a very wide range of distribution types: some orchid species are widely distributed but rare, while others are narrowly distributed but abundant (Crain and Tremblay, 2014; Zhang et al., 2015). However, most orchids are narrowly distributed in specific habitats (Fay, 2018). In addition, habitat fragmentation and changes in land management have decreased the distribution and abundance of many orchid species (e.g., Parra-Tabla et al., 2011; Vogt-Schilb et al., 2015).

We propose thresholds for orchid distribution and abundance relevant to decision-making for harvest at the local scale. These thresholds are by no means universal and need to be adapted to the species and local context. However, a pragmatic tool that is useful to local managers and harvesters pressed with making decisions with limited information requires some kind of threshold. The ones we present here were appropriate for the range of species and contexts we trialed, and likely hold for many others.

3.3.1 Distribution

The key recognizes that populations of orchids that are outside of their native habitat and are considered invasive, have high potential for sustainable harvest. This is because they tend to be abundant and harvest does not affect the population persistence in their native habitat (**Table 4b, Step 1**). JD. Ackerman (pers. comm.) has identified 33 invasive terrestrial and epiphytic orchid species globally, across diverse habitats. Some appear to have been imported accidentally (e.g., *Oeceoclades maculata*, González-Díaz and Ackerman, 1988), but most have been introduced because of their ornamental value (e.g.*Arundina graminifolia*, Kolanowska and Konowalik, 2014; *Spathoglottis plicata* (Ackerman, 2007)).

The key also suggests that harvest of populations from human-modified environments is generally preferable over harvest from natural forests, grasslands and protected areas (**Table 4b, Step 2**). Many orchids that grow in natural areas (e.g., forests, grasslands) also grow well in human modified environments, including agricultural and agroforestry systems (e.g., García-González et al., 2016; Solis-Montero et al., 2005), cemeteries (Löki et al., 2015), roadsides (Fekete et al., 2017) and plantations (Süveges et al., 2019). Many tuberous terrestrial orchids benefit from open spaces rather than densely forested environments. Therefore, in some geographic regions, management practices that control the regrowth of forests, such as mowing and certain types of grazing regimes, like low-density sheep grazing (e.g., Damgaard et al., 2020; Köhler and Tischew, 2016) can favor orchid abundance. This is especially true for the European orchid flora, for which a considerable number of species are found in grasslands, forest openings, maquis, and other non-forested managed areas (Delforge, 2006; Kühn, et al., 2019).

The key takes into account that, within their native ranges, orchid species with wider distributions are less at risk of overharvest, because there is a higher chance that populations in some locations will remain unharvested and because species with wider distributions have a lower chance of extinction (Mace et al., 2008). Since legal permissions for orchid harvest are issued at the national level, we assess distribution by dividing those species found in >1 province or state from those found in only one (i.e. an administrative rather than ecological approach; **Table 4b, Steps 4 and 5**). However, this threshold can be adapted to fit the local context; for example, in a small country with many small provinces or vice versa, it may not be appropriate.

3.3.2. Abundance

The key reinforces that, regardless of distribution, if abundance is low, harvesting increases the risk of population extirpation (**Table 4b, Steps 6-8**). Sustainable harvest is more likely to occur when there are many individuals or patches of individuals within a location. Small populations, or those with few patches have a higher chance of extinction due to demographic and environmental stochasticity, as well as inbreeding depression (Angeloni et al., 2011; Mace et al., 2008); and harvest may exacerbate this. Since decisions to harvest any given population are made by harvesters or managers at the local level, we focus on this local level to assess abundance.

Given the distinct life histories of many terrestrial tuberous orchids, the key assesses their abundance in a different way from other orchids (Table 4a, Step 4). In particular, many tuberous terrestrial species—including some the most commercially-harvested species used for *salep, chikanda* and in Ayurvedic medicine—often grow in large populations. Many also have a type-III survival strategy, involving high mortality in early life history stages (Charitonidou and Halley, 2020), more like mushrooms (Egli et al., 2006). Organisms with this type of survival strategy may be less vulnerable to overharvest than Type I organisms (e.g., large mammals) that depend critically on population sizes relative to the minimum viable population (MVP). According to several studies, a global population of any plant taxa should contain thousands of individuals to be viable (Reed, 2005; Traill et al., 2007). Based on this, we draw a threshold of a minimum local population size of 1,000 unique individuals for tuberous terrestrial orchids. This represents a conservative limit (errs on the side of caution), provided the species is geographically widespread (see distribution above). However, as the estimation of the MVP remains a subject of vigorous debate (Flather et al., 2011), even such a conservative concession should be exposed to regular monitoring to confirm the robustness of the population. Importantly, not all tuberous terrestrial orchids meet these conditions, and the literature reflects an unsurprising research bias towards studying species and populations with large numbers of easily-observed individuals.

