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YAM MELLISSA PINEDA TORRES

DIRECTOR

SANTIAGO MADRIÑÁN

CODIRECTOR

IVÁN JIMÉNEZ

UNIVERSIDAD DE LOS ANDES

FACULTAD DE CIENCIAS

DEPARTAMENTO DE CIENCIAS BIOLÓGICAS

LABORATORIO DE BOTÁNICA Y SISTEMÁTICA

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THE NATURE OF *ESPELETIA* SPECIES

Yam M. Pineda¹, Andrés J. Cortés², Santiago Madriñán³ and Iván Jiménez⁴

¹ ³ Departamento de Ciencias Biológicas, Universidad de los Andes, Bogotá, Colombia,

² Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden, ³ Jardín Botánico de Cartagena “Guillermo Piñeres”, Turbaco, Colombia, ⁴ Center for Conservation and Sustainable Development, Missouri Botanical Garden, St. Louis, MO, USA

INTRODUCTION

Species are often regarded as basic units of biodiversity in ecology, evolution, biogeography and conservation biology, following the presumption that they are real, discrete natural entities (Coyne and Orr 2004; Barraclough and Humphreys 2015). But some biologists, most notoriously botanists, have persistent doubts about the existence of species. They see species as arbitrary divisions of biological diversity that do not necessarily correspond to discrete natural groups of organisms (Levin 1979; Raven 1986; Bachmann 1998). Darwin seemed to have developed a similar view (see Mayr 1982; Mallet 2013): “...we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect, but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species” (Darwin 1859, page 485). Indeed, Darwin’s view about the nature of species may have been largely shaped by interactions with botanists (Mayr 1982). Moreover, botanists could have been overly impressed by a few examples of fuzzy species limits (e.g., blackberries, dandelions and oaks) and wrongly assumed these “botanical horror stories” to be representative of plant species overall (Diamond 1992).

Attempts to empirically solve this controversy about the nature of species would ideally address two related but separate issues. One is whether individual organisms form sympatric, distinct groups in nature (Coyne and Orr 2004; Barraclough and Humphreys 2015). Sympatry is stressed in this context because it implies opportunity for the groups to merge into one (Coyne and Orr 2004), via genetic or demographic exchangeability (Templeton 1989). Thus, sympatric, discrete groups or organisms are widely accepted as evidence of distinct, real units in nature (Mayr 1992; De Queiroz 2007; Mallet 2007,

2008). The second issue is the degree to which taxonomic classification at the species level accurately reflects distinct groups of individual organisms or constitute arbitrary divisions (Rieseberg et al. 2006). Thus, to address the problem of the nature of species, it is paramount to distinguish the idea of species taxa (i.e., taxonomic divisions at the species level) from the notion of species as biological units in nature (Hey et al. 2003). Species taxa presumably exist in the sense of human-made divisions, documented in taxonomic treatments. And, yet, species may not occur in nature as discrete sympatric groups of individual organisms (Levin 1979; Raven 1986; Bachmann 1998). Moreover, even if species do occur in nature as discrete sympatric groups of individual organisms, human-made taxonomic classification at the species level may not reflect such groups.

The first issue above, whether individual organisms form distinct, sympatric groups in nature, may be empirically addressed in the context of multiple, potentially contrasting species definitions (*sensu*, De Queiroz 1999). In particular, species could be real units in terms of different properties acquired during lineage divergence, include ability to interbreed, ecological divergence and reciprocal monophyly among others. Despite the variety of possible species definitions, there has been enduring interest in the reality of species in terms of two criteria: phenotypic and genome-wide distinctiveness (Dobzhansky 1951; Grant 1957; Mayr 1963; Ehrlich and Raven 1969; Levin 1979; Gould 2002; Coyne and Orr 2004; Rieseberg et al. 2006; Mallet 2013). Several kinds of species may be distinguished when simultaneously considering these two criteria (Fig. 1). One kind includes species that show very little if any phenotypic distinctiveness but differ in allele frequencies across many loci (Fig. 1A). These species are likely reproductively isolated and known as “sibling” (Mayr 1963) or “cryptic” species (Bickford et al. 2007; Fišer et al. 2018; Struck et al. 2018). A second kind of species is characterized by phenotypic distinctiveness in the absence of differences in allele frequencies across most loci (Fig. 1D). “Syngameons” are examples of this second kind of species, where phenotypic distinctiveness is due to few loci, preserved despite interbreeding (Lotsy 1931; Grant 1971; Rieseberg and Burke 2001; Wu 2001) and the basis of meaningful ecological and evolutionary units (Van Valen 1976; Templeton 1989) (Fig. 1D). Yet another kind of species is that of phenotypically distinct lineages that have different allele frequencies throughout the genome. Such species are likely reproductively isolated and,

thus, are sometimes referred to as “good species” (Fig. 1B, (Templeton 1989; Allmon 2016)). Finally, some species may be characterized by discordant sets of distinct phenotypes and genome-wide allele frequencies (Fig. 1C). In these latter case, phenotypes and genome-wide allele frequencies might reflect contrasting evolutionary histories incorporated into a single species (Doyle 1997; Maddison 1997; Szilosi et al. 2015).

The degree of concordance between distinctiveness in phenotype and genome-wide allele frequencies (Fig. 1) have played a central role in debates about the nature of species (Grant 1957; Ehrlich and Raven 1969; Levin 1979; Diamond 1992; Coyne and Orr 2004; Rieseberg et al. 2006). Yet, there seem to be few empirical studies addressing the controversy by formally testing whether individual organisms form sympatric, distinct groups in nature according to these two criteria (Barraclough and Humphreys 2015; Coyne and Orr 2004), and assessing the correspondence of such groups (if any) to species level taxonomic divisions (but see Rieseberg et al. 2006). The paucity of such studies may partly reflect that methods to formally infer the number of distinct groups in a sample of individuals, with no a priori information about group membership, were developed relatively recently for both phenotypic (Ezard et al. 2010; Cadena et al. 2017) and genome-wide data (Pritchard et al. 2000; Huelsenbeck and Andolfatto 2007; Raj et al. 2014; Verity and Nichols 2016; Cadena et al. 2017). Thus, until recently, there was little empirical guidance for studies attempting to formally assess the nature of species in terms of concordance between distinctiveness in phenotype and genome-wide allele frequencies. But even outstanding species delimitation studies, employing state-of-the-art methods (e.g. (Spriggs et al. 2019)), are commonly based on geographically sparse sampling, characterized by well-separated collection localities and few specimens per locality. Such sampling has been traditionally used to accumulate invaluable collections in natural history museums (ter Steege et al. 2011) required for global taxonomic assessments of monophyletic clades. However, geographically sparse sampling is often insufficient to rigorously determine if individual organisms form distinct, sympatric groups in terms of phenotypes and genome-wide allele frequencies. Consequently, the debate about the nature of species remains unsatisfactorily addressed by empirical studies. Yet, understanding such nature is a major and long standing issue in evolutionary

biology (Barraclough et al. 2003; Coyne and Orr 2004; Rieseberg et al. 2006; Barraclough and Humphreys 2015) with significant implications for basic and applied fields in biology (Richards 2010; Sigwart 2018).

Here we contribute to empirically address the debate about the nature of species by providing a carefully worked example, characterized by geographically dense sampling of organisms to determine whether individual organisms form sympatric, distinct groups in nature. We used formal approaches to i) infer sympatric groups of organisms in terms of phenotype and genome-wide allele frequencies, ii) measure the degree of concordance between distinctiveness in phenotype and genome-wide allele frequencies (Fig. 1), and iii) the concordance between species taxa (i.e., taxonomic divisions at the species level) and distinctiveness in phenotype and genome-wide allele frequencies. We are unaware of empirical studies about the nature of species that employ these approaches on a geographically dense sampling of individual organisms.

We focused on *Espeletia*, a genus of plants endemic to the northern Andes (Monasterio and Sarmiento 1991; Rauscher 2002; Cuatrecasas 2013; Diazgranados and Barber 2017) and often dominant in high elevation ecosystems known as “páramos” (Ramsay and Oxley 1997). This genus appears to have undergone a very rapid radiation starting around 2.7 Ma (Madriñán et al. 2013; Pouchon et al. 2018). *Espeletia* species are suspected to commonly produce inter-specific hybrids, even between distantly related species (Pouchon et al. 2018), and, nevertheless, maintain phenotypic and ecological integrity (Berry et al. 1988; Diazgranados 2012; Cuatrecasas 2013; Diazgranados and Barber 2017). In one of the (two) prefaces of the most recent *Espeletia* monograph (Cuatrecasas 2013), Harold Robinson wrote: "The recent origin, the high specialization and the complex structure of the often large plants, added to the few barriers to hybridization in addition to geography, even at the intergeneric level, presented many complications for the monographic study." Indeed, along with other plant genera (e.g., oaks, irises, pines, aspen, eucalyptus, dandelions and blackberries (Lenz 1959; Van Valen 1976; Sutton et al. 1991; Alice et al. 2001; Field et al. 2009; Cronk and Suarez-Gonzalez 2018)), *Espeletia* may be a “botanical horror story” (Diamond 1992) from which we may learn much about the nature of plant species.

MATERIALS AND METHODS

Study region and taxa

We studied plants of the genus *Espeletia* occurring in the páramo de Sumapaz. This páramo encompasses 1780 km² in the Cordillera Oriental of the Colombian Andes, south of Bogotá, and includes the high elevation areas of Parque Nacional Sumapaz. Annual average temperature varies spatially between 2 ° and 10 ° C and annual rainfall between 500 and 2000 mm. According to the most recent *Espeletia* monograph (Cuatrecasas 2013), seven *Espeletia* species occur in the páramo de Sumapaz: *Espeletia argentea* Humb. & Bonpl., *Espeletia cabrerensis* Cuatrec., *Espeletia grandiflora* H. & B., *Espeletia killipii* Cuatrec., *Espeletia miradorensis* (Cuatrec.) Cuatrec., *Espeletia summapacis* Cuatrec. and *Espeletia tapirophila* Cuatrec. The monograph also mentions infra-specific taxa occurring in the páramo de Sumapaz for three of the species: *Espeletia argentea* fma. *phaneractis* (S.F.Blake) A.C.Sm., *E. grandiflora* spp. *grandiflora* var. *attenuata* Cuatrec., *E. grandiflora* spp. *subnivalis* Cuatrec. and *Espeletia killipii* var. *chiscana* Cuatrec.

Specimen collection

To sample *Espeletia* species we defined the limit of the páramo de Sumapaz as the 3,000 m elevation isocline, based on the Aster digital elevation model with 30 m resolution (<https://asterweb.jpl.nasa.gov/gdem.asp>). Thus defined, the páramo de Sumapaz was divided into quadrants of 2 x 2 km. We sampled 34 of these quadrants by randomly choosing two 30 × 30 m grid cells (of the Aster digital elevation model) in each band of 100 m elevation (Fig 2). We sampled a total of 219 grid cells of 30 × 30 m. In each grid cell we collected one specimen of each seemingly different phenotype. Additionally, we also collected specimens opportunistically to further document the occurrence of different phenotypes across the páramo de Sumapaz. In total we collected 540 specimens of reproductive *Espeletia* plants, all deposited in triplicate at the herbarium of the Jardín Botánico de Bogotá (JBB).

Phenotypic distinctiveness

Morphological characters

We measured thirteen morphological characters to measure phenotypic distinctiveness among *Espeletia* species from the páramo de Sumapaz (Table 1). Except perimeter of the synflorescence axis, all these characters were discussed by Cuatrecasas (2013) as useful traits to delimit *Espeletia* species from the páramo de Sumapaz. We additionally included the perimeter of the synflorescence axis because in the field this character seemed useful to distinguish some putative species.

Whenever possible, we measured all morphological characters above in each of the 540 specimens we collected. Additionally, we measured as many of the morphological characters as possible in each of 156 specimens from páramo de Sumapaz, or from taxa known to occur there, that were collected by other researchers and deposited in the Herbario Nacional Colombiano (COL), at the Instituto de Ciencias Naturales, Universidad Nacional de Colombia. Out of these 156 specimens, 127 were explicitly mentioned in the *Espeletia* monograph by Cuatrecasas (2013), including types for all but one (*Espeletia argentea*) species taxa that, according to Cuatrecasas (2013), occur in the páramo de Sumapaz. When it was possible, each one of the morphological characters was measured in three separate structures per specimen (as mentioned before, specimens were collected in triplicates), and analyses were based on average values per specimen to account for intra-individual variation (Hou and Li 2010; Lim et al. 2012). The length of synflorescence axis was measured in the field to the nearest centimeter. All other measurements were done in the herbarium after the specimens were dried. To measure leaf blade length and width we took photographs on a standard background including a millimeter ruler and then processed them using the measure tool in the *Image J* program (Schindelin et al. 2012). Capitulum diameter, length and width of the corolla of the flowers of the disc, length of the corolla of the flowers of the ray, and length of the tubes of the disc were measured with a three-digit precision gauge.

Estimating morphological groups

To estimate the number phenotypic groups among the measured *Espeletia* specimens, as well as the assignment of specimens to such groups, we used the R package *Mclust* 5.0

(Scrucca et al. 2016) to fit normal mixture models (NMM, McLachlan and Peel 2000) to our morphological data. NMMs conceptualize phenotypic variation as a mixture of different normal distributions. This model assumes polygenic inheritance and random pairing; under these assumptions, gene frequencies would be close to Hardy-Weinberg equilibrium, two or more loci would be near linkage equilibrium, and phenotypic variation among individuals of a single species would tend to be normally distributed (Templeton 2006; Cadena et al. 2017). The parameters of a NMM (e.g., means, variances and covariances) describe each morphological group as a (possibly multivariate) Gaussian distribution and can be estimated using maximum likelihood from data on phenotypic measurements, without *a priori* knowledge of species limits, using the algorithm of expectation-maximization (McLachlan and Krishnan 2008).

We used the Bayesian Information Criterion (BIC, Schwartz 1978) to estimate the number of phenotypic groups among the specimens we measured, as well as the location and spread of such groups in morphological space. BIC measures empirical support for NMMs that differ in parameter values, including number of morphological groups (Fraley and Raftery 2002). We fitted NMMs that covered a wide range of the parameter defining the number of morphological groups, at one extreme some NMMs assumed a single morphological group and at the other up to ten groups. This latter number of groups is three more than the number of species expected in the study according to Cuatrecasas (2013). To define the morphological space to be considered in the MMNs, we first rotated the data on thirteen morphological characters (Table 1) using a principal component analysis on the covariance matrix of the natural logarithm of the original data. One of these characters (i.e., pairs of sterile leaves per synflorescence) took on zero values, so we added one to this variable before the logarithm transformation. We used R package *Clustvarsel* (Scrucca and Raftery 2018) to reduce the dimensionality of the data by selecting the most useful set of principal components for the discrimination of groups in NMMs, without a priori information about the groups (Raftery and Dean 2006; Maugis et al. 2009; Cadena et al. 2017).

Genome-wide allele frequencies distinctiveness

DNA Extraction and Genotyping-by-Sequencing

Genomic DNA was extracted using the QIAGEN DNeasy Plant Mini Kit (QIAGEN, Germany). DNA concentration was quantified in R Qubit dsDNA HS Fluorometer (Life Technologies, Sweden). One 96-plex genotyping-by-sequencing libraries were performed with MsiI digestions according to (Elshire et al. 2011) and sequenced at LGC Genomics (Berlin, Germany). Readings were aligned following Cortés et al. (2018) using a cluster of 283 *Espeletia* samples, built with 192 samples from that study in addition to 96 samples (specimens) from this study. Filtering of variants was done using a GBS-specific rule set with > 5 read count for a locus, $> 5\%$ minimum allele frequency across all samples, and an observation of genotype frequency of at least 80%. This filtering reduced the initial sample of 99 specimens to 77. The filtered dataset was inspected with TASSEL v. 3.0 (Glaubitz et al. 2014), resulting in a final set of 2,098 single nucleotide polymorphisms (SNPs).

Estimating groups according to genome-wide allele frequencies

To infer the number of groups according to genome-wide allele frequencies among genotyped *Espeletia* specimens, and assign specimens to such groups, we implemented ancestry models in R *Maverick* package in R 3.3.1. (Verity and Nichols 2016). These models assume that groups are in the Hardy Weinberg equilibrium with their own set of allele frequencies and that all loci are in linkage equilibrium (Pritchard et al. 2000). *Maverick* uses thermodynamic integration to estimate the number of groups, based on the posterior probability of models, given the data and a prior distribution of model parameters (Verity and Nichols 2016). This method distinguishes *Maverick* from other approaches that rely on less formal, heuristic methods to evaluate the number of groups according to genome-wide allele frequencies.

We evaluated models postulating a wide range of number of groups among *Espeletia* specimens, from a single group up to ten. Again, the latter number is three groups more than expected by the number of species occurring in the páramo de Sumapaz according to Cuatrecasas (2013). All models allowed admixture.

Species taxa

To determine the extent to which species taxa corresponded to phenotypic groups and groups based on genome-wide allele frequencies, we assigned specimens to species taxa based detailed descriptions in Cuatrecasas (2013). In particular, for all species taxa expected to occur in Sumapaz, according to Cuatrecasas (2013), we obtained the maximum and minimum values for all the 13 characters in Table 1 except but one perimeter of the synflorescence axis. As already mention, this character was not considered by Cuatrecasas (2013). Then, for each specimen in our sample, we determined if the measured values for the 12 characters fell within the ranges of each taxa species. We assigned a specimen to a species taxa if the measurements for all 12 characters fell within the respective ranges provided by Cuatrecasas (2013).

Concordance between groups defined by phenotype, genome-wide allele frequencies and species taxa

To estimate the degree of concordance between the groups of specimens defined according to phenotypes, genome-wide allele frequencies and species taxa we used Goodman and Kruskal tau statistic (GKtau), as implemented in R package '*GoodmanKruskal*' version 0.0.2 (Pearson 2016). GKtau is a measure of asymmetric association between two classifications. Asymmetry in these kind of association may arise because one classification, say based on phenotypic characters, may predict the assignment of individuals in another classification better than the latter may predict the former (Pearson 2016). Therefore, we performed two tests to gauge concordance between a given pair of classifications. The first examines the degree to which the assignment of specimens to groups according to the first classification (e.g., based on phenotype) predicts the assignment of specimens to groups according to the second classification (e.g., based on genome-wide allele frequencies). The other tests the degree to which specimen assignment to groups according to the second classification predicts specimen assignment according to the first classification. We evaluated the statistical significance of both tests using 1,000 iterations of a null model that randomized the assignment of specimens to groups in one of the two classifications being compared. We We calculated GKtau for each iteration of the null model and thus constructed a null distribution of

1,000 GKtau values. We estimated p-values for each test as the fraction of GKtau values in the null distribution that were at least as extreme as the observed GKtau value.

Sympatry

We adopted an operational definition of sympatry based on a concept reflecting both gene flow and geography (Mallet et al. 2009). According to this concept, populations are sympatric when they have geographic distributions within the normal cruising range of individuals of each other (Mayr 1947), so that gametes of individuals are physically capable of encountering one another with moderately high frequency (Futuyma and Mayer 1980). The normal cruising range of individuals is determined by the distribution of distances between the sites of birth and breeding of individual organisms (Mallet et al. 2009). Thus, both pollen and seed dispersal are relevant to this operational definition of sympatry, although in *Espeletia* seed dispersal is thought to be fairly limited (Berry and Calvo 1989; Diazgranados 2012; but see Gallego Maya and Bonilla Gómez 2016). In sharp contrast, the pollen of *Espeletia* is thought to travel considerable distances via bumblebees (genus *Bombus*) and, potentially, hummingbirds (Fagua and Gonzalez 2007); except in some species that seem to be pollinated by wind (Berry and Calvo 1989;). Bumblebees home back to their nests from places 9.8 km away (Goulson and Stout 2001) and regularly perform flights covering > 1 km (Greenleaf et al. 2007; Pope and Jha 2018). Thus, we considered inter-group distances < 1 km as definitively small enough for sympatry and inter-group distances < 5 km as likely small enough for sympatry. Accordingly, to estimate the degree of sympatry between a given pair of groups (phenotypic or defined by genome-wide allele frequencies), we measured the geographic distance between each specimen and the nearest specimen that did not belong to the same group. We examined the resulting distribution of inter-group distances to determine if groups were separated by < 1 km, < 5 km or longer distances.

RESULTS

Phenotypic distinctiveness

The morphological analysis included only 295 out of 696 specimens measured in this study, because several specimens were missing values for at least one of the 13 characters

studied (Table 1). This was mainly due to the fact that not all specimens exhibited flowers anthesis.

Reducing the dimensionality of the data from a total of 13 principal components to nine (1, 2, 3, 5, 6, 7, 8, 9, 10) or twelve (1 through 12) seem to be equally useful for the discrimination of groups in normal mixture models (NMMs). The reduction to nine axes had the highest empirical support when implementing the procedure for reduction of dimensionality (*Clustvarsel*, see Methods) based on a forward algorithmic search of principal components, whereby axes (i.e., principal components) were progressively added to NMMs. In contrast, the reduction to twelve axes had the highest empirical support when using a backward algorithmic search that begins with all 13 available axes and progressively discards axes to examine NMMs with lower dimensionality. Although NMMs based on these two alternatives (nine and twelve principal components) differed in details regarding the location and spread of groups in morphological space as well as the assignment of specimens to groups, both models yielded the same results in terms of the number of sympatric morphological groups, concordance with other classifications (based on genome-wide allele frequencies and species taxa). Therefore, given that the main conclusions were insensitive to the choice between the NMM with nine and twelve principal components, for simplicity here we focus on the former model.

We found support for the existence distinct phenotypic groups among the *Espeletia* specimens from páramo de Sumapaz. In particular, the best NMM identified seven morphological groups and had substantially more empirical support than models assuming 1-6 and 8-10 groups ($\Delta\text{BIC} > 10$, Fig. 3A). In this best model, the morphogroups appear to be fairly distinct, because assignment of specimens to morphogroups entailed little uncertainty. For all but three specimens in the analysis, the probability of assignment to their corresponding morphogroup exceeded 0.9. Put another way, in a probability scale, assignment uncertainty exceeded 0.1 in only three specimens out of 296.

In the best model, four groups were easily distinguished in the morphological space defined by the first two principal components, mainly determined by four characters: number of capitula per synflorescence, number of sterile leaves per synflorescence,

length of the cyma peduncle and sterile phyllary width (Fig. 4A). At one extreme of this space, morphogroup 1 had the narrower sterile phyllaries and shortest cyma peduncles (lower right in Fig. 5A). At another extreme, morphogroup 4 was characterized by the widest sterile phyllaries, many capitula for synflorescence and several pairs of sterile leaves per synflorescence (central upper part in Fig. 5A). Finally, morphogroups 6 and 7 were distinguished from the rest by having long cyme peduncles, few capitula per synflorescence and no sterile leaves along the synflorescence (extreme left in Fig. 5A). These last two morphogroups (6 and 7) differed from each other most clearly in terms of the width of sterile phyllaries. The three remaining morphogroups were most easily distinguished in the morphological space defined by principal components 2 and 3, mainly determined by leaf blade width, number of capitula per synflorescence, number of sterile leaves per synflorescence, sterile phyllary width and length of the tubes of the flowers in the disc (Fig. 4C). In this space, morphogroups 3, 5 and 2 were located along a gradient of increasing values for the number of sterile leaves per synflorescence (Fig. 5C).