For epiphytic, lithophytic and non-tuberous terrestrial species, the key uses the number of patches within a single location in which an orchid species is found, as a measure of abundance. This is because for many of these species, it is difficult to accurately count the number of individuals in a population, and since most orchid species have patchy distributions. To ensure that the key is usable for local harvesters and managers, we consider location to be a point of harvest. The key draws a threshold at <3 patches, but this can be adapted to species and context. For example, a point of harvest is often a parcel of land owned or managed by an individual or a community with a known population of the species of interest. If the parcel happens to be very large and the species of interest is/are distributed across the whole area, one might increase the threshold. Similarly, for a widespread species which tends to have few individuals per patch, one might increase the threshold. This step requires discussion for each context and has the potential to be misused; however, given the current state of knowledge, there is no “one size fits all” measure that can be used. For narrowly distributed species, regardless of the number of patches, the key recommends no harvest for naturally rare species and/or those known to be declining.

For epiphytic orchids, the abundance of host trees is also an important consideration for sustainable harvest (**Table 4b, Step 9**). Epiphytic orchids need their host trees to survive since they provide them with the habitat they require to fulfill their life cycle. However, not all host trees are equal: morphological (e.g., bark roughness, branch angles), phenological (e.g, length and timing of leaf loss), chemical (e.g., bark, pH and surface, allelopathic compounds) and nutritional characteristics of the host tree can lead to host bias (e.g., Marler, 2018; Rasmusssen and Ramussen, 2018; Vegara-Torres et al., 2010; Wagner et al., 2015). Most orchid species are not limited to a specific host tree, but some species show strong host bias (Tremblay et al., 1998; Wagner et al., 2015; and references within), including some of those that are heavily harvested, such as *Laelia speciosa* (Flores-Tolentino et al., 2020; Hernández-Apolinar, 1992). Host bias, however, can vary within species across environmental conditions (e.g., Borrero et al., 2022; Tremblay et al., 1998). If host trees are rare or declining or themselves harvested, then orchid harvest is unlikely to be sustainable in the long-term.

3.4 Local management context

The key considers that for orchids, like other NTFPs, the capacity of a population to withstand harvest can depend heavily on the local management context, including management of the species and its habitat (Ticktin, 2015). A local population that is currently abundant might be at risk if its habitat or host species is at risk or if it is harvested in a destructive manner.

3.4.1 Habitat management

For epiphytic species, if habitat management negatively affects host trees, or the species directly, then the key indicates that harvest will be unsustainable (**Table 4b, Steps 10-11**). Multiple types of land-use can affect the potential for sustainable harvest of orchids. For example, for epiphytic orchids, timber harvest can result in the decline and local extirpation of entire populations (Bautista et al., 2014). In coffee and citrus plantations, epiphytes are often removed from host trees to increase tree growth, which can lead to population decline (Raventós et al., 2018; Solis-Montero et al., 2019). Epiphytic orchids can also be subject to grazing by domestic animals (Ackerman et al., 2020).

Terrestrial orchids can be impacted by native and introduced herbivores or florivores (e.g., Coates et al., 2006; Faast and Facelli, 2009; Hutchings, 2010). Grazing can have both positive and negative effects: one the one hand, some habitats only persist if there is grazing, on the other hand, high stocking densities, especially of cattle, may severely disrupt orchid habitats (Alexander et al., 2010; Köhler et al., 2016). The addition of nitrogen and other fertilizers (e.g., phosphorus, potassium) have been shown to have a negative effect on *salep* orchid populations (e.g., Dijk and Olff, 1994; Erickson et al., 2006; Walker et al., 2004), as most of the species harvested for salep prefer habitats with nitrogen-poor soils (e.g., *Dactylorhiza sambucina*, see

Jersáková et al., 2015). Other management issues include weed invasion, fire and trampling (Phillips et al., 2020). For some species, appropriate habitat management can allow populations to recuperate. This is especially true for species with dormant stages, as this characteristic can allow some individuals to escape harvest or grazing, and thus enable the population to recover (e.g, Molnár et al., 2017a).

3.4.2 Harvest type and species traits

The key recognizes that the harvest method is one of the strongest determinants of sustainable use for wild plant species (Shackleton et al., 2015; Ticktin, 2015). For epiphytic orchids, as for other vascular epiphytes (Francisco-Ventura et al., 2018; Mondragon and Ticktin, 2011), the harvest of individuals that have fallen from trees or tree falls represents the most sustainable practice, as these orchids can be considered dead from a demographic perspective (Damon, 2017; Francisco-Ventura et al., 2018; Matelson et al., 1993) (**Table 4b, Step 12**). The natural fall of epiphytic orchids is a common process since branches, bark and even trees frequently fall, and tree falls are common in hurricane impacted regions (Mondragón et al. 2011; Tremblay, 2008). Some orchids are also detached by animals (Matelson et al., 1993; Sarmento-Cabral et al., 2015).

The key flags that, at the other end of the spectrum, the removal of entire plants, which is very common across all orchid harvest contexts, is likely unsustainable for most epiphytic species and populations (with the exception of invasive species). Meta-analyses of demographic studies have demonstrated that the persistence of populations of long-lived perennials is sensitive to small declines in adult survival (Franco and Silvertown, 2004). Both empirical observations of orchid populations subject to whole plant harvest, and modeling approaches are consistent with this finding (Mondragon, 2009; Ticktin et al., 2020). As such, our key currently recommends *no* harvest of whole plants for epiphytic species. Globally, the majority of documented commercial harvest of epiphytic orchids involves whole plant harvest, and is therefore likely unsustainable.