Distinctiveness in genome-wide allele frequencies

We found support for the existence of more than one genomic group among the *Espeletia* plants we sampled from the páramo de Sumapaz. In particular, an ancestry model with three groups had the highest empirical support, with posterior probability of almost one (Fig. 3-B). In this best ancestry model, however, the genomic groups did not seem particularly distinct. One of these groups had only six specimens, all with a relatively low proportion of alleles from other groups (Fig. 7A). However, the other two groups were much larger (32 and 39 specimens) and included specimens with fairly high proportions of mixed ancestry. Indeed, in both these groups specimens with more than 10% admixture were nearly half the group (19 and 21, respectively), and fairly high values of admixture (>20 %) were not uncommon (Fig. 7A).

Species taxa

Our procedure to assign species to specimens resulted in only one specimen being assigned to any species taxa, out of a total of 296 specimens with data for all 12 relevant measurements (i.e., all characters in Table 1 except perimeter of the synflorescence axis).

In particular, one specimen was assigned to *Espeletia killipii* Cuatrec. All other specimens fell outside the ranges specified by Cuatrecasas (2013) for the species expected to occur in the páramo de Sumapaz. This remarkable result, whereby all but one of the *Espeletia* specimens in our sample could not be formally assigned to any species taxa, meant that it was not possible to apply a test of concordance between species taxa and groups defined by phenotypic distinctiveness and genome-wide allele frequencies. Such concordance was null, because the morphological space defining species taxa (according to Cuatrecasas 2013) was nearly void of specimens.

Concordance between distinctiveness in phenotype and genome-wide allele frequencies

The analysis of concordance between the classifications based on two different operational criteria only included 46 specimens, because several specimens included in the genetic analysis were not in anthesis and, therefore, did not enter the morphological analysis. While the association between the classifications was not very strong, it was statistically significant in one direction. The groups according to allele frequencies were not predictive of specimen assignment to phenotypic group (GKtau = 0.147, p-value > 0.001 Fig. S1). On the other hand, phenotypic groups did predict to some degree the assignment of specimens to groups based on allelic frequencies (GKtau = 0.382, p-value < 0.001 Fig. S2). Thus, knowledge of phenotypic groups conferred significant but poor ability to predict group based on genome-wide allele frequencies (GKtau ranges from zero to one). This weak concordance seems mainly due to the complete inclusion of morphogroups 4 and 7 into single genomic groups, and to the complete inclusion of one genomic group within morphogroup 1 (Fig. 7A and B). However, five out of seven morphogroups straddled two genomic groups, and two out of three genomic groups included multiple morphogroups (Fig S2).

Sympatry

All the seven morphological groups seemed largely sympatric. Under the assumption that inter-group geographic distances ≤ 5 km allowed gamete exchange via pollen dispersal by bumblebees, all pairs of morphogroups were sympatric, because all inter-group geographic distances were less than 2 km. Moreover, out of 21 morphogroup pairs only

five exceeded 1 km (Fig. 6). Therefore, under the assumption that geographic distances $\leq$ 1 km imply sympatry, six morphogroups (1, 2, 3, 5, 6 and 7) were sympatric with at least four other morphogroups and one morphogroup (4) was sympatric with two other morphogroups (Fig. 6, S3).

The groups according to the allele frequencies are sympatric, given that all inter-group distances were $\leq$ 1 km (Fig. 8, S4)

DISCUSSION

To our surprise, we found that species taxa delimited by Cuatrecasas (2013) were mostly empty in the sense that they contained only one of the 296 *Espeletia* specimens from Sumapaz in our analyses. In other words, we did not find the species taxa of Cuatrecasas (2013) in nature. However, analysis of data on thirteen morphological characters did reveal fairly distinct, sympatric phenotypic groups among the *Espeletia* from Sumapaz. On the other hand, analysis of genome-wide allelic frequencies indicated somewhat indistinct, sympatric groups with seemingly high levels of admixture among the *Espeletia* from Sumapaz. These phenotypic and genomic groups were only weakly concordant. Therefore, among the various possible scenarios regarding the nature of species, our data is only consistent with those in Fig. 1C. The *Espeletia* from Sumapaz seem to form discordant sets of distinct phenotypes and seemingly less distinct groups of genome-wide allele frequencies, suggesting that phenotypes and genome-wide allele frequencies reflect contrasting evolutionary histories incorporated into a single species. Next we explore implications of these results and potential caveats in our analyses.

Normal mixture models (NMMs) revealed distinct, sympatric morphological groups, which suggests the existence of seven, non-cryptic *Espeletia* species in Sumapaz, thus ruling out scenarios depicted in Fig1A and E. This conclusion is based on the assumptions needed to apply NMMs to species delimitation based on phenotypic characters (Cadena et al. 2017), including polygenic inheritance. We are not aware of studies of the genetic architecture of morphological characters in *Espeletia*. However, studies of quantitative trait loci (QTL) in confamilial species suggests that morphological characters (including some in Table 1) are determined by QTL of small effects (relative to the variance of inter-specific backcross populations, Lexer et al. 2005), as expected for

polygenic inheritance. Two additional assumptions implicit in the application of NMMs to our context are that morphological groups do not reflect ontogenetic variation or phenotypic plasticity (Cadena et al. 2017). Given that all specimens included in the analysis were adult reproductive plants, we expect only negligible ontogenetic effects. Also, morphogroups seemed to share environments, at least broadly defined, as suggested by extensive sympatry (Fig. 6 and Fig. S3). In sum, the assumptions required by the application of NMMs seem to be reasonable for our study system.

We found evidence of three sympatric groups of *Espeletia* specimens from Sumapaz, characterized by different allelic frequencies across the genome. However, in contrast to the morphological groups, these genomic groups seemed indistinct and characterized by high levels of admixture. Moreover, the admixture proportions of different specimens seem to form a gradient from north to south (Fig. 7C), suggesting a pattern of isolation by distance. Yet, the ancestry models we used assume Hardy-Weinberg equilibrium and linkage equilibrium within groups (Pritchard et al. 2000). These models are likely a useful but rough approximation to reality, and it may be unwise to place much emphasis on any single value for the number of genomic groups (in our case 3). It may be more useful to consider the entire distribution of posterior probabilities for the number of genomic groups (Verity and Nichols 2016). Nonetheless, in our case the posterior distribution for the number of groups takes a value close to one for three groups and close to zero for all other values (Fig. 3-B), by which we conclude that there is strong support for three genomic groups. However, these groups seem indistinct due to admixture and may partly reflect isolation by distance across all *Espeletia* from Sumapaz.

The weak concordance between phenotypic and genomic groups suggests that the nature of *Espeletia* species in Sumapaz resembles that depicted in Figure 1C. However, the genomic groups are poorly differentiated (Fig. 7A) and the geographic distribution of admixture proportions suggests an overall effect of isolation by distance (Fig. 7C). Therefore, the nature of *Espeletia* species in Sumapaz may also be similar to the model depicted in Fig 1D, a syngameon. In both cases (Fig. 1 C and D) phenotypic but and genetic distinctiveness reflect contrasting evolutionary histories (Doyle 1997; Maddison 1997; Szilosi et al. 2015). This lack of agreement may be due to the fact that a general scan of the allele frequencies across the genome may not represent small and atypical

parts of the genome that determine phenotypic distinction, as seems to be the case on oaks (Hipp et al. 2019). These results are in line with previous studies that inferred hybridization between distantly related taxa (Pouchon et al. 2018), measured high inter-specific crossability (Berry et al. 1988) and observed pupative hybrids between several species pairs (Cuatrecasas 2013; Diazgranados and Barber 2017).

We did not find the species taxa described in the most recent monograph of *Espeletia* (Cuatrecasas 2013) for the páramo de Sumapaz. This result suggests that species taxa are not even arbitrary divisions of biological diversity, as proposed by botanists (Levin 1979; Raven 1986; Bachmann 1998) and suggested by Darwin (1859). Far more disconcerting, species taxa in *Espeletia* appear to largely miss biological diversity, delineating mostly empty phenotypic space. We wonder if this result is unique to our study taxa and region. We note, however, that formal, specimen-based exploration of the multidimensional phenotypic space proposed in the taxonomic monographs is rarely carried out. In this study we provide a simple example of how such exploration may be accomplished. This is no small matter, given that species are considered basic units of biodiversity in ecology, evolution, biogeography and conservation biology (Coyne and Orr 2004, Barraclough and Humphreys 2015, Richards 2010; Sigwart 2018). In any case, our findings regarding species taxa strongly suggest the need to revise species limits in *Espeletia*, in addition to the taxonomic changes above the species level suggested by Pouchon et al. 2018).

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TABLES

Table 1: The thirteen morphological characters that we use to measure the phenotypic distinction between *Espeletia* species of páramo de Sumapaz

Morphological character	
1	leaf blade length
2	leaf blade width
3	number of capitula per synflorescence
4	capitulum diameter
5	number of pairs of sterile leaves per synflorescence
6	length of the synflorescence axis
7	perimeter of the synflorescence axis
8	length of the cyma peduncle
9	sterile phyllary length
10	sterile phyllary width
11	length of the corolla of the flowers in the disc
12	length of the corolla of the flowers in the ray
13	length of the tubes of the flowers in the disc

FIGURES

Figure 1. Possible scenarios of the nature of species in which the study specimens can be found under two operational criteria: phenotypic distinction and frequency of alleles. The points are individuals located in the space given by two morphological features, the colors are morphological groups and the lines represent the structure of the population. A) There are three groups with molecular structure, however there is no phenotypic distinction. B) Three morphological groups that belong to the genetic structure. C) There are three distinguishable morphological groups and there is a genetic structure, but the structure does not correspond to the morphological groups. D) There are three distinguishable phenotypic groups, but there is no genetic structure. E) It is a scenario where there is no genetic structure neither phenotypic distinction.

Figure 2. Topographic map of the study region, bounded by the altitude of 3,000 m, based on the digital Aster elevation model. The study region was divided into quadrants of 2 x 2 km (gray grid), of which we sampled 34 (black squares). In each of these 34 quadrants, we sampled two 30 x 30 m cells in each band of 100 m altitude, chosen randomly based on the Aster digital elevation. For example, the 2 x 2 km quadrant shown to the left of the figure has five elevation bands (as indicated by the color scale). Therefore, we sampled 10 cells of 30 x 30 m, two in each elevation band of 100 m, as indicated by the black squares within the 2 x 2 km quadrant.

Figure 3. Empirical support to determine the number of groups: morphological and groups according to genome-wide allele frequencies. A) Analysis of strongly supported morphological data. The graph shows the empirical (ordered) support for the normal mixture models (NMM), assuming 1 to 10 different morphological groups. The empirical support was measured as the difference in BIC in relation to the best model (ΔBIC). The two models with the most empirical support assumed seven and eight different morphological groups. B) Analysis of data according to the allelic frequencies (Maverick). The graph shows the empirical support for the different K, assuming 1 to 10 groups according to genome-wide allele frequencies. The empirical support was measured by the posterior probability that numbers close to one have a higher empirical support. The model with the most empirical support assumed three groups according to allele frequencies.

Figure 4. The contribution of the morphological features measured to the first three main components, measured by the loads of each feature in each main component (ie, elements of normalized eigenvectors). The circles show the length of the expected arrows if the thirteen features contributed equally to the spaces of two-dimensional main components; arrows that exceed this expectation contribute more significantly. A) Principal components analysis 1 (41.9%) and 2 (17.4%), these explain 59.3% of the total variation, PC1 and PC2 reflect general aspects of the number of capitula per synflorescence, number of pairs of sterile leaves per synflorescence, sterile phyllary width and length of the cyma peduncle. B) Principal components analysis 1 (41.9%) and 3 (11%), these explain 52.9% of the total variation. PC1 and PC3 reflect general aspects of capitulum diameter, number of pairs of sterile leaves per synflorescence and length of the cyma peduncle. C) Principal components analysis 2 (17.4%) and 3 (11%), these explain 28.4% of the total variation. PC2 and PC3 reflect general aspects 2, 4, 5, 10, 13 (Table1).