However, many epiphytic orchids can be, and are, harvested by cutting pseudobulbs and/or flowers (e.g., See review by Ticktin et al., 2020; R. Bashyal, pers. comm.), which leaves the plant alive and potentially able to reproduce the following year (Emeterio-Lara et al., 2021a; Liu et al., 2014; Orozco-Ibarrola et al., 2020). Based on the persistence of populations harvested this way for centuries, such as those used in local religious and cultural celebrations in Mexico (Table 2), demographic models (Ticktin et al., 2020) and experimental harvest trials (e.g., Emeterio-Lara et al., 2021b; Orozco-Ibarrola et al., 2020), this type of harvest can likely be sustainable under certain conditions and for species with certain traits.

One of the traits most important in conferring resilience to partial plant harvest is the ability to branch and reproduce vegetatively. This includes species that have more than one active growing front, or that branch after disturbance, as well as species that can reproduce vegetatively through keiki (Lee, 2018) or that have stolonoid roots. The key therefore takes into account that species with these traits are likely to recuperate faster from harvest (**Table 4b, Step 13**). However, more research is needed on how different types of harvest of vegetative structures (e.g., plants with one versus several pseudobulbs; cutting a bulb in half) and of inflorescence harvest, affect long-term persistence of species across a range of life histories (Table 5).

3.5 Population structure

Ultimately, to be considered sustainable, the key emphasizes that harvest must allow populations to remain stable (or grow) in size over the long-term. Population structure, or the proportion of individuals of each age or stage class in a population, reflects the response of the population to the conditions of its ecosystem over time, including biotic and abiotic variables, and has long been used as a proxy to assess the viability of long-lived perennial plants (Rabotnov, 1985). For orchids, it has been used to assess the effect of disturbance, vegetation features, climate, protection status and harvest (e.g., Chapagain et al., 2021; Emeterio-Lara et al., 2021b; Nurfadilan, 2020) among other variables.

At one end of the spectrum, a "dynamic" population has a higher proportion of individuals in the immature stages (i.e., seedling, juvenile) than adults (reproductive stages). This indicates good recruitment and that the population is likely growing (0ostermeijer et al.,1994; Rabotnov, 1985). A "static" population is one with a uniform distribution of individuals in all the stages, suggesting that the population is possibly stable. A "senescent" population is predicted when the majority of individuals are in the adult stage, as this structure suggests poor recruitment. Harvest may be sustainable if it maintains populations that are considered "dynamic" as this illustrates adequate regeneration despite harvest (**Table 4b, Steps 14-15**).

However, using population structure as an indicator can be misleading in some situations, such as if there is a higher proportion of juveniles in the wild because the adults have been harvested, or in the case of long-lived species with long intervals between sporadic recruitment events. The best way to assess viability is with long-term demographic studies (e.g., Acevedo et al., 2020; Hutchings, 2009; Schödelbauerová et al., 2010; Zotz and Schmidt, 2006) but time and labor required to make them is impractical for informing harvest decisions at the local level. We therefore use population structure as the best proxy currently available, and assess it annually.

3.6. Augmentation and reintroduction

The sustainable harvest of many NTFPs not only involves extraction using regenerative methods such as partial harvest, but also activities to increase populations sizes and ranges, for example by dispersing propagules within populations, or translocating them to new areas (e.g., Ticktin et al., 2006; Tuner et al., 2000). Planting propagules to enlarge existing population ('augmentation') or to reintroduce extirpated populations ('reintroduction') are also well recognized as potentially effective measures for rare and endangered species recovery (Godefroid et al., 2011; Maschinski and Haskins, 2012), including orchids (e.g., Emeterio-Lara et al., 2021; Liu et al., 2015; Reiter et al., 2016; Reiter and Menz, 2022; Segovia-Rivas et al., 2018; Yam et al., 2010). These measures can be applied to wild or semi-wild orchid populations to promote sustainable harvest and native forest conservation while supporting livelihoods (Ashton et al., 2014; Liu et al., 2014). For epiphytic orchids that are used for adornment and decorations (Ticktin et al., 2020), reintroduction or augmentation by replanting pseudobulbs (Lemus-Herrera, 2013; Viedma-Vásquez, 2017) is a potentially viable strategy for communities to help ensure harvest sustainability

Population reintroductions using adult size pseudobulbs initially circumvent vulnerable orchid life stages such as germination and seedling survival, thus allowing for high initial survivorship and growth. However, creating and maintaining ecological environments that can facilitate subsequent recruitments is critical in establishment of a truly self-sustaining population (Swarts and Dixon, 2009). There are no studies to date that have followed a reintroduced or translocated orchid population through the entire lifecycle and reported success in establishing multiple self-sustaining generations. Therefore, augmentation and reintroduction hold high potential as effective management tools for sustainable harvest and are therefore included in the key, but need more research, experimentation, and optimization.

Beyond the unknown long-term efficacy of augmentation and reintroductions, these practices need to be undertaken with some caution. For example, using propagules of inappropriate genetic provenance can potentially reduce local adaptation and species level genetic diversity. Concerns about genetic preservation and maintenance in wild plant populations has led many to recommend using only local seed sources (McKay et al., 2005; Vallee et al., 2004), although there is a lack of consensus, considerable complexity, and each species needs individual consideration (McKay et al., 2005). For species that have experienced dramatic population declines and fragmentation, inbreeding depression is common (Angeloni et al., 2011) and mixing local and non-local populations as planting source materials is sometimes recommended in restoration (Frankham et al., 2011). For species that have a long history of wild harvest, casual enrichment plantings using mixed local and non-local seed sources may have been practiced for decades, and insisting on using local materials can be misleading (Burkhart et al., 2021). Finally, mixing genetic materials for reintroductions may be increasingly attractive under future climate change and extreme climate events.

If not done carefully, augmentation and reintroduction may generate unintended impacts on recipient forests, such inadvertently introduced pathogens or invasive species (Dreaden et al. 2020). To minimize impacts, augmentation and reintroduction activities can prioritize forests or other habitats that are already prone to human activities, such as in many community and private forest areas. Nevertheless, reintroduction is low impact if done properly, and carrying it out in reserves where harvest is prohibited access can also be an important strategy for developing 'insurance populations'.

3.7 Demand

The key recognizes that increasing demand is a well-documented driver of unsustainable orchid harvest (e.g., Hinsley et al., 2018). Increases in human population size and purchasing power are among the main reasons driving increase in market demands on wild species, which in turn drive moves from localized to regional collection. Examples include medicinal orchids in China (Liu et al. 2014), edible orchids in Sub-Saharan Africa, (Davenport and Ndangalasi 2003), and ornamental orchids in Southeast Asia (Phelps and Webb, 2015). Changes in international immigration are also likely increasing demand, including as a result of diaspora communities (e.g. salep, Kasparek and Grimm, 1999). Other factors that can alter demand include new development initiatives (e.g., China's Belt and Road Initiative, Hinsley et al., 2020), emergence of novel products (e.g., Dendrobium sports supplements, Kedia et al., 2014), new patents for orchid-containing products, Masters et al., 2020), and the ease of online international trade (e.g., Masters et al., 2022). Such increases and shifts are rarely quantified, but evidence from other taxa highlights that rapid changes in social drivers of wildlife demand, including distal drivers such as changes in technologies, policies and demographic factors, can be early predictors of impending shifts (see Hicks et al., 2016). In such cases, additional interventions such as augmentation, reintroduction and/or cultivation, along with greater regulation and enforcement, are likely required to ensure sustainability– regardless of whether a given population is stable or growing (**Table 4b, Step 16**). This is because the chance of poaching increases, and because other populations of the species will likely be heavily harvested or overharvested.

4. Discussion

Legal and illegal harvest of thousands of wild orchids is occurring across the globe, sometimes in massive quantities (Gale et al., 2019; Hinsley et al., 2018; Phelps et al., 2014; Ticktin et al., 2020). Through this review, we generated a set of considerations to guide management decisions to move towards greater sustainability of existing orchid harvest. The dichotomous key that emerged does not provide prescriptive instructions, but rather sets of considerations that harvesters and managers can use, experiment with, and adapt to local contexts, to improve the management of local orchid flora.

The key involves a minimum of quantitative prescriptions on harvest quantities and avoids quota-setting. This is because most of the characteristics that we identified as salient vary across species, sites and over time (Table 3). Indeed, our review highlighted that different life-histories and ecologies lead to different tolerances to harvest; that even if species could be grouped, the required demographic information to identify generic harvest ranges is lacking; and that within any given single species the potential for sustainable harvest varies across sites and over time. Instead, the review suggests the need for annual assessment of whether a given population can withstand harvest, thus allowing for adaptive management in the context of changing environmental, management and trade conditions (Shackleton et al., 2015).

Notably, the review identified some key conditions under which harvest is very unlikely to be sustainable. This includes many protocols that involve harvest of the whole plant; harvested populations that fail to show adequate regeneration; and species under very high demand. These situations characterize many existing trade systems, and should be a source of conservation concern. Equally though, and less widely recognised, the key distinguishes these systems from harvest regimes that may be more sustainable and highlights how unsustainable systems might be improved through actions such as partial harvesting of plants, harvest of fallen epiphytes, augmentation and reintroduction of populations, as well as cultivation. As demand continues to rise, these activities will be increasingly critical to ensure greater sustainability.

Our key is aimed exclusively at orchids *currently* in trade; not to identify new species to be harvested. Improving sustainability of species currently in trade will also require addressing the large gaps in our knowledge of orchid responses to harvest, and the governance of related systems (Laird et al., 2010). While more research on all the factors listed in Table 3 will improve our understanding of the potential for sustainable harvest, we don't have the time to wait for these to be filled. Our review highlighted some areas of high priority (Table 5), especially given the lack of studies on orchid management and harvest systems (Hinsley et al., 2018; Ticktin et al., 2020). Notably, there is a need to understand what traits or conditions allow for population persistence in those species that have withstood harvest over generations, as well as to identify how different types of partial plant harvest protocols (e.g. harvest of 1 or more pseudobulbs versus no harvest) affect demographic rates across species with different life histories. This will require establishing long-term demographic studies. Drawing on the local and traditional ecological knowledge of harvesters who hold long histories of such use, and who often continue to experiment, will be of crucial importance.