Figure 5. Seven morphological groups of *Espeletia* identified using normal mixture model (NMM) based on all the characters, but the components (1,2,3,5,6,7,8,9,10) that showed the clust-vasel as useful (A - C). It shows the groups in the space defined by the three most useful main components for group discrimination (PC1 - PC3). The colored symbols represent specimens assigned to different morphological groups and the ellipses show 95% of high density regions for normal distributions that represent each morphological group.

Figure 6. Map of occurrences of the specimens, the colors and symbols correspond to the seven groups that the NMM revealed. The continuous line of the relationship graph means that the two groups that connect the line with the nearest neighbor are less than one kilometer away. The dotted line means that the two groups are at a distance with the nearest neighbor greater than one kilometer but less than five kilometers.

Figure 7. Comparative analysis between allele frequencies, morphological groups and their latitude position. A) There are 77 samples organized by their admixture percentage. The colors refer to the three groups with more empirical support according to the allele frequencies. In the upper part with a continuous line, each of the three groups is delimited and with a dotted line three levels of admixture are drawn: (0.1.0.5 and 0.9). From right to left is group 1 according to the allele frequencies and it is observed how the admixture increases to the left with group 2 (red) and finally group 3 in blue. B) The colored symbols represented specimens assigned to the seven morphological groups of the NMM, and are organized on the x axis by the position of the samples of the analysis of allele frequencies, to compare between the morphogroup and the genetic group to which each specimen belongs. C) The colored symbols represented specimens assigned to the seven morphological groups of the NMM and the gray points are specimens that are part of the analysis of allelic frequencies but were not assigned to a morphogroup. In the axis and Latitude (degrees north), that is to say that having a high number, the geographical position is more to the north (small numbers, more to the south). In the x-axis are organized by the position of the samples of the analysis of allelic frequencies which allows us to observe the position of the groups allelic geographically.

Figure 8. Map of occurrences of the specimens, classified according to allele frequencies groups. The continuous line of the relationship graph means that the two groups that connect the line with the nearest neighbor are less than one kilometer away.

SUPPLEMENTARY MATERIAL

Supplementary Figure 1. Comparison of the groups according to allele frequencies and the morphogroups provided with the NMM. A) In the first morphogroup there are 6 specimens which are found: two in the genetic group 1 and three in the genetic group 3. B) In the second morphogroup there are 5 specimens; one in the genetic group 1 and four in genetic group 2. C) In the third morphogroup there are 11 specimens; eight in the genetic group 1 and three in genetic group 2. D) The fourth morphogroup the 6 specimens belong to the genetic group 1. E) In the fifth morphogroup there are 6 specimens; three in the genetic group 1 and three in genetic group 2. F) In the sixth morphogroup there are 7 specimens; three in the genetic group 1 and four in genetic group 2. G) The seventh morphogroup the 5 specimens belong to the genetic group 1. H) The null hypothesis of no association between the two classifications, represented by the Goodman-Kruskal tau distribution, produced by a null model of randomization of the data. Significance of how the group given by the allelic frequencies predicts the morphological group. The red line is the value $\tau_{yx} 0.147$ of the test ($p\text{-value} > 0.001$).

Supplementary Figure 2. Comparison of the classifications provided with the NMM and the groups according to allele frequencies. A) In the first genetic group there are 28 specimens which are found: two in the morphogroup 1, one in the morphogroup 2, eight in morphogroup 3, six in the morphogroup 4, three in the morphogroups 5 and 6, and five the morphogroup 7. B) In the second genetic group there are 14 specimens; four in the morphogroup 2, three in morphogroup 3, three in group 5 and four in group 6. C) The third genetic group the four species belong to the morphological group 1. D) The null hypothesis of no association between the two classifications, represented by the Goodman-Kruskal tau distribution, produced by a null model of randomization of the data. Significance of how the group given by the allelic frequencies predicts the morphological group. The red line is the value $\tau_{xy} = 0.382$ of the test ($p\text{-value} < 0.001$).

Supplementary Figure 3 Box-plots of the geographical distance to the nearest neighbor between pairs of groups of the seven moroghroups revealed by the NMM.

Supplementary Figure 4. Box-plots of the geographical distance to the nearest neighbor between pairs of groups of the three groups according to allele frequencies.

Supplementary table of morphological data

Colector	C	Number	Longitud	Latitud	Length.L	Width.La	Length.S	Perimet	ε	Numb	Numbe	Length.C	Diamete	Length.S	Width.St	Ray.Flow	Disc.Flow	Disc.Flower	Tube
Pineda Yam	73	-74.345	3.8261	26.9	3.085	48	2.8	0	3	14.667	4.6	24.267	6.6167	16.423	9.5267	2.25			
Pineda Yam	75	-74.349	3.8067	24.6	3.2367	66	2.3	2	11	2.4767	2.025	12.503	8.1533	12.383	7.2267	1.5767			
Pineda Yam	76	-74.349	3.8067	31.25	3.045	56	2.5	1	11	3.28	1.8333	14.567	5.2133	9.45	6.8267	2.3733			
Pineda Yam	77	-74.349	3.8067	22.25	3.5	43	2	1	18	2.45	1.675	10.723	4.1667	7.7767	6.0067	1.93			
Pineda Yam	78	-74.357	3.8161	11.933	0.896	21	0.8333	3.67	5.33	1.45	1.2333	9.8467	3.13	6.6533	4.39	2.02			
Pineda Yam	79	-74.373	3.8258	33.167	4.3567	64.667	2.1333	0	18.7	1.7	1.245	8.3133	2.84	6.27	5.7867	1.8267			
Pineda Yam	81	-74.187	4.2443	31.7	3.05	71	2.2333	1	13	3.4883	1.58	13.917	4.4433	10.68	6.1967	1.9033			
Pineda Yam	88	-74.174	4.2174	43.46	3.6977	87	2.3667	1	14.3	4.3867	1.6975	10.71	4.9967	8.6433	5.9833	1.36			
Pineda Yam	90	-74.174	4.2174	21.307	1.1333	44.5	1.35	2	11.5	3.346	1.0625	5.32	3.35	3.4733	2.7467	1.16			
Pineda Yam	91	-74.174	4.2175	20.609	1.6933	56.5	1.2	2	18	2.1333	1	5.31	3.67	4.8467	4.0667	1.5033			
Pineda Yam	99	-74.175	4.2197	33.514	1.338	101.5	2.0667	3	10.3	5.8833	1.1	5.4167	3.4667	5.4367	3.57	1.1467			
Pineda Yam	146	-74.188	4.2413	34.864	3.243	87.333	1.9	1.5	13.3	1.1433	1.9975	14.757	5.23	13.727	5.8	1.4267			
Pineda Yam	152	-74.184	4.2206	29.918	3.873	70.667	1.6667	1.5	8.67	2.7667	1.6125	11.747	4.7233	7.2	5.8833	1.9733			
Pineda Yam	156	-74.184	4.2205	21.171	2.0827	57.25	1.1	1.5	12	1.8567	1.096	5.4733	3.0333	3.16	3.7133	1.5733			
Pineda Yam	157	-74.184	4.2205	28.012	2.9363	73.333	2.5667	2	14	4.075	1.5125	5.8567	4.1567	9.5067	5.6933	1.8667			
Pineda Yam	164	-74.201	4.2232	33.677	3.2467	80.333	1.3667	3	5.67	3.3333	1.5875	16.033	5.6367	13.327	6.5267	2.26			
Pineda Yam	166	-74.201	4.2231	38.321	4.3127	87.333	2.6333	2	11.7	3.1067	2.425	16.88	7.2233	12.867	7.06	2.61			
Pineda Yam	176	-74.176	4.215	39.844	4.9937	57.667	2.2333	0.5	15.3	3.1967	2.1267	9.3	4.94	15.64	6.2967	2.1267			
Pineda Yam	178	-74.176	4.215	40.323	5.4917	104.67	2.2667	2	18.7	4.055	1.764	10.353	4.4033	10.935	5.9867	1.5667			
Pineda Yam	181	-74.176	4.2123	37.328	2.7787	53.333	1.45	1	21.5	1.7067	1.3975	4.6333	3.5067	4.5967	3.5633	1.84			
Pineda Yam	183	-74.176	4.2122	35.408	4.241	51	1.7	0.5	7.67	3.5433	2.0983	12.743	6.2	13.05	5.27	2.475			
Pineda Yam	184	-74.177	4.2061	41.418	4.3525	73.667	1.9	1	19	4.33	1.7563	10.557	4.9867	8.1267	6.0967	1.7067			
Pineda Yam	186	-74.177	4.2063	29.906	1.9807	108.67	1.6667	2	20	1.07	1.3675	5.3233	3.4133	2.9233	4.11	1.58			
Pineda Yam	190	-74.18	4.2049	37.274	4.375	75.5	1.6333	1	9	3.1917	1.85	11.473	3.5333	9.82	5.8633	1.9633			
Pineda Yam	191	-74.18	4.2049	24.595	2.5117	65	1.55	1	8	1.2738	1.3075	14.09	5.9133	11.14	5.7733	1.57			
Pineda Yam	193	-74.18	4.2049	30.54	3.7467	40.75	1.4333	0.5	11	1.9617	1.815	14.447	6.1067	6.9167	5.49	1.605			
Pineda Yam	195	-74.18	4.2049	32.744	3.507	79.667	1.2333	3	8.67	1.345	1.6875	13.917	6.2033	14.467	7.0733	2.5167			
Pineda Yam	197	-74.18	4.2049	36.178	4.068	85.567	2.0333	3	8	2.6933	1.775	14.973	8.7833	11.33	6.1667	1.6333			
Pineda Yam	199	-74.18	4.2049	34.354	5.2437	49.633	2.5333	4	7	1.2	1.91	15.94	10.253	10.093	5.9333	2.0667			
Pineda Yam	201	-74.248	4.2126	41.663	5.608	62.5	3.35	0	5	6.8333	3.0375	35.387	16.593	17.45	9.5567	6.6567			
Pineda Yam	204	-74.253	4.2078	26.692	4.4333	61.667	2.4	0.5	11.3	2.3417	1.4275	10.347	6.74	9.4033	7.26	3.2633			
Pineda Yam	207	-74.259	4.2022	32.942	5.4553	55.333	2.0333	1	5.33	7.6683	2.71	17.713	15.593	10.09	6.7767	4.5367			
Pineda Yam	218	-74.287	4.2177	35.078	3.7787	53	1.9667	1	17.7	2.31	1.1725	7.0833	3.5033	7.4433	6.0133	2.28			
Pineda Yam	220	-74.286	4.2184	45.976	2.8663	79	2.7667	0	6.33	6.4683	2.675	22.77	14.967	13.117	8.5967	5.4133			
Pineda Yam	222	-74.286	4.2184	24.066	3.277	62.333	1.6667	1	7.33	1.1817	1.1575	13.09	5.89	10.18	5.8433	1.8567			
Pineda Yam	238	-74.256	4.2163	29.701	3.14	90.333	2.1333	1	11.3	2.005	1.584	9.53	4.7733	11.007	4.97	3.1367			
Pineda Yam	246	-74.264	4.2005	20.727	2.91	40.667	1.6333	1	9.33	2.4833	1.4225	10.88	5.54	11.213	5.7967	2.14			
Pineda Yam	247	-74.264	4.2	26.799	3.544	63.333	1.9	2	9.67	2.595	1.925	17.027	5.2967	12.757	7.02	2.08			
Pineda Yam	251	-74.265	4.2003	13.265	2.2413	40.333	1.3667	1	7	1.1275	1.8225	12.28	5.7	9.7833	6.3033	4.1467			
Pineda Yam	253	-74.272	4.1975	18.601	2.9123	49.333	1.4667	0.5	9.33	1.125	1.915	12.77	6.47	9.0433	5.6633	2.13			
Pineda Yam	255	-74.277	4.1997	23.724	3.2287	61.667	1.75	3	7	1.4867	1.9875	12.32	5.3867	12.42	7.2933	2.6967			
Pineda Yam	259	-74.284	4.2025	40.861	3.9957	79.333	2.2333	0	5	3.4083	2.8775	24.683	20.27	16.717	9.4433	5.65			
Pineda Yam	260	-74.282	4.2064	41.398	4.4353	79.667	3.5667	0	5	5.4933	2.83	24.447	14.357	15.917	9.83	6.9967			
Pineda Yam	263	-74.293	4.2188	36.046	6.2197	69.5	1.75	0	12	1.7767	1.31	10.477	6.3567	9.26	6.4267	2.1633			
Pineda Yam	287	-74.264	4.1956	26.981	3.6703	86.667	1.7667	2	16.3	2.0617	1.8375	12.003	6.9767	8.44	6.0733	1.4833			
Pineda Yam	288	-74.263	4.1955	29.741	3.253	66	2.2	2	11	3.55	2.0975	20.933	12.383	11.607	7.57	2.2933			
Pineda Yam	290	-74.266	4.2158	39.242	5.2333	91.333	2.0667	1	21.7	1.4633	1.8175	12.623	6.52	13.433	5.9533	4.47			
Pineda Yam	292	-74.231	4.2056	31.511	4.404	81	2.1667	1	17	2.895	1.6925	12.367	4.27	10.73	6.0167	0.87			
Pineda Yam	294	-74.235	4.2043	24.74	2.971	54.667	1.8	2	7	1.68	1.9125	14.397	7.3567	12.61	5.7533	1.3767			
Pineda Yam	295	-74.235	4.2023	25.081	4.7797	73.333	2.0333	1.5	12.3	2.1567	2.175	15.093	6.31	12.86	6.6033	4.27			
Pineda Yam	296	-74.236	4.2012	25.858	5.4843	56.5	2	2	7	3.07	1.8267	15.33	8.37	12.787	6.1433	5.2367			
Pineda Yam	298	-74.236	4.1997	29.034	5.387	57.333	2.8333	1.5	9	1.9	2.015	17.463	16.95	9.33	6.2733	3.8067			
Pineda Yam	303	-74.238	4.1977	35.749	5.011	58.667	2.8333	1	5.67	11.03	2.405	15.94	11.46	11.283	7.7967	1.85			
Pineda Yam	304	-74.251	4.1947	34.716	3.666	84.333	2.7333	2	16	3.3	2.1125	14.107	8.02	8.03	5.85	1.57			
Pineda Yam	306	-74.263	4.1839	30.201	3.4783	110.33	2.0333	3.5	12	2.4633	1.61	16.393	5.5333	9.2367	5.7867	1.6267			
Pineda Yam	308	-74.266	4.1825	21.885	2.9273	57	1.65	2.5	10.5	1.435	1.755	13.623	6.7533	8.36	6.3867	2.1433			
Pineda Yam	310	-74.27	4.1778	30.497	3.8677	76.333	2.4333	2.5	21	2.89	1.7525	10.407	6.3867	8.8733	5.8433	2.0033			
Pineda Yam	312	-74.279	4.1814	35.033	4.0247	73.333	1.7	0	14	2.6733	1.555	15.45	8.0867	10.45	6.3967	3.3133			
Pineda Yam	314	-74.278	4.1822	19.714	3.0323	41	3.7	0	31	2.3633	1.7367	11.127	4.92	10.327	6.64	1.9733			
Pineda Yam	316	-74.339	3.8651	17.833	1.6333	58	1.5	5	26	2.135	1.42	9.36	3.8033	7.94	5.3133	4			
Pineda Yam	321	-74.262	4.1878	28.917	4.9387	90.667	2.4667	1.5	19.3	2.39	1.855	15.227	5.67	10.937	8.5967	6.7333			

Pineda Yam	323	-74.262	4.1878	21.774	3.0787	50.667	1.9	1	13	1.4783	1.4925	10.987	7.45	10.177	6.0367	1.6967
Pineda Yam	325	-74.269	4.1905	33.274	4.7367	50	2.4667	1	6.33	1.966	2.0025	22.03	12.107	13.577	7.68	2.74
Pineda Yam	328	-74.269	4.1905	26.498	3.4603	62.333	1.4	2	9.67	2.3233	2.18	13.293	7.0267	9.56	6.6667	2.1767
Pineda Yam	331	-74.278	4.1903	38.34	2.7057	56.333	2.4667	0	5	4.8467	2.8925	19.127	15.1	13.97	8.2	1.85
Pineda Yam	337	-74.277	4.1892	20.129	3.6927	52	1.5	2	10	2.5433	1.3675	9.31	5.0833	8.2267	5.6233	2.01
Pineda Yam	338	-74.431	3.8214	22.565	3.1013	38.667	1.6333	0	8	2.155	1.59	14.237	3.0333	9.2733	5.67	4.38
Pineda Yam	351	-74.446	3.837	32.329	4.9177	60	1.9	0	20.3	1.7133	1.7	11.51	3.02	11.257	5.7633	4
Pineda Yam	353	-74.44	3.83	34.203	4.955	52.667	1.8	0	13.7	3.78	1.6225	13.043	2.7467	8.6967	6.8867	5.09
Pineda Yam	355	-74.425	3.8255	42.767	11.417	52.667	3.1667	2.5	13	3.9133	2.49	20.07	13.297	15.717	11.483	5.1467
Pineda Yam	356	-74.446	3.8309	32.827	4.198	48.25	1.9667	0	10	2.5717	1.955	11.57	2.6367	7.8767	5.96	4.2133
Pineda Yam	364	-74.295	4.2126	43.466	5.3627	106.33	2.0333	1	13.3	1.71	1.795	13.973	6.0833	9.3067	7.84	4.9033
Pineda Yam	378	-74.335	3.8339	30.202	3.861	43	1.7	0	7.67	2.2867	2.375	12.37	4.275	11.14	7.5267	2.14
Pineda Yam	382	-74.333	3.8255	38.41	4.4775	58.667	3.4333	0	3	21.467	3.7425	34.72	13.49	12.59	9.5667	6.54
Pineda Yam	383	-74.332	3.825	34.513	3.979	61	2.4667	0	3	9.4167	3.525	20.42	6.44	12.96	8.2567	1.51
Pineda Yam	387	-74.333	3.8247	33.245	5.9333	44	1.77	0	9	9.3783	2.685	23.76	6.5667	12.753	8.1333	2.6
Pineda Yam	388	-74.333	3.8257	32.746	4.0383	54.667	2.2	1	14.7	2.3517	1.65	11.323	5.4167	11.177	7.5333	5.1333
Pineda Yam	389	-74.333	3.8257	33.5	4.343	41.333	3.1667	0	6.33	6.0817	1.8225	18.91	7.6033	13.567	7.5	2.19
Pineda Yam	394	-74.29	4.2025	26.304	3.2633	72	2.0667	1	12.3	1.1867	1.6938	8.96	4.67	8.93	6.3167	3.5833
Pineda Yam	396	-74.29	4.2003	31.227	3.3157	85.333	1.7	1	11	2.05	1.65	9.9867	3.8633	10.09	6.15	4.2533
Pineda Yam	405	-74.294	4.1989	44.095	5.2633	93.667	2.5	0	15.3	2.66	1.2263	12.587	5.9933	8.6233	6.5833	1.9333
Pineda Yam	410	-74.22	4.2836	31.785	4.363	75	2	0	6.5	6.225	3.15	19.993	13.49	25.503	10.483	2.8833
Pineda Yam	411	-74.288	4.2124	43.371	3.547	143	1.9667	1.5	28	1.66	1.54	10.087	4.6167	7.7633	6.2133	2.7267
Pineda Yam	412	-74.296	4.2043	24.75	3.4353	81	2.5	3.5	50	2.3333	1.5725	12.287	5.4467	9.7933	7.6	4.3067
Pineda Yam	413	-74.3	4.2005	42.379	5.572	121.67	2.3	0	22.3	1.9517	1.64	13.2	5.89	10.037	7.8067	2.6233
Pineda Yam	414	-74.293	4.2178	46.474	5.6867	107.33	2.3667	0	25.3	2.5533	1.6925	12.323	6.52	10.493	6.37	2.5433
Pineda Yam	415	-74.291	4.2097	46.783	3.7163	83.333	2.7667	0	5	8.7833	2.83	20.797	14.03	17.113	8.5367	2.19
Pineda Yam	416	-74.291	4.2023	25.205	2.7517	57.333	1.3333	1	7	2.1567	1.44	8.8067	3.49	9.3433	6.0233	2.6067
Pineda Yam	417	-74.29	4.2004	32.804	3.7837	83	2.75	1	6.5	6.072	2.8525	21.237	14.893	16.153	10.473	2.9567
Pineda Yam	418	-74.29	4.2004	37.412	4.434	78.667	2.2333	0	10	2.3917	1.5575	12.533	7.9067	9.1833	6.5533	2.26
Pineda Yam	420	-74.221	4.2833	34.044	5.0847	71.333	2.0333	4	9.33	1.88	1.9025	14.077	9.5033	10.923	6.3667	1.9467
Pineda Yam	468	-74.189	4.2928	18.03	2.813	40.333	1.7	0	6.33	2.816	2.1375	14.207	6.26	10.73	6.6733	5.8533
Pineda Yam	487	-74.203	4.2764	19.891	3.0947	57.333	2.1	0	12	3.6067	1.84	9.27	4.2667	8.3333	5.38	4.68
Pineda Yam	497	-74.188	4.2928	19.35	2.8897	43.5	1.7	0	11	1.615	1.7288	9.39	4.37	11.32	6.8367	2.2667
Pineda Yam	506	-74.253	4.0378	37.546	3.8313	56.667	2.1	0	3	4.6783	3.27	24.29	4.8967	14.957	7.4733	1.8633
Pineda Yam	511	-74.255	4.0536	24.89	2.7413	67	1.7333	1	17.3	2.7467	1.4425	14.163	6.01	10.027	5.99	2.0333
Pineda Yam	519	-74.266	4.0414	24.734	3.06	47	2.1333	0	14.7	2.3817	2.0538	11.28	5.11	9.0933	6.57	1.6933
Pineda Yam	521	-74.266	4.0414	28.089	4.3087	53.333	1.5333	0	4	3.8017	2.0925	10.74	5.47	8.9833	6.5767	2.0133
Pineda Yam	525	-74.266	4.0414	23.785	3.4347	41	1.9667	2	11.7	1.9233	1.59	10.827	4.97	10.893	6.2567	1.8067
Pineda Yam	535	-74.337	3.8213	27.883	4.2163	49.667	2	0	3	4.915	2.85	19.543	4.62	17.023	9.55	1.9733
Pineda Yam	538	-74.336	3.8139	23.17	3.3847	46	4.2333	0	7.33	6.3367	2.89	21.747	4.7367	10.35	7.0433	5.0767
Pineda Yam	544	-74.338	3.8105	26.402	4.556	55.5	2.3	3	14	1.625	2.13	11.703	7.2333	15.813	6.1933	1.5367
Pineda Yam	545	-74.338	3.8107	23.371	4.5987	49.333	2.4667	3.5	9.33	1.2517	1.185	12.883	9.5167	11.61	7.3333	5.89
Pineda Yam	546	-74.338	3.8112	33.382	3.233	48.667	3.7	0	9	10.212	2.185	17.2	8.04	11.4	8.04	5.4533
Pineda Yam	549	-74.331	3.8138	35.161	5.6687	64.333	3	2	15.7	2.455	2.3025	13.563	5.7167	11.417	6.79	2.8167
Pineda Yam	550	-74.335	3.8039	33.963	4.308	62.333	2.1333	1	16	2.4467	1.7333	12.41	4.2267	11.783	6.3433	2.1833
Pineda Yam	561	-74.169	4.2939	22.36	2.9193	41.667	2	1	7	1.85	1.3825	8.3623	3.84	8.76	5.9	2.3333
Pineda Yam	601	-74.439	3.8142	42.587	3.484	57.333	2.3333	0	3	11.533	3.27	29.04	8.96	15.493	8.86	1.9367
Pineda Yam	602	-74.439	3.8142	35.306	4.0333	90.5	2.7667	4	14.3	3.935	1.7525	13.367	9.06	10.777	6.13	2.05
Pineda Yam	603	NA	NA	40.196	5.182	59.833	1.6667	0	12	1.9717	1.5925	9.74	3.93	8.72	6.6333	1.69
Pineda Yam	606	-74.439	3.8142	33.163	3.695	47	1.5333	0	9.33	3.035	1.525	8.7967	2.88	7.58	5.73	1.53
Pineda Yam	609	-74.439	3.8139	31.035	4.0827	50.667	1.8	0	8.67	2.25	1.82	10.493	3.4633	9.4933	5.4133	2.1567
Pineda Yam	613	-74.445	3.8078	30.257	6.1363	51.333	1.8667	0	13	1.8783	1.75	12.3	4.3	9.2333	5.9367	1.9967
Pineda Yam	615	-74.436	3.8055	38.284	7.213	61	1.8333	0	15.3	2.3117	1.655	12.02	1.9567	7.3667	5.9433	2.2033
Pineda Yam	619	-74.433	3.8062	27.942	2.722	59	3.2	1	84	2.6617	1.3375	8.4267	3.1	9.02	5.49	5.0767
Pineda Yam	620	-74.432	3.8062	7.093	1.175	52.25	4.45	0	25	1.926	1.9175	10.213	3.5833	7.7	6.0467	5.0833
Pineda Yam	633	-74.335	3.8035	30.461	3.7897	51.333	1.7667	0	13	1.745	1.5688	13.297	3.0467	8.2867	5.6667	1.64
Pineda Yam	638	-74.205	4.2995	26.423	3.4107	55.5	2.05	0	11	1.755	1.7125	10.127	4.87	8.8967	6.46	5.0333
Pineda Yam	644	-74.212	4.307	22.911	3.881	58.5	2.25	0	12.5	2.22	1.775	10.853	4.27	10.72	6.1067	4.6
Pineda Yam	646	-74.213	4.3056	18.738	2.5413	48	1.3	1	6	0.94	1.3867	10.26	5.4433	9.03	4.9733	1.4767
Pineda Yam	650	-74.201	4.2991	27.031	4.3177	69.333	2.7333	2	19	3.206	1.7825	8.4233	3.9033	11.627	5.34	4.55
Pineda Yam	685	-74.206	4.2974	41.971	4.19	76.333	2.6333	0	5	6.8	3.0225	24.077	14.48	17.2	8.59	6.8933
Pineda Yam	686	-74.212	4.307	24.378	3.3033	52.667	1.6333	0	7	3.0017	1.5025	8.84	4.56	10.627	6.06	5.88