5. Conclusion

Faced with widespread trade of orchids that is often unsustainable, we integrated available literature from orchid taxa across the world to propose an initial, pragmatic approach to making harvest evaluations. This, however, is just the first step. There is now a need to trial, refine, and adapt this to different species and populations. This process should also involve collaborative experimentation with harvesters and local decision makers to see how populations respond to existing harvest regimes, and to new protocols informed by this decision-key. Our knowledge is incomplete. Nevertheless, we have refined the number of variables that should be considered, given the complexity and diversity of life histories of orchids. These may help move existing harvest systems towards greater sustainability and should be considered prior to harvesting, setting quotas, awarding harvest permits or approving CITES export permits for orchids globally.

Table 1. Examples of heavily harvested wild orchids and estimated trade volumes

Use	**Species or Genera**	**Region**	**Habit**	**Quantity harvested**
Food (*salep*)	*Dactylorhiza*, *Orchis Anacamptis* & others	Turkey	Terrestrial	10-20 million bulbs/year[1]
Food (*chikanda*)	Some *Disa*, *Habenaria* and *Satyrium*	Tanzania	Terrestrial	2-4 million bulbs/year[2]
Medicine	*Dendrobium hancockii*	China	Epiphytic	4500 stems (200 kg)/day[3]
Medicine	*Dendrobium nobile*	China	Epiphytic	4500 stems (150 kg)/day[3]
Ornamental	*Prostechia squalida*	Mexico	Epiphytic	>80,000 plants or plant parts/year[4]
Ornamental	*Euchile karwinskii*	Mexico	Epiphytic	>60,000 plants or plant parts/year[4]
Ornamental	*Laelia autumnalis*	Mexico	Epiphytic	>60,000 plants or plant parts/year[4]

[1] Kasparek and Grimm, 1999; [2] Davenport and Ndangalasi, 2003; [3] Gale et al., 2019; [4] Ticktin et al., 2020.

Table 2. Examples of heavily-harvested orchid species that fall at either end of the continuum from unsustainable to sustainable harvest. "Probably sustainable" harvest refers to current levels of harvest and is evidenced by long-term persistence of populations without observed decline.

Species	Habit	Type of trade	Evidence of sustainable or unsustainable use	
Bulbophyllum kwangtun-gense	Lithophytic	Medicinal	**Probably sustainable:** Harvested as folk medicine for local markets over centuries (National Compilation Board, 1975), yet still recorded in >56 national and provincial nature reserves and is still listed as Least Concern in the recent Chinese Red List (Liu et al., 2020). In recent years, small scale cultivation using wild sourced pseudobulbs is becoming common.	
Cypripedium calceolus	Terrestrial	Ornamental	**Unsustainable**: Previously abundant (but never common) in the UK, but local populations were extirpated due to over-collection by orchid enthusiasts and even botanists (for herbarium specimens) (Kull, 1999; Rankou and Bilz, 2014). Listed as 'Critically Endangered' in the UK (Cheffings and Farrell, 2005).	
Dactylorhiza sambucina	Terrestrial	Food (salep)	**Probably sustainable**: Traditionally among the most harvested salep orchids in NW Greece, yet remains abundant (Tsiftsis and Antonopoulos, 2017). Local communities have not reported any severe decline in populations (Charitonidou et al., 2019).	

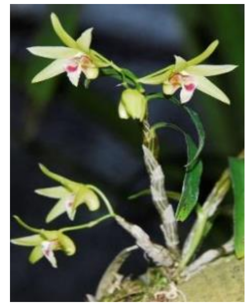
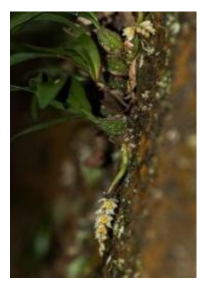
Dendrobium catenatum	Lithophytic, Epiphytic	Medicinal	**Unsustainable**: Market data show declines and unpublished reports of local extirpations (Liu et al., 2014) Large scale cultivation since the 1980s.	
Prosthechea karwinskii	Epiphytic	Ornamental	**Previously sustainable:** Harvested for centuries in large quantities for cultural and religious uses and remained abundant until recent increases in commercial harvest (Dutra-Elliott 2014; Solano et al., 2010).	
Gastrodia elata	Terrestrial	Medicinal	**Unsustainable**: Market data show declines and unpublished reports of local extirpations (Liu et al., 2010). Large scale cultivation since the 1980s.	
Laelia speciosa & L. autumnalis	Epiphytic,Lithophytic	Ornamental	**Previously sustainable**: Widely harvested for centuries for cultural, religious and ornamental purposes but remained abundant until recent increases in commercial harvest (Beltrán-Rodríguez et al., 2012; Hernández-Apolinar, 1992;, Emeterio-Lara et al., 2021b)	
Pholidota chinensis & P. cantonensis	Lithophytic, Epiphytic	Medicinal	**Probably sustainable:** Harvested as folk medicine for local markets over centuries(National Compilation Board, 1975), yet still listed as Least Concern in the recent Chinese Red List (Liu et al., 2020)	

Photo credits (in order of photos: P.Kumar, B. Hempton, K.Stara, Z. Liu, E. Pérez García, Z. Liu, E.Pérez García, P.Kumar)

Table 3. List of characteristics hypothesized to be important to population-level harvest decisions. Characteristics included in the decision-key are marked with bold lettering.