Pineda Yam	690	-74.213	4.3056	22.43	2.8377	43.333	1.2667	0	8.67	1.55	1.69	9.9867	5.4	11.837	5.3167	4.89
Pineda Yam	694	-74.256	4.0231	40.993	4.4607	72.333	2.5	0	3	9.7667	3.8625	19.22	6.2	11.853	6.9167	5.5933
Pineda Yam	706	-74.265	4.0513	36.932	6.3313	53.667	2.5667	1	12	2.9167	2.0971	19.413	10.523	10.147	7.53	5.1433
Pineda Yam	707	-74.265	4.0513	29.672	3.966	73.5	2.25	2	5.5	2.575	1.93	17.23	8.7667	11.4	8.41	3.1367
Pineda Yam	709	-74.264	4.0475	31.425	6.045	56.667	2.0667	0	10.7	3.535	2.105	10.5	5.7	7.54	6.16	2.0133
Pineda Yam	713	-74.262	4.0458	30.64	4.487	63	2.5333	0	13.3	2.2375	1.7825	9.4133	3.6067	8.1867	5.9533	2.1267
Pineda Yam	717	-74.249	4.0189	42.01	3.5863	65.333	2.2	0	3	7.7333	3.405	22.4	7.24	15.58	7.905	7.305
Pineda Yam	719	-74.25	4.023	25.446	2.5453	60	2.2667	3	16.3	2.28	2.155	17.363	8.0933	10.63	6.9633	5.8667
Pineda Yam	721	-74.25	4.023	30.29	2.9127	49.667	2.8333	2	14.3	1.7683	1.4167	13.563	9.9133	11.2	6.4433	2.3133
Pineda Yam	722	-74.25	4.023	25.219	2.485	37	3.5333	0	8	5.335	2.8175	15.5	6.4067	11.527	7.9233	5.6467
Pineda Yam	724	-74.261	4.0475	35.487	6.23	85.667	3.0667	0	20	1.665	1.8125	11.287	3.9067	7.5867	6.11	4.3667
Pineda Yam	726	-74.261	4.0475	35.45	4.061	74.667	1.6667	0	25.3	1.615	1.34	7.5433	4.6333	5.6	4.4333	4.43
Pineda Yam	731	-74.255	4.02	31.351	3.4927	66.333	2.7	2	10.7	2.3983	1.8505	15.57	8.0867	8.26	5.6	1.3067
Pineda Yam	734	-74.26	4.0252	21.513	3.3523	45.667	2.3667	2	9.67	1.7017	1.435	12.18	5.7667	7.23	5.2667	1.9067
Pineda Yam	737	-74.26	4.0324	18.144	2.7737	50.667	2.3333	2	14.3	2.44	1.6125	13.103	5.94	11.413	6.2733	2.0233
Pineda Yam	738	-74.261	4.0325	24.177	2.7027	49.667	2.2333	2	8.67	1.6267	1.73	12.477	8.1133	11.117	6.25	1.97
Pineda Yam	742	-74.258	4.0364	27.12	3.7307	51	2.7333	2	15	1.7817	1.725	12.563	7.7167	9.32	6.3433	2.0467
Pineda Yam	744	-74.267	4.0405	31.396	7.4333	74.333	2.8667	2	11.3	3.7417	1.9175	16.017	9.4733	12.84	7.9267	5.16
Pineda Yam	745	-74.267	4.0402	33.16	6.1333	67.667	3.6333	2	12.3	4.1233	1.705	16.343	9.19	10.933	7.6367	4.2333
Pineda Yam	746	-74.271	4.0383	24.452	4.8	50.333	2.1	0	11.5	1.8083	1.9125	12.447	6.1067	7.2	6.0767	2.0567
Pineda Yam	748	-74.271	4.0383	23.695	2.9	41	1.6333	1	6.33	1.8817	1.7243	11.003	4.7167	13.31	5.8767	1.7333
Pineda Yam	749	-74.271	4.0383	21.709	3.1667	57	1.9	0.5	13.3	2.43	1.605	11.273	4.82	8.1933	4.78	1.5233
Pineda Yam	750	-74.271	4.0383	34.261	5.2333	92	2.2333	0	14.7	2.39	1.8875	10.67	5.0933	9.1667	5.6733	1.2267
Pineda Yam	751	-74.427	3.8296	38.609	9.65	77.5	4.2	1.5	14	4.7	1.68	15.743	9.31	12.3	7.9133	5.3667
Pineda Yam	753	-74.427	3.8256	30.182	5.6	58	2.15	0	12	1.047	1.8675	8.0433	2.42	9.5533	6.4833	2.61
Pineda Yam	755	-74.424	3.8283	46.232	4.4	55	2.1	0	16.7	2.82	1.9175	10.197	2.97	8.65	6.0133	2.05
Pineda Yam	757	-74.422	3.8292	31.968	4.2333	66.667	1.9667	0	18.7	1.455	1.115	7.2533	2.3433	6.7467	5.72	1.7233
Pineda Yam	761	-74.418	3.8203	30.718	4.4333	63.5	2.3333	0	22.7	0.9333	1.225	8.48	2.9433	6.0267	6.1767	1.7333
Pineda Yam	774	-74.427	3.8081	31.521	5.2333	53.667	1.9667	0	17	1.8783	1.6	9.5567	3.81	8.4033	5.56	2.04
Pineda Yam	776	-74.427	3.8081	36.874	7.1665	84.667	2.9	1	21.3	4.488	2.2413	12.56	5.9567	10.22	7.3933	5.71
Pineda Yam	782	-74.425	3.8033	30.934	3.694	61.667	1.9	0	16.7	1.2483	1.2225	9.1967	3.5267	6.5833	5.2467	1.9733
Pineda Yam	788	-74.26	4.065	31.003	3.853	53	3.1333	2	23.3	2.2767	1.325	9.32	5.0733	8.3733	5.9733	4.3933
Pineda Yam	789	-74.26	4.0669	26.189	3.457	54.667	2.6333	4	16.3	2.3233	1.625	12.623	7.31	9.31	6.8633	4.8333
Pineda Yam	792	-74.258	4.0735	36.548	7.907	75.667	2.3667	0	20.7	1.6017	1.925	11.327	6.24	8.7767	7.0167	3.1533
Pineda Yam	795	-74.268	4.0583	30.63	5.3107	41.333	2	0	12	1.0133	1.655	11.37	6.9567	9.86	6.6067	2.2833
Pineda Yam	797	-74.26	4.0769	38.639	4.7573	52.333	1.9667	1	10	2.3517	1.7613	14.127	5.14	9.0433	6.14	4.7967
Pineda Yam	803	NA	NA	32.477	5.031	74.5	2.3	0	12	2.6167	2.0025	9.88	4.3067	8.4633	5.9433	1.7233
Pineda Yam	804	NA	NA	22.208	3.5273	56.45	1.75	1	7.5	1.4283	2.035	11.393	4.8433	10.393	6.1033	1.6467
Pineda Yam	805	NA	NA	28.795	4.8043	45.25	2.25	1	10.5	1.34	1.8386	11.06	5.77	8.03	5.94	1.41
Pineda Yam	806	NA	NA	25.437	4.9993	56.5	2.15	0	9	1.432	2.0433	13.183	4.78	11.047	5.8833	1.5667
Pineda Yam	807	-74.266	4.0606	27.657	5.1497	62.5	2.2	0	13.3	3.4317	1.655	12.697	5.8767	10.523	6.5633	1.9133
Pineda Yam	808	-74.266	4.0606	20.247	2.701	46	1.8	2	12.3	1.1083	1.6675	13.947	6.9	9.8433	6.56	1.7167
Pineda Yam	812	-74.266	4.0606	28.012	4.841	39.667	5.9	0	6	7.845	2.7	16.453	9.6467	13.163	7.57	1.8367
Pineda Yam	814	-74.266	4.0605	34.555	4.5173	64.667	2.7	0	3	20.25	3.5375	32.2	11.543	18.07	9.1533	2.4367
Pineda Yam	820	-74.268	4.0608	36.917	4.6207	68.333	3.1667	0	3	12	2.75	26.427	8.2867	13.04	7.6867	2.1267
Pineda Yam	822	-74.268	4.0608	30.749	3.235	49.667	2.1667	2	15.3	2.8483	1.63	13.987	9.2933	9.14	6.58	2.6233
Pineda Yam	823	-74.268	4.0522	35.082	4.703	53	2.9333	0	3	13.917	3.7575	32.597	9.2833	17.683	8.6333	2.4133
Pineda Yam	824	-74.269	4.0597	35.483	3.913	79.667	2.8667	0	3	12.083	3.6275	21.157	6.6067	13.493	7.96	1.6633
Pineda Yam	825	-74.27	4.0575	40.465	6.0497	68	3	0	3	9.6667	3.775	26.573	9.4967	17.597	8.35	2.11
Pineda Yam	826	-74.27	4.0575	21.412	3.6583	51.667	2.3333	2	15	1.74	1.375	13.133	8.0933	13.983	6.6167	2.6933
Pineda Yam	828	-74.269	4.0572	19.726	3.2293	41	2.1333	2	12	1.6833	1.4	13.007	6.0633	11.79	6.1767	2.32
Pineda Yam	830	-74.201	4.2782	25.921	4.0477	66.667	1.7	1	9.67	2.575	2.3975	14.637	5.63	9.5167	6.21	1.6733
Pineda Yam	831	-74.198	4.2822	41.067	4.5927	91.267	2.8	0	6.67	3.3733	2.72	22.57	11.247	13.54	8.9	2.1467
Pineda Yam	834	-74.202	4.187	32.532	1.873	74	1.6333	2	13.3	0.61	0.7675	4.1933	3.3367	4.02	2.05	1.0233
Pineda Yam	835	-74.265	4.1825	37.042	4.46	75.333	2.4667	3	13.7	1.86	2.0475	15.893	6.4033	10.917	6.3367	1.87
Pineda Yam	836	-74.226	4.1862	33.387	2.1717	84	1.7667	3.5	13.3	0.9333	1.0075	5.2	2.8767	6.15	3.41	1.785
Pineda Yam	838	-74.237	4.1375	33.986	4.422	60.833	2.5333	3	11.7	1.74	1.81	11.393	4.78	7.83	5.1867	1.5433
Pineda Yam	840	-74.247	4.2129	39.336	4.8983	69.667	2.8667	0	5	6.8283	3.45	25.947	17.377	23.527	10.497	3.9767
Pineda Yam	841	-74.247	4.2129	27.787	3.1367	67.333	2.0667	0	8.67	1.23	1.67	12.647	4.7933	8.5333	6.12	2.1433
Pineda Yam	842	-74.247	4.2123	32.911	3.0477	61.333	2.1333	0	6.33	2.0717	2.7275	16.613	12.313	11.233	7.6633	1.7433
Pineda Yam	846	-74.404	3.8555	34.664	4.133	63.5	2.4	0	23.3	1.9167	1.3275	9.3867	3.2067	5.2233	5.3067	1.67
Pineda Yam	848	-74.425	3.8256	34.138	8.7127	67.5	3.05	2	30	3.535	2.1075	22.863	12.103	14.827	8.7467	2.5567

Pineda Yam	849	-74.425	3.8256	38.741	10.346	81.5	3.4	2	17	3.7633	2.2425	23.377	12.02	12.987	10.033	3.8933
Pineda Yam	850	-74.425	3.8256	40.572	8.6567	71.5	3.615	0.5	28.5	2.185	2.12	19.553	10.453	11.683	9.0067	4.14
Pineda Yam	851	-74.425	3.8245	49.785	9.602	88.5	3.7	1.5	26.5	3.6383	2.1475	16.65	8.59	15.71	8.62	3.3033
Pineda Yam	852	-74.425	3.8243	33.556	4.435	69.25	2.3	0	14.5	0.9933	0.8725	9.7433	3.68	8.6733	5.9	2.1733
Pineda Yam	853	-74.432	3.8291	40.792	6.8407	78.5	3	2	10.5	3.2133	2.1825	19.08	12.593	13.847	7.6333	3.1533
Pineda Yam	854	-74.432	3.8293	40.8	9.1787	68	3.65	1	23.5	3.0283	2.2275	19.567	11.933	10.053	8.2567	3.14
Pineda Yam	855	-74.432	3.8293	48.538	9.2647	92	4.15	2	22	1.6533	2.125	18.91	10.923	12.55	9.2133	4.7333
Pineda Yam	856	-74.432	3.8293	36.393	11.06	94	3.8	2	36	5.29	2.0767	20.063	10.137	12.4	7.3933	2.5533
Pineda Yam	857	-74.404	3.8582	33.62	2.3487	123	2.5	2	37.3	3.7133	0.8375	4.5133	2.8667	5.3667	4.1867	1.8467
Pineda Yam	859	-74.404	3.8584	32.298	2.9293	75	2.41	2.5	24	0.945	0.675	5.6767	3.48	7.2167	5.3867	2.03
Pineda Yam	860	-74.404	3.8583	40.119	2.482	92	2.95	2	22.5	1.88	1.035	5.8333	3.8167	6.1367	5.99	1.9667
Pineda Yam	861	-74.404	3.8583	26.979	3.387	59.5	2.3	0	29	1.6383	1.22	10.33	2.5267	6.8033	5.6333	2.5867
Pineda Yam	862	-74.404	3.8582	38.974	4.188	78.5	2.35	1	21.5	1.2933	0.8375	4.3233	3.2033	5.1633	4.2133	1.6467
Pineda Yam	864	-74.336	3.8246	32.702	4.0017	61.333	2.4333	0	3	7.0083	2.775	15.043	3.91	14.003	6.99	1.9933
Pineda Yam	865	-74.336	3.8246	29.662	4.2523	56	2.4	0	4.5	8.4383	2.24	15.02	3.53	11.603	6.9367	2.16
Pineda Yam	866	-74.336	3.8238	32.643	4.3693	79.833	3.2	0	3.67	15.15	2.8725	27.063	4.4167	16.587	8.1933	2.0833
Pineda Yam	867	-74.336	3.8233	27.314	3.299	54.667	2.3	0	3.67	11.7	2.8025	24.27	3.95	11.69	7.35	1.81
Pineda Yam	868	-74.336	3.8231	30.35	3.816	66.833	2.9	0	3	14.383	3.0275	24.743	2.5433	16.68	8.6433	1.9267
Pineda Yam	869	-74.335	3.8229	36.651	4.354	52.833	2.5	0	3	18.267	3.1167	19.14	5.78	14.533	8.5333	2.3767
Pineda Yam	870	-74.335	3.8225	32.905	3.9237	54.167	2.05	0	3	5.6867	2.8275	22.81	4.6567	12.927	7.1433	1.7133
Pineda Yam	871	-74.249	4.1237	32.717	3.3	65	2.2333	3.5	18	3.3167	1.3	10.807	4.38	12.9	6.3067	2.1033
Pineda Yam	872	-74.294	4.0613	69.777	14.203	103.5	4.95	2	22	5.4333	2.57	23.26	15.453	14.797	9.3	2.7867
Pineda Yam	873	-74.294	4.0611	36.279	7.4947	62	2.4	0	25	0.7833	1.475	9.8267	3.77	8.1167	5.61	1.9
Pineda Yam	874	-74.294	4.0866	36.618	3.474	63	2.4333	3	19.3	1.5167	1.55	16.133	7.2433	12.913	6.4733	2.14
Pineda Yam	875	-74.257	4.0868	41.785	2.909	78	2.9333	4	15.7	1.9	1.875	11.74	4.68	10.77	6.7867	2.13
Pineda Yam	876	-74.247	4.2111	32.577	3.8917	86	2.3	1	16.5	2.9167	2.025	14.91	6.89	10.257	5.22	1.6867
Pineda Yam	877	-74.247	4.2117	53.003	4.321	65.5	3.25	0	7	1.75	2.45	17.123	10.337	14.053	10.423	3.6067
Pineda Yam	878	-74.253	4.1954	33.812	3.351	61.667	2.8	4.5	15.3	2.15	1.6	13.293	7.3667	10.48	6.92	2.52
Pineda Yam	879	-74.253	4.1953	32.807	3.342	72	2.3667	5	11.3	2.9567	2.125	14.687	9.66	12.317	7.8633	2.7333
Pineda Yam	880	-74.253	4.1959	43.648	5.6557	71.333	2.6333	4	17.7	3.9083	1.8625	10.247	7.29	11.417	7.1967	2.6833
Pineda Yam	881	-74.252	4.1978	40.815	5.0277	98.333	2.9667	2.5	27.3	3.1	1.7125	14.913	10.973	12.837	6.7667	1.94
Pineda Yam	882	-74.247	4.2115	49.582	5.7007	89.667	3.7	0	7	9.3333	2.675	18.233	13.35	13.417	9.5933	2.62
Pineda Yam	883	-74.247	4.0611	48.476	3.0463	71.333	2.8	0	4.33	4.1333	2.85	21.34	17.14	11.223	8.61	1.49
Pineda Yam	884	-74.23	4.1834	38.499	5.3123	57	2.3333	3	10.7	1.1237	1.315	13.323	10.27	14.31	8.07	2.5767
Pineda Yam	885	-74.23	4.1835	38.779	5.4493	80.433	2.7	3	19	1.7333	1.4875	13.14	8.4167	10.063	5.06	0.9533
Pineda Yam	886	-74.231	4.1836	41.192	5.9617	91.667	2.5333	3.5	13.3	3.15	1.49	14.747	7.6867	13.827	8.2667	2.4533
Pineda Yam	887	-74.231	4.1837	40.318	5.4177	74	2.2333	2	15.3	3.3383	1.44	15.85	7.83	14.34	7.4	2.06
Pineda Yam	888	-74.231	4.1834	40.784	4.71	110.33	2.6667	4	17	3	1.665	10.623	9.2633	11.093	5.47	1.6333
Pineda Yam	889	-74.229	4.1839	42.92	4.1533	99.667	2.7333	5.67	23.7	2.338	1.8525	16.727	8.3267	13.607	6.5967	1.8333
Pineda Yam	890	-74.189	4.2802	36.058	4.3273	58	1.9	0	7	2.95	1.52	21.907	18.97	18.017	8.5267	3.4967
Pineda Yam	891	-74.189	4.2802	27.652	4.6553	71	1.7	0	9	2.47	1.475	11.02	6.2933	11.077	6.7433	1.5967
Pineda Yam	892	-74.187	4.2804	23.104	3.3153	64.5	1.5	0.5	7	1.6867	1.37	9.5233	4.1067	9.1623	5.76	1.6233
Pineda Yam	893	-74.185	4.2826	21.227	2.6307	54.667	2.1	1	5	1.3733	1.275	7.5667	3.8	10.487	6.5333	1.4667
Pineda Yam	894	-74.184	4.283	37.063	5.3027	54.667	1.8667	0	5	5.13	2.2075	14.84	10.06	13.833	9.4733	2.46
Pineda Yam	895	-74.184	4.2829	47.435	5.1123	66.5	2.15	0	5	4.898	2.085	25.003	11.92	10.757	8.9667	2.67
Pineda Yam	896	-74.184	4.28	35.511	4.872	71.3	2.3	1	9.67	2.065	1.3775	11.657	4.22	12.677	6.4467	6.3933
Pineda Yam	897	-74.183	4.2831	38.931	4.7607	75.667	2.9	0	7	3.3067	2.2275	15.233	10.75	19.603	9.4967	2.8433
Pineda Yam	898	-74.182	4.2825	36.384	5.1077	52.75	2.7	0	5	3.3933	2.3425	17.813	9.0267	11.75	8.3567	1.9433
Pineda Yam	899	-74.182	4.2825	42.341	5.6377	82.5	2.55	0	5	5.686	2.8175	20.75	11.277	15.087	9.7133	8.89
Pineda Yam	900	-74.176	4.2839	40.568	4.162	61.55	1.9667	0	5	3.9017	2.1	16.453	13.053	16.767	9.6633	3.3167
Pineda Yam	901	-74.175	4.2847	35.213	4.4197	52.5	3.45	0	7	2.6333	1.8975	16.963	11.947	14.21	8.3667	2.3433
Pineda Yam	902	-74.181	4.2821	29.637	3.599	57.167	1.7333	0.67	6	0.6917	1.37	12.88	5.4633	10.127	6.8033	2.4967
Pineda Yam	903	-74.259	4.0824	38.373	4.7163	67	2.6667	3	33.7	2.2183	1.3075	12.18	5.9567	9.6367	7.7767	6.96
Pineda Yam	904	-74.259	4.0824	45.002	6.4313	80.333	2.3667	0	14.3	4.6933	1.6525	12.327	5.6033	11.173	7.0333	2.76
Pineda Yam	905	-74.253	4.0997	38.256	4.416	65.8	2.9667	2	12.7	2.8617	1.4675	11.893	6.6967	14.39	7.58	2.3967
Pineda Yam	906	-74.251	4.1094	38.453	3.917	84	2.1	3.67	22.3	3.6467	1.4225	9.7267	4.76	12.36	7.4767	2.1433
Pineda Yam	907	-74.249	4.1248	37.895	4.3863	63.833	2.5	3	13.3	3.1433	1.3925	10.423	4.2633	14.033	1.95	2.2067
Pineda Yam	908	-74.249	4.125	33.543	3.7783	72.833	1.9	2	20.3	2.915	1.43	10.11	6.4167	9.4533	7.24	1.9433
Pineda Yam	909	-74.241	4.1432	34.721	4.4543	83.3	3.0667	2.33	21.7	2.7017	1.5175	11.927	4.6067	13.237	5.91	1.8233
Vergara	8	-74.238	4.1947	24.6	1.7	64.7	1.45	2	20	2.63	1.065	4.69	5.14	7.43	6.2433	1.8067
Cuatrecasas	27070	NA	NA	47.5	2.3033	85.5	1.7	3	16	1.68	1.272	6.2167	4.64	5.7933	4.965	2.03
Idrobo & Hernar	2756	NA	NA	41.1	2.075	134	2.2	3	28	3.67	1.3975	9.9567	5.0433	8.6	5.25	1.3367