Characteristic	**Rationale**	**Position in decision-key (Table 4b, unless otherwise indicated)**
Distribution and abundance		
Invasive status	Harvesting populations of species that are invasive outside their native range does not pose a threat to population persistence in their native range.	Step1
Distribution	For species growing in both natural and agricultural areas, harvest only from agricultural areas may allow for better conservation of natural populations. Species with very narrow distributions are more vulnerable to overharvest since they are at higher risk of extinction naturally (Mace et al., 2008).	Steps2-5
Substrate specificity	Species and populations growing in an environment where they are obligate to one substrate (e.g. epiphyte vs terrestrial vs lithophyte) may be more vulnerable to whole plant harvest than those that can colonize > 1 substrates. This may vary across sites (Flores-Tolentino et al., 2020).	Excluded: covaries with abundance and distribution
Habitat specificity	Species that rely on specific abiotic or biotic conditions are likely to have narrower distributions and lower abundance (Tremblay et al., 1998), and therefore may be more vulnerable to harvest.	Excluded: Lack of knowledge of biotic conditions needed for most species (e.g., pollinators, mycorrhizae)
Abundance	Species and populations with very low abundance (current and/or historical), regardless of distribution, habitat specificity or market volume, are likely vulnerable to harvest because they have a greater risk of extinction (Mace et al., 2008).	4, 6-8

Host bias abundance	Epiphytic species and populations that grow on only one type of host may be more vulnerable to harvest if their host species is at risk.	8
Number of Johansson life-zones (within a tree; epiphytes only)	Generalist species found across 3 or more Johannsson life zones tend to be more abundant (e.g., Nurfadilah, 2016) and may have higher probability of recolonization after harvest, especially if found in the highest life-zone, where pressure from humans and other organisms may be lower (e.g., Einzmann et al., 2021).	Excluded: covaries with abundance
Population structure	Populations with a structure that indicates adequate regeneration are more likely able to withstand harvest.	14-15, but excluded for terrestrial species: dormant stages make it impossible to assess
Species characteristics and traits		
Life history	For terrestrial orchids, species with tubers are more harvested than the rhizomatous ones. A complex life cycle with significant below-ground phases and mechanisms like dormancy can shield terrestrial orchids from overharvesting since plants are 'hidden' for significant periods of time.	4
Sexual system	Semelparous species are expected to be more vulnerable to harvest than iteroparous species, since they may get harvested before they reproduce.	Excluded: very few species have this characteristic (e.g., *Erycina*); most orchids are iteroparous
Time to Reproduction	Species that take a long time to reach reproductive age are expected to be more vulnerable to whole plant harvest than those that can reproduce quickly (Mace et al., 2008)	Excluded: little information on time to reproduction for most species, therefore only included indirectly through population structure (14,15)

Fecundity	Species and populations with low fecundity are less likely to sustain harvest pressures (Tremblay, 1997). Equally, those with high fecundity may actually be at higher risk because fluctuation of mortality is also higher (Charitonidou and Halley, 2020).	Excluded: little information on fecundity patterns in natural populations, but included indirectly through population structure (14,15)
Size of inflorescence relative to plant size	Harvesting flowers of species with large inflorescence relative to plant size (e.g., *Oncidium sphacelatum*, *Sophronitis*) may have a large impact because of the larger energy investment in reproduction.	Excluded: relatively few species with this characteristic. It is hard to specify what “large” vs “small” means
Presence of seedbanks	Species with long-lived seedbanks may be more resilient to harvest because they can withstand adverse conditions (Whigham et al., 2006) and may stock for recovery following harvest events.	Excluded: little information available on seedbanks and their contributions to population growth. Most epiphytic species do not have persistent seedbanks (apparently)
Shoot to root ratio	For species with low shoot:root biomass ratios, (e.g., some *Sobralias*, *Epidendrums*, *Barkeria*s, *Chiloschista*) harvest of pseudobulb requires harvest of all the roots and is likely unsustainable.	Excluded: applies to relatively few species
Ability to branch and/or to reproduce vegetatively	Species that have the ability to branch or to reproduce vegetatively (e.g. >1 active growing front; branch after disturbance; regenerate from back-bulbs; produce keiki; are clonal through stolonoid roots) may be able to recuperate faster from partial harvest (harvest of structures) than those that don’t.	13
Length of rhizomes	Species with long rhizomes with widely-spaced pseudobulbs or shoots may be harvested more sustainably because they allow for harvest of a single flowering structure, leaving more of the plant behind to recover.	Excluded: pseudobulbs from some species with short (<~3cm)

		rhizomes are also harvested by cutting one flowering structure
Dormancy	Species with the capacity for dormant stages may be less vulnerable to overharvest because they may avoid harvest detection and withstand adverse conditions (Shefferson et al., 2018, 2020)	Included by separating terrestrial tuberous species from epiphytes
Local management context		
Habitat management	Populations growing in areas where management negatively affects the substrate (e.g., timber harvest for epiphytes; fertilizers or excessive grazing for some terrestrials) reduce regeneration and abundance and will be more vulnerable to overharvest (see "abundance" above).	10,11
Harvest type	**Harvesting** whole adult plants is most likely unsustainable because populations of long-lived perennials tend to be highly sensitive to decreases in adult survival (Franco and Silvertown, 2004). Partial-plant harvest (e.g., flowers, pseudobulbs) may be at lower risk assuming that the non-harvested portion of the plant has the potential to recuperate.	12
Management of cultivated populations	Cultivation operations that rely on continual harvest of wild-collected individuals are less likely to be sustainable than those that do not.	Table 4a
Population restoration	Augmentation or translocation (existing populations are supplemented with nursery-grown individuals grown from seed or plant material from the same or different locations), and reintroduction (nursery-grown individuals or pseudobulbs divided from mature individuals are outplanted in areas where the populations were extirpated) can enhance the potential for sustainable harvest by increasing population abundance and improving regeneration.	6-9, 11, 14-16
Demand		

Demand	Where demand is increasing (and/or prices are rising), whether for commercial or subsistence use or for local, regional or international markets, the potential for sustainable harvest is low unless appropriate governance is in place (Laird et al. 2010).	16

Table 4. Dichotomous key to guide more sustainable orchid harvest decisions for species currently in trade, at a given harvest site. The key is designed to be used each harvest season.

a) Species that are cultivated

1. Cultivation relies on supply of wild-collected plants, tubers or cuttings on a regular basis……2 Cultivation is "closed system" that does not rely on regular supply of wild-collected material (e.g., propagation vegetative, seed or tissue culture)**…….Promote ex-situ cultivation**
2.Target species cultivated commercially at large-scale (multiple commercial greenhouses)…..**See wild species key** Target species in small-scale cultivation (community greenhouse, backyards)….**Promote ex-situ cultivation, limiting inputs of wild plants**

b) Species that are wild harvested

1. Target species is invasive……**Harvest** Target species is native……2
2. Target species grows in both natural (forests, grasslands) and human-dominated (eg. agricultural) areas……**Harvest from human-dominated areas only** Target species grows primarily in natural areas…...3
3. Species is obligate terrestrial and has tubers (e.g., *Dactylorhiza, Disa, Gastrodia, Satyrium*)……4 Target species is epiphytic, lithophytic or terrestrial without tubers (e.g., *Paphiopedilum, Cypripedium*)…….5
4. Target population has >1000 individuals……**Harvest, leaving at least 1000 individuals unharvested** Target population has < 1,000 individuals or is distributed in only 1 province or state……**Do not harvest**
5. Target species is distributed across only 1 province or state……6 Target species is distributed across > 1 province or state……8
6. Target species is found in > 3 patches at proposed harvest site……7 Target species is found in < 3 patches at proposed harvest site……**No harvest; Augment and/or reintroduce**
7. Target species is abundant (many individuals per patch) ……8 Target species has naturally low abundance or is declining……**No harvest; Augment and/or reintroduce**

8. Target species is found in >3 patches at proposed harvest site……9
Target species is found in < 3 patches at proposed harvest site……**No harvest; Augment and/or reintroduce**

9. Host trees are locally abundant; or species is lithophytic or (non-tuberous) terrestrial…10
Host trees for epiphytic species are is declining...**Augment and/or reintroduce host tree**

10. Habitat is managed by people (logging, grazing, harvest of NTFPs)……11
Habitat is not managed……12

11. Habitat management negatively impacts host trees or substrate…… **For epiphytes, limit harvest to fallen orchids. For terrestrials, do not harvest: augment and/or reintroduce**
Habitat management does not negatively impact host tree or substrate……12

12. Harvest involves partial removal of the individual (pseudobulb(s), flowers)……13
Harvest involves removal of whole individual……**Do not harvest; enforce conservation**

13. Target species has more than one growing front and/or produces offshoots/keiki……14
Target species has only one growing front and does not produce offshoots/keiki……15

14. Population structure shows adequate regeneration (number of juveniles is greater than the number of adults (individuals big enough to flower) ……**Harvest and augment and/or reintroduce**
Population structure does not show adequate regeneration……**Do not harvest; augment and/or reintroduce**

15. Population structure shows adequate regeneration (number of juveniles is greater than the number of adults (individuals big enough to flower) ……16
Population structure does not show adequate regeneration ……**Do not harvest; augment and/or reintroduce**

16. Demand is increasing……**Harvest combined with augmentation, reintroduction and/or cultivation**
Demand is not increasing……**Harvest**

‘Augment’ refers to supplementing existing populations with locally sourced seeds or outplants.
‘Reintroduce’ refers to restoration of populations that were extirpated.

Table 5. Key knowledge gaps and priority research questions to inform sustainable harvest

Gaps	**Research questions**
Persistence of historically harvested populations (indicating potentially sustainable harvest)	● What demographic traits allow for population persistence in species that have withstood harvest over generations? ● What characterizes governance of orchid populations that withstood harvest over generations? ● How do historically harvested populations respond to increased harvest levels? ● What stewardship practices are used in populations that have withstood harvest over generations?
Adaptive management	● How do different levels of harvest and types of partial plant harvest (e.g., plants with one versus several pseudobulbs; cutting a bulb in half) affect survival, subsequent reproduction and population viability? How do responses vary with changing conditions? ● Which kinds of orchids (i.e., suites of characteristics) may benefit from this kind of approach and which may not? ● What are the best approaches to augmentation and reintroduction of harvested orchid populations? ● Which restoration strategies are feasible and economically-viable for communities that harvest orchids or manage orchid habitats?
Population structure and demography	● Is population structure a good predictor of population dynamics for orchids?
Consumer dynamics	● Under what conditions does cultivation reduce demand for wild-harvested plants? ● What are the social drivers of changes in demand?

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors

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Appendix Table 1. Description of experts

Name	Institution	Area(s) of orchid expertise	Geography
Martha Charitonidou	University of Ioannina	Orchid population dynamics; ecology and effects of harvesting on edible *(salep)* orchids	Greece, Eastern Mediterranean
Julia Douglas	University of Hawaii at Manoa	Reintroduction of epiphytic orchids; local drivers of orchid abundance	Mexico, Costa Rica
John Halley	University of Ioannina	Population dynamics; European orchids	Europe
Mariana Hernández-Apolinar	Universidad Nacional Autónoma de México	Population dynamics & harvest of orchids	Mexico
Hong Liu	Florida International University	Population ecology; wild orchid trade; sustainable use of high value plants	China, USA
Demetria Mondragón	Instituto Politécnico Nacional de México	Demography and phenology of epiphytic orchids	Mexico
Eduardo Pérez-García	Universidad Nacional Autónoma de México	Orchid growing, taxonomy and reintroduction of epiphytic orchids	Mexico
Jacob Phelps	Lancaster University	Orchid/wildlife trade dynamics, conservation impacts of propagation, orchid pollination ecology	Costa Rica, Thailand
Tamara Ticktin	University of Hawaii at Manoa	Population dynamics & harvest of epiphytic orchids; local orchid trade	Mexico

Raymond Tremblay	University of Puerto Rico	Population dynamics and evolutionary processes	Puerto Rico, Australia & global

Appendix Table 2. Wild-harvested orchid species used to identify characteristics that influence the potential for sustainable harvest (Table 3) and that could be used practically to make harvest decisions by local managers and harvesters (Table 4).

Species	**Primarily harvested for:**	**Habit**	**Distribution**
Anacamptis morio	Food (salep)	Terrestrial	Europe & Anatolia (up to Iran)
Anacamptis pyramidalis	Food (salep)	Terrestrial	Europe (mainly in the Mediterranean) up to Anatolia (Iran)
Artorima erubensis	Ornamental	Epiphytic	Mexico
Aspidogyne stictophylla	Ornamental	Epiphytic	Mexico
Barkeria scandens	Ornamental	Epiphytic, Lithophytic	Mexico
Brassavola nodosa	Ornamental	Epiphytic	Mexico, Central & South America; Carribean
Bulbophyllum kwangtungense	Medicinal	Lithophytic	Southern China
Cymbidium goeringii	Medicinal	Terrestrial	China, Bhutan, India, Japan, Korea
Dactylorhiza sambucina	Food (salep)	Terrestrial	Europe
Dendrobium fimbriatum	Medicinal	Epiphytic	China, Bhutan, India, Myanmar, Nepal, Thailand, Vietnam
Dendrobium loddigesii	Medicinal	Lithophytic, epiphytic	China, Laos, Vietnam
Dendrobium catenatum	Medicinal	Lithophytic, epiphytic	China & Japan
Encyclia alata	Ornamental	Epiphytic	Mexico & Central America
Guarianthe aurantiaca	Ornamental	Epiphytic, Lithophytic	Mexico &Central America
Laelia albida	Ornamental	Epiphytic	Mexico

Laelia autumnalis	Ornamental, cultural	Epiphytic, Lythophytic	Mexico
Laelia dawsonii	Ornamental	Epiphytic	Mexico
Laelia speciosa	Ornamental, cultural	Epiphytic	Mexico
Oncidium sphacelatum	Ornamental	Epiphytic, Lithophytic	Mexico & Central America
Oncidium unguiculatum	Ornamental	Epiphytic	Mexico
Orchis italica	Food (salep)	Terrestrial	Mediterranean
Orchis mascula	Food (salep)	Terrestrial	Europe, NW Africa and the Middle East
Prostechea karwinskii	Ornamental, cultural	Epiphytic	Mexico
Prosthechea cochleata	Ornamental	Epiphytic	Mexico, Central & South America; Carribean
Rhynchostele maculata	Ornamental	Epiphytic, Lithophytic	Mexico &Central America
Stanhopea hernandezii	Ornamental	Epiphytic, Lithophytic, Terrestrial	Mexico
Trichocentrum cosymbephorum	Ornamental	Epiphytic	Mexico

Appendix Table 3. Species used to trial (iteratively) the dichotomous key (Table 4)

Species	**Primarily harvested for:**	**Habit**	**Distribution**
Bulbophyllum kwangtungense	Medicinal	Lithophytic	Southern China
Cymbidium goeringii	Medicinal	Terrestrial	China, Bhutan, India, Japan, Korea
Dactylorhiza sambucina	Food (salep)	Terrestrial - tuberous	Greece
Dendrobium catenatum	Medicinal	Epiphytic & lithophytic	China & Japan
Laelia speciosa	Ornamental, cultural	Epiphytic	Mexico
Prostechea karwinskii	Ornamental, cultural	Epiphtyic	Mexico