Cleef	8301	NA	NA	47.4	4.3467	74.5	2.15	4	14	2.9375	1.685	10.567	5.0533	6.9067	4.595	1.705
Betancur	8093	-74.214	4.0873	33.5	4.7	79	3.3	2	14	2.07	2.2167	15.515	9.5	11.093	7.0467	1.43
Uribe	5537	NA	NA	30.25	4.605	105	2.4	1	14	1.32	1.7025	17.71	7.915	12.137	6.14	1.325
Uribe	4505	NA	NA	33.75	4.425	47.75	2.2	2	12.5	1.7067	1.925	12.915	9.1	11.743	8.2133	2.5233
Garcia-Barriga	17193	NA	NA	29.667	2.27	78.167	1.5667	2	10.5	2.7417	1.91	11.53	7.57	13.067	7.2	2.9033
Cuatrecasas	5517	NA	NA	34.85	4.5	109	1.9	1	10.5	1.8575	1.7871	15.237	8.6	14.047	6.0467	2.17
Garcia-Barriga	8103	NA	NA	34.75	7.285	126	2.8	1	10	2.4467	2.1825	20.02	11.547	19.765	7.4933	2.7333
Cuatrecasas et al.	25567	NA	NA	27.55	4.325	75	1.5	1	9	2.34	2.38	17.51	10.57	16.953	7.7767	2.6533
Uribe	2473	NA	NA	41.5	6.595	60.5	1.7	1	10	4	2.1833	18.707	10.133	17.263	8.07	2.96
Humbert et al.	26849	NA	NA	46	7.06	79.5	1.6	1	6	5.3167	2.56	23.325	17.995	21.71	6.125	1.74
Garcia-Barriga	13390	NA	NA	32.167	4.5667	71	2.1	1	9	1.2	1.8833	11.7	8.76	12.617	7.795	2.55
Bardlay & Juajib	6137	NA	NA	43.533	3.7667	79	2.4	0	5	6.855	3.52	18.43	9.685	20.1	8.39	3.56
Fernandez & Jar	1486	NA	NA	38.9	3.2	70.5	3	0	7	5.03	3.2	19.63	10.93	17.647	9.3333	2.95
Uribe	6786	NA	NA	40.333	4.2567	74	2.2	0	5	4.12	2.5467	24.76	16.48	16.84	9.74	2.92
Bardlay et al.	3258	NA	NA	39	4.33	68	2.6	0	4.5	5.45	2.4833	18.51	11.18	12.007	8.8433	3.09
Humbert et al.	26904	NA	NA	41.133	4.87	79.2	2.6	0	5	5.32	2.735	20.67	11.27	11.125	7.865	2.565
Dugang	2965	NA	NA	35.5	4.2533	60.6	2.1	0	5	3.655	3.5	20.885	11.72	13.077	8.2467	2.6733
Garcia-Barriga	17392	NA	NA	38.35	4.91	68	2.1	0	5	6.6467	2.45	23.4	9.89	11.4	8.1733	3.405
Cleef	1575	NA	NA	40.95	3.5	60.5	2.5	0	3	7.22	3.2067	28.84	5.33	17.757	9.42	2.99
Cleef	1573	NA	NA	37.6	3.1	45	1.8	0	3	8.1	3.185	18.33	8.55	13.1	7.94	2.5567
Diaz et al.	2873	NA	NA	39.433	3.51	65	2.6	0	3	18	2.99	2.18	6.04	15.457	8.44	1.8067
Uribe	7033	NA	NA	30.5	2.95	51.167	2.1667	0	3	7.115	3.115	20.513	5.5533	14.857	8.5033	1.69
Cuatrecasas & J	28785	NA	NA	38.4	3.24	53	2.1	0	3	12.76	3.365	17.94	8.15	15	10.64	1.585
Cuatrecasas & J	28789	NA	NA	38	4.05	63	2	0	3	6.6	2.85	21.79	8.42	13.427	8.9033	1.7733
Garcia-Barriga	8117	NA	NA	39.167	4.38	53.667	1.9	0	4.67	7.2567	2.5825	25.967	11.287	13.58	9.4533	3.47
Uribe & Jaramill	6895	NA	NA	45.433	4.5933	54.3	2.9	0	3	10.35	3.7133	18.04	7.015	15.79	9.19	1.7567
Cuatrecasas	9527A	NA	NA	25.95	5.195	106	1.4	3	8	2.1967	1.7275	11.64	6.09	10.277	5.8733	2.4033
Cuatrecasas	9527	NA	NA	37.233	7.89	100	2.6	1	26	3.0433	1.58	12.52	7	11.347	6.0033	2.3633
Cuatrecasas & J	25908	NA	NA	42	4.4167	69	1.95	3.5	9	1.45	2.49	13.56	8.22	1.46	8.06	2.755
LATP	10	NA	NA	37.167	5.2333	92.333	2.3	0	15.3	2.37	2.0914	13.86	5.1433	7.3833	6.6433	2.51
LATP	9	NA	NA	41.667	5.3667	95	2.45	0	15.7	2.072	1.79	14.08	5.1367	8.0167	6.5967	2.34
LATP	6	NA	NA	38.167	4.9	96	2.2	0	27	1.515	1.5973	9.0533	4.1	7.0167	4.6067	1.9633
LATP	11	NA	NA	47.333	5.4667	111	2.5667	0	23.7	1.8817	1.405	10.28	3.5733	7.12	5.61	1.53
Granados David	823	NA	NA	33.267	3.8667	74	2.4333	0	5.67	11.138	2.5025	19.62	11.297	15.07	9.7367	2.5833
Granados David	812	NA	NA	38.967	3.5	69.533	3.2	0	7.67	2.43	2.7675	25.167	15.413	15.58	9.05	2.3867
Granados David	808	NA	NA	47.7	3.7333	92	2.4	0	7	2.87	2.0275	19.723	12.283	14.833	10.163	2.45
Granados David	825	NA	NA	39	3.1733	45.667	2.5667	0	5	3.885	2.3325	17.75	11.373	17.2	9.6567	3.0967
Granados David	822	NA	NA	39.767	3.5	66	3	0	5	10.75	3.3633	22.8	13.6	16.983	10.153	2.8733
Granados David	819	NA	NA	36.333	3.6733	57	2.0667	0	3.33	6.222	2.67	20.7	11.37	8.8767	8.4933	2.77
JLMA	1	NA	NA	33.867	2.9	84.667	1.8667	3.67	17	1.053	1.6825	10.847	5.3	8.97	6.1867	1.6567
LATP	7	-74.165	4.2203	30.2	3.4	82.633	2.1667	4	21.7	2.7433	1.5075	12.237	5.5567	9.9933	7.2067	0.92
Granados David	811	NA	NA	32	3.6667	63.167	1.2	1.33	7	1.302	1.2403	12.037	5.2067	10.553	6.0367	1.1967
Granados David	814	-74.166	4.4941	23.667	2.8333	88	1.5	2	9	1.0367	1.63	12.415	6.985	10.923	6.89	1.79
SAV	1	-74.183	4.4407	30.3	4.4667	99	1.95	2	15	1.605	1.1675	7.605	3.96	10.19	6.48	1.4067
Granados David	824	-74.232	4.2355	20.667	3.7333	63.75	1.6	1	14.5	1.118	1.6025	4.9433	4.8967	11.097	5.39	1.1733
LATP	8	-74.165	4.2077	34.567	2.9667	74.3	2.1	3	18.3	2.075	1.6275	12.297	8.17	12.347	7.5467	2.63
Granados David	863_S152	NA	NA	30.8	3.9333	79	1.9667	3	12.3	6.4	1.435	12.277	5.5833	10.04	7.3233	2.9367
Granados David	840	-74.345	3.9193	25.833	1.7333	71.5	2.15	4	44	3.205	1.1875	4.9433	3.1133	6.4067	5.0033	1.7933
Granados David	837	-74.308	4.0547	39.1	7.1333	91.533	2.3667	0	21.7	2.895	1.6825	13.537	6.11	8.4367	7.44	2.3733
Granados David	833	-74.414	3.8751	43.733	5.2333	80.933	2.9	1	19.7	1.1375	1.36	9.6633	3.46	8.2767	6.5933	2.4833
Granados David	841	-74.338	3.9479	41.4	5.4333	71.2	3	2	17	3.49	1.6875	17.07	9.9933	13.063	10.063	4.18
Granados David	832	-74.428	3.7872	33.667	6.3667	63	2	1	19.5	1.0033	1.385	8.7433	2.5433	6.7767	5.315	2.55
Granados David	842	-74.335	3.948	41.267	4.4333	89.7	2.6	0	24.3	1.28	1.5375	12.5	3.7433	6.7133	5.8033	1.7367
Granados David	831	-74.394	3.9014	45.9	8.1667	100.25	3.65	3	18	1.8017	1.6575	16.3	10.167	10.87	7.5933	2.4
Granados David	835	NA	NA	53.067	8.1	90	3.35	1.5	19	5.03	1.8875	21.847	12.957	11.773	9.1433	3.38
Granados David	834	NA	NA	46.767	7.1667	92	3.4	3	12	4.87	1.8225	16.853	7.47	14.197	8.9933	3.1733
Granados David	846	NA	NA	50.667	10.4	70.5	2.9333	3.33	11	3.7067	2.06	14.54	9.7433	13.98	7.7267	1.71
Granados David	845	NA	NA	38.133	3.7	68.9	1.7	0	5	3.1667	1.7875	16.64	9.86	13.73	7.5633	2.73
Granados David	855_S84	NA	NA	40.433	3.9333	69	3.5	0	9	3.5667	2.9275	26.013	18.66	15.14	9.5067	2.5867
Granados David	856	NA	NA	27.833	3.09	56	2.3	1	12	2.26	1.545	10.037	5.1367	9.5633	6.9933	1.